

TURUN YLIOPISTON JULKAISUJA
ANNALES UNIVERSITATIS TURKUENSIS

SARJA - SER. B OSA - TOM. 345
HUMANIORA

“IT’S ALL RIGHT”

**Multimodal rightward spatial bias
modified by age and praxis**

by

Fia Takio

TURUN YLIOPISTO
UNIVERSITY OF TURKU
Turku 2012

From Division of Psychology and Centre for Cognitive Neuroscience
Department of Behavioural Sciences and Philosophy
University of Turku
FIN-20014 Turku
Finland

Supervised by

Professor Heikki Hämäläinen
Division of Psychology and Centre for Cognitive Neuroscience
Department of Behavioural Sciences and Philosophy
University of Turku

Docent and Academy Research fellow Mika Koivisto
Division of Psychology and Centre for Cognitive Neuroscience
Department of Behavioural Sciences and Philosophy
University of Turku

Reviewed by

Professor Synnöve Carlson
Brain Research Unit
O. V. Lounasmaa Laboratory
Aalto University School of Science,
and
Neuroscience Unit
Institute of Biomedicine/Physiology
University of Helsinki

Professor Teija Kujala
CICERO Learning,
and
Cognitive Brain Research Unit
Institute of Behavioural Sciences
University of Helsinki

Opponent

Professor Kimmo Alho
Institute of Behavioural Sciences
Department of Psychology
University of Helsinki

ISBN 978-951-29-4979-3 (PRINT)
ISBN 978-951-29-4980-9 (PDF)
ISSN 0082-6987
Painosalama Oy – Turku, Finland 2012

Mää joskus otin oikee assiaksen ajatel...

CONTENTS

ABSTRACT	6
LIST OF PUBLICATIONS	8
ABBREVIATIONS	9
1 INTRODUCTION	11
1.1. Functional brain asymmetries	13
1.1.1. Motor asymmetries and handedness	13
1.1.2. Perceptual asymmetries	14
1.1.3. Language lateralization	16
1.1.4. Sex differences in handedness, brain asymmetry, and language lateralization	18
1.2. Cognitive neuroscience of attention	19
1.2.1. Alerting and orienting	20
1.2.2. Asymmetry of attentional mechanisms	22
1.2.3. Executive functions	26
1.2.4. Perceptual asymmetry and executive functions: Dichotic listening (DL) paradigm	29
1.2.5. Modification of executive functions by training	31
2 AIMS	33
3 METHODS	34
3.1. Dichotic listening test	34
3.2. Auditory Go/No-Go Spatial Attention test (AGSA)	34
3.3. Auditory Divided Spatial Attention test (ADSA)	35
3.4. Visual Go/No-Go Spatial Attention test (VGSA)	35
3.5. Visual Divided Spatial Attention test (VDSA)	36
3.6. Other cognitive tests	36
4 SUMMARY OF THE STUDIES	37
4.1. Description of participants	37

4.2.	The effect of age on attentional modulation in Dichotic listening (Study I)	37
4.3.	Auditory rightward spatial bias varies as a function of age (Study II)	39
4.4.	Visual rightward spatial bias varies as a function of age (Study III)	41
4.5.	Blind individuals show enhanced perceptual and attentional sensitivity for identification of speech sounds (Study IV)	44
5	DISCUSSION	46
5.1.	The role of age and praxis in perceptual tasks: summary of the results	46
5.1.1.	Children	46
5.1.2.	Young and middle-aged adults	48
5.1.3.	Old adults	48
5.1.4.	Blind participants	49
5.2.	Multimodal rightward spatial bias – underlying mechanisms	49
5.3.	Effect of age and praxis as evidence for the role of executive functions in perceptual asymmetries	51
5.4.	The model of interaction of cognitive functions underlying the age- and praxis-related change in rightward spatial bias	57
5.5.	Gender differences	60
5.6.	Conclusions	62
5.7.	Limitations and suggestions for future research	63
	ACKNOWLEDGEMENTS	66
	REFERENCES	68
	ORIGINAL PUBLICATIONS	77

Abstract

The general goal of the present work was to study whether spatial perceptual asymmetry initially observed in linguistic dichotic listening studies is related to the linguistic nature of the stimuli and/or is modality-specific, as well as to investigate whether the spatial perceptual/attentional asymmetry changes as a function of age and sensory deficit via praxis.

Several dichotic listening studies with linguistic stimuli have shown that the inherent perceptual right ear advantage (REA), which presumably results from the left lateralized linguistic functions (bottom-up processes), can be modified with executive functions (top-down control). Executive functions mature slowly during childhood, are well developed in adulthood, and decline as a function of ageing. In Study I, the purpose was to investigate with a cross-sectional experiment from a lifespan perspective the age-related changes in top-down control of REA for linguistic stimuli in dichotic listening with a forced-attention paradigm (DL). In Study II, the aim was to determine whether the REA is linguistic-stimulus-specific or not, and whether the lifespan changes in perceptual asymmetry observed in dichotic listening would exist also in auditory spatial attention tasks that put load on attentional control. In Study III, using visual spatial attention tasks, mimicking the auditory tasks applied in Study II, it was investigated whether or not the stimulus-non-specific rightward spatial bias found in auditory modality is a multimodal phenomenon. Finally, as it has been suggested that the absence of visual input in blind participants leads to improved auditory spatial perceptual and cognitive skills, the aim in Study IV was to determine, whether blindness modifies the ear advantage in DL. Altogether 180-190 right-handed participants between 5 and 79 years of age were studied in Studies I to III, and in Study IV the performance of 14 blind individuals was compared with that of 129 normally sighted individuals.

The results showed that only rightward spatial bias was observed in tasks with intensive attentional load, independent of the type of stimuli (linguistic vs. non-linguistic) or the modality (auditory vs. visual). This multimodal rightward spatial bias probably results from a complex interaction of asymmetrical perceptual, attentional, and/or motor mechanisms. Most importantly, the strength of the rightward spatial bias changed as a function of age and augmented praxis due to sensory deficit. The efficiency of the performance in spatial attention tasks and the ability to overcome the

rightward spatial bias increased during childhood, was at its best in young adulthood, and decreased as a function of ageing. Between the ages of 5 and 11 years probably at first develops movement and impulse control, followed by the gradual development of abilities to inhibit distractions and disengage attention. The errors especially in bilateral stimulus conditions suggest that a mild phenomenon resembling extinction can be observed throughout the lifespan, but especially the ability to distribute attention to multiple targets simultaneously decreases in the course of ageing. Blindness enhances the processing of auditory bilateral linguistic stimuli, the ability to overcome a stimulus-driven laterality effect related to speech sound perception, and the ability to direct attention to an appropriate spatial location. It was concluded that the ability to voluntarily suppress and inhibit the multimodal rightward spatial bias changes as a function of age and praxis due to sensory deficit and probably reflects the developmental level of executive functions.

List of publications

- I. Takio, F., Koivisto, M., Jokiranta, L., Rashid, F., Kallio, J., Tuominen, T., Laukka, S.J., & Hämäläinen, H. (2009). The effect of age on attentional modulation in Dichotic listening. *Developmental Neuropsychology*, 34, 225-239.

- II. Takio, F., Koivisto, M., Laukka, S.J., & Hämäläinen, H. (2011). Auditory rightward spatial bias varies as a function of age. *Developmental Neuropsychology*, 36, 367-387.

- III. Takio, F., Koivisto, M., Tuominen, T., Laukka, S.J., & Hämäläinen, H. (2012). Visual rightward spatial bias varies as a function of age. *Laterality, e-pub*, 1-24.

- IV. Hugdahl, K., Ek, M., Takio, F., Rintee, T., Tuomainen, J., Haarala, C., & Hämäläinen, H. (2004). Blind individuals show enhanced perceptual and attentional sensitivity for identification of speech sounds. *Cognitive Brain research*, 19, 28-32.

Abbreviations

ADSA auditory divided spatial attention

AGSA auditory Go/No-Go spatial attention

BVF both visual fields

CERAD the Consortium to Establish a Registry for Alzheimer's Disease

CV consonant-vowel

DL dichotic listening

EF executive functions

FL forced-left condition

FR forced-right condition

ISI inter-stimulus interval

LEA left-ear advantage

LVF left visual field

MCI mild cognitive impairment

NF non-forced attention condition

REA right-ear advantage

RVF right visual field

VDSA visual divided spatial attention

VGSA visual Go/No-Go spatial attention

WMS-R Wechsler Memory Scale- Revised

1 Introduction

Both cerebral hemispheres typically have at least some competence to process a similar kind of perceptual-cognitive information to a reasonable extent, but they both also display superiority in some processes of various domains (for review, see Dien, 2009). In other words, both sides of the brain are superior to each other for different, and sometimes contradictory, aspects of a task or process (e.g. Hellige, Laeng, & Michimata, 2010). This tendency for certain processes to be more highly developed on one side of the brain than the other is called lateralization. A history of neurocognitive research on the functional and structural lateralization of the brain has provided consistent findings on the developmental and sensory deficit related changes in individuals' behavioural phenotype. Still many basic questions regarding the nature and the lifelong development of the left-right asymmetries remain. The purpose of the present work is to investigate perceptual asymmetries presumably related to the lateralization of the brain, and the changes in these left-right asymmetries as a function of age and praxis due to sensory deficit.

Different theoretical approaches have opened up the discussion on the development of hemispheric asymmetry; whether it is predetermined before birth, or develops as a function of maturation and age. The invariant approach (for review, see Boles, Barth, & Merrill, 2008) proposes that lateralization, which is fixed in advance by nature, emerges always in the same way in normal development of the brain and is completed by the end of infancy. However, this approach has not achieved much support in recent studies showing that some asymmetries are more apparent in adults than in children (for review, see Boles et al., 2008). According to the progressive approach, hemispheres are equivalent in infancy, but due to maturation, lateralization is a phenomenon of growth and development, and many different perceptual functions become lateralized by the end of adolescence (e.g. Lenneberg, 1967). Results, for example, from increasing language lateralization during childhood (Andersson & Hugdahl, 1987; Hiscock & Kinsbourne, 1977, 1980; Sexton & Geffen, 1979) and strengthening of lateralization in visuospatial functions (Everts et al., 2009) have provided support for this approach. However, the variable results of the development of the asymmetries in the literature make it difficult to determine the exact timing of lateralization of different processes. Moreover, the functional motor asymmetries observed already in fetuses suggest that some lateralization may occur even before birth

(McCartney & Hepper, 1999). The modular approach (Boles et al., 2008) suggests that the hemispheric asymmetry results from a complex interaction of biological and environmental factors and can take a different course in different individuals. The developmental timing for lateralization may vary in different domains, some processes lateralizing earlier than others (Boles et al., 2008). To test this hypothesis, research approaches should focus on more than one cognitive or perceptual domain at the same time. Unfortunately, most of the earlier studies have focused on asymmetries either in motor, visual, auditory, or tactile processes separately.

Age-related changes in hemispheric asymmetry are not restricted to childhood or adolescence: changes in human structural and functional hemispheric asymmetry continue into old age (e.g. Dolcos, Rice, & Cabeza, 2002). For example, ageing seems to reduce not only the performance in perceptual or in cognitive tasks, but also has an impact on the brain asymmetry. In the “right hemi-ageing” model the right hemisphere shows stronger decline than the left hemisphere, while the “hemispheric asymmetry reduction in old age” (HAROLD) model proposes that frontal activity during cognitive processes is less lateralized in older than in younger adults (for review, see Daselaar & Cabeza, 2005; Dolcos et al., 2002).

Previously, one of the main assumptions in neurocognitive research has been that lateralization of the brain enhances cognitive processing and that the higher the degree of lateralization, the more advanced the cognitive performance (e.g. Boles et al., 2008; Hirnstein, Leask, Rose, & Hausmann, 2010). Nonetheless, the maturation of lateralization does not guarantee better performance in perceptual-cognitive tasks (Boles et al., 2008): extreme lateralization of, e.g. language (left hemisphere) or face perception (right hemisphere) is not always related to the enhanced cognitive performance in perceptual tasks (Hirnstein et al., 2010). In this work I propose that the development of executive functions, which is often neglected in earlier studies of perceptual and functional asymmetries, modulates asymmetry differently at different periods of the lifetime (e.g. Hiscock & Kinsbourne, 1977; Hugdahl & Andersson, 1986). The term executive function is generally agreed to be an umbrella term encompassing the skills necessary for goal-directed behaviour which have been shown to develop slowly during childhood and adolescence, to be advanced in adulthood and to decline as a function of ageing (e.g. Burke & Barnes, 2006; Jurado & Rosselli, 2007; Madden, Whiting, & Huettel, 2005; Span, Ridderinkhof, & van der Molen, 2004; Tsujimoto, 2008). A key assumption in the present work is that the complex interactions between

the maturation of the lateralized processes and the development of the executive functions (top-down processes) (see Posner, 2008; Posner & Raichle, 1994; Teshiba et al., 2012) both influence the perceptual-cognitive performance in adult populations, and that the development/decline of these different processes at both ends of the lifespan modifies the age-related differences in perceptual-cognitive asymmetries.

First the previous findings related to functional and structural asymmetries in humans will be reviewed. Then a general picture will be drawn of the literature concerning when, in what way and how the asymmetries and the executive functions are thought to change as a function of age and sensory deficit. After that, the aims of the present work and a brief summary of the four studies forming this work will be presented. Finally, the present results will be discussed in light of earlier findings and current theoretical views, and a schematic proposal of the possible underlying mechanisms behind the present findings will be presented.

1.1. Functional brain asymmetries

1.1.1. Motor asymmetries and handedness

Functional asymmetries exist at the body level already in the very early stages of development. Motor asymmetries have been found even in fetuses, which have led to the conclusion that in the prenatal period, the lateralization of motor asymmetries is not under cortical control, but perhaps under spinal or muscular control (McCartney & Hepper, 1999). In infants, rightward asymmetries of movements have been found in head-turn preferences or in primitive involuntary Moro responses triggered by a sudden change in the environment (Ginsburg, Fling, Hope, Musgrove, & Andrews, 1979; Rönnqvist, 1995; Rönnqvist & Hopkins, 1998; Rönnqvist, Hopkins, van Emmerik, & de Groot, 1998; Turkewitz, Gordon, & Birch, 1965). Asymmetries in newborns' stepping responses have been found to be present in terms of spatial and temporal organization of movement, as well as in intralimb coordination (Domellöf, Rönnqvist, & Hopkins, 2007). Short right-side reaching and grasping preference as early as eight months of age (for review, see Fagard, Spelke, & von Hofsten, 2009) correlates with a later right-sided preference at the age of three years (Corbetta & Thelen, 1996, 1999). As a matter of fact, it has been proposed that the later emerging right-hand preference would arise from an early right-side reaching preference (Rönnqvist & Domellöf, 2006; Domellöf et al., 2007), and that functional motor asymmetries may predate structural brain asymmetries

related to handedness (Hepper, McCartney, & Shannon, 1998).

In adults, it has been estimated that about 90 % of individuals are right-handed, such that the right arm is preferred over the left when performing tasks such as reaching for or manipulating an object (for review, see Corballis, 2009). Besides the well observable preference for using and being more skilled with one hand versus the other in complex motor tasks requiring accuracy (Flowers, 1975; Goble & Brown, 2008), there is still no consensus on the neuro-anatomical and behaviour-based asymmetries of handedness. At the anatomical level, both hemispheres are active prior to movement initiation and seem to contribute to the control of goal-directed movements (for review, see Goble & Brown, 2008). Recently, several theoretical approaches suggest that each hemisphere is specialized for different aspects of movement control. For example, it has been proposed that visual feedback is of greater importance for the control of a preferred arm reaching movement, while proprioceptive feedback favours the control of a non-preferred hand's targeted movements. Furthermore, in right-handed individuals the left hemisphere is proposed to be dominant at cortical level for controlling complex movements with either arm, while the right hemisphere dominance exists for the allocation of attentional resources or specification of the spatial aspects of the movement to be performed (for review, see Goble & Brown, 2008; Haaland, 2006; Haaland & Harrington, 1996). As a conclusion, the effect of handedness on behaviour is rather intrinsic already from early life on, and seems to result from a complex interaction of different levels of the central nervous system.

1.1.2. Perceptual asymmetries

In the auditory modality, it has been proposed that dichotically presented sounds of musical instruments induce a stronger activity in the right than left temporal lobe, producing a left-ear advantage (Hugdahl et al., 1999). However, contradictory results concerning hemispheric asymmetry in the perception of music or non-linguistic stimuli have been found (for review, see Ivry & Robertson, 1998). Already some early studies of pure tones (Efron, Koss, & Yund, 1983; Galbraith & Arroyo, 1993; Gregory, Efron, Divenyi, & Yund, 1983; Murray, 1986; Obrzut, Conrad, & Boliek, 1989) reveal that specific parametric alterations of the stimulus material, such as the differences in the frequency of the two dichotic stimuli compared to the centre frequency (spatial and perceptual complexity) and/or temporal patterning, have remarkable consequences on the ear/side dominance observed. For example, when two dichotic tone pairs of equal

intensity and close in frequency are presented (Efron et al., 1983; Gregory et al., 1983; Murray, 1986) and the participant reports hearing a single sound image located in the midline (the two stimuli cannot be distributed perceptually), the left-ear advantage is observed (see also Obruzt et al., 1989; Murray, 1986). In turn, if the difference in these specific parameters becomes so much larger that a single intertone is no longer heard, the ear advantage shifts toward the right-ear dominance (Efron et al., 1983; Gregory et al., 1983).

In the visual modality, there is reasonable evidence that the two hemispheres are not equal in different aspects of visual information processing. The left hemisphere is proposed to be superior for processing local aspects of visual stimuli that are carried by high spatial frequencies, and of categorical spatial relationships (i.e. abstract relation between objects' spatial difference), while the right hemisphere is proposed to be dominant for the processing of global aspects of visual stimuli that are carried by low spatial frequencies, and of coordinate spatial relationships (i.e. quantitative relation between objects' spatial difference) (for review, see Hellige et al., 2010; Ivry & Robertson, 1998). For example, leftward asymmetry, related to the right hemisphere dominance, has been observed in both children and adults in visuospatial positional processing (e.g. dot localization), visual search functions, mental rotation of objects, face-processing and emotional processing (Boles et al., 2008; Chiang, Ballantyne, & Trauner, 2000; Everts et al., 2009; Harris et al., 2000). There are also results showing that in enumeration tasks, the non-verbal stimuli (e.g. dots, bargraphs) are more accurately identified in the left than in the right visual field (e.g. Kimura, 1966; see also Boles, 1986; Boles et al., 2008). For example, Young and Bion (1979) studied hemispheric laterality effects in an enumeration task where children aged 5, 7, and 11 were asked to enumerate collections of 2, 3, 4, 5 or 6 dots presented briefly in their left or right visual hemifield. They reported a general left visual field (right hemisphere) superiority that did not interact with age. However, the evidence and results for some of the claims above remain equivocal and diverse. For example, Alivisatos and Petrides (1997) found not right but left hemisphere dominance for mental rotation of objects, and related the right hemisphere activity to general visuospatial processing necessary for the discrimination of transformed views of stimuli. Also, left hemisphere superiority in visuospatial quantitative processing has not always gained support (e.g. Boles, 1986) and attempts to find a consistent locus of activation in the right hemisphere during visual search tasks have failed (for review, see Everts et al., 2009). As a matter of fact,

Martin and co-workers (2008) observed right hemisphere activation in both coordinate and categorical spatial tasks. They proposed that the two coding types rely essentially on the same neural networks, not on different ones, and that the right hemisphere activation asymmetry observed is related to the lateralization of spatial attention mechanisms rather than to the lateralization of coding mechanisms (Martin, Houssemand, Schiltz, Burnod, & Alexandre, 2008). In face processing, it is widely accepted that humans have right hemisphere dominance in specialized cognitive and neural mechanisms dedicated to the perception of faces (Kanwisher & Yovel, 2006), even though such a face-specificity hypothesis is still questioned (e.g. Hellige et al., 2010). To summarise, the evidence and empirical support for most of the perceptual asymmetries and for the hemispheres' separate spatial coding remain equivocal. In particular, knowledge about the development of the right hemispheric functions is scarce. It seems that the two hemispheres make complementary contributions to many perceptual information processes, and apparently many of the observed perceptual asymmetries depend on a number of requirements and computations demanded in different tasks.

1.1.3. Language lateralization

Over 90 % of right-handers are left-hemisphere dominant for language (for review, see Corballis, 2009). Strong left hemisphere dominance in the processing of linguistic stimuli in auditory and visual modalities develops already at an early age, producing a rightward perceptual asymmetry (e.g. Andersson & Hugdahl, 1987; Boles et al., 2008; Hiscock & Kinsbourne, 1977, 1980). For example, already in newborns, the auditory cortex is asymmetrically sensitive to the temporal frequency structure of the acoustic signal (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; Telkemeyer et al., 2009). The strength of the language lateralization also changes as a function of age and development: e.g. an fMRI study revealed that the left lateralization of language increases in childhood and adolescence (between ages of 5 and 20 years), is stable in young adulthood, and decreases slowly between the ages of 25 to 70 years (Szaflarski, Holland, Schmithorst, & Byars, 2006).

In the visual modality, visual half-field experimental setups have been frequently applied to study perceptual asymmetries, such as linguistic asymmetry. For example, studies investigating visual lexical processing have typically presented words, multiple digits, or letters, either unilaterally or bilaterally, requiring recognition. A typical

finding in children and in adults in the lateralized word recognition task is that words are recognized faster and more accurately in the right visual field (RVF) than in the left visual field (LVF) (for review, see Boles et al., 2008; Calvo & Nummenmaa, 2009; Koivisto, 1997), indicating a left hemisphere advantage for processing visual verbal stimuli. For example, increasing rightward asymmetry (left hemisphere recognition advantage) of visual verbal stimuli (e.g. words, letters) has been found to occur between the ages of 7 and 11 (Miller, 1981, 1984; for review, see Boles et al., 2008).

In the auditory modality, the dichotic listening (DL) procedure with linguistic stimuli has been broadly used to estimate the language lateralization both in child and in adult participants (e.g. Andersson & Hugdahl, 1987; Asbjørnsen & Helland, 2006; Hiscock & Decter, 1988; Hiscock & Kinsbourne, 1977; Hugdahl, 2003). DL generally refers to an experimental arrangement in which the two ears simultaneously receive distinct acoustic inputs. In DL with linguistic stimuli (e.g. words, syllables) a standard finding in a normal right-handed participant when attention is not voluntarily directed to either ear (non-forced attention condition, NF) is a right ear advantage (REA). The REA has been explained to be due to different neuronal pathways from the ears to the left hemisphere's language-dominant areas: the contralateral pathway from the right ear works faster and more efficiently than the ipsilateral pathway from the left ear (Hugdahl, Bodner, Weiss, & Benke, 2003; Kimura, 1967; see also Bryden, 1988) (Figure 1). More precisely, it has been proposed that contralateral auditory pathways suppress ipsilateral input at the level of the brainstem, thereby inducing a left hemispheric advantage for auditory processing of verbal input (Asbjørnsen & Hugdahl, 1995; Beaton, Hugdahl, & Ray, 2000). An alternative hypothesis is that the attentional functions explain more profoundly all perceptual asymmetries (Kinsbourne, 1970): since the left hemisphere orients towards the contralateral space and is specialized in the processing of linguistic stimuli, the expectation of linguistic stimuli automatically orients the attention towards the right hemispace. Thus, in DL with linguistic stimuli, the REA would be caused by an attentional bias to the right auditory space caused by the expectation of the linguistic stimulus material. Hugdahl (2003) suggests that the REA is produced by the inherent bottom-up processing and reflects the language specialization of the left hemisphere. In bottom-up processing, attentional functions are driven mainly by the characteristics of the stimulus and its sensory context (see also Westerhausen et al., 2010).

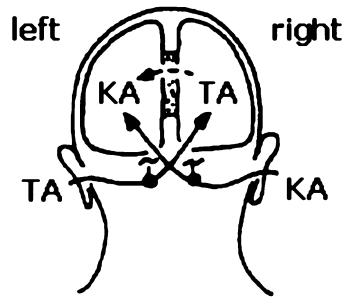


Figure 1. An example of dichotic listening procedure, where two linguistic stimuli (e.g. syllables KA and TA) are presented simultaneously to both ears. The mechanism behind the right-ear advantage for the linguistic stimuli has been explained to be due to different neuronal pathways from the ears to the left hemisphere's language-dominant areas: The right-ear syllable KA has direct access to the language-dominant left hemisphere while the left ear TA goes first to the right hemisphere and then needs to travel through the corpus callosum to the left hemisphere's language dominant areas.

The REA toward the right auditory space has been found already early in childhood as young as at 2 ½ years of age (for review, see Boles et al., 2008), and observed throughout the lifespan (Hugdahl et al., 2009). A deficit in phonological awareness, such as dyslexia, influences the early perceptual asymmetry in DL (Hugdahl, Helland, Færevaa, Lyssand, & Asbjørnsen, 1995; Helland & Asbjørnsen, 2001; for normal development of phonological awareness, see also Carroll, Snowling, Hulme, & Stevenson, 2003). Dyslexic children show a weaker degree of asymmetry than healthy children towards the right-ear linguistic stimuli in DL, and there seem to be anatomical differences in brain activation between the dyslexic and healthy children (e.g. Hugdahl et al., 1995; Helland & Asbjørnsen, 2001; Penolazzi, Spironelli, Vio, & Angrilli, 2006).

1.1.4. Sex differences in handedness, brain asymmetry, and language lateralization

The inconsistency of results concerning sex differences in handedness, brain asymmetry, and language lateralization has induced an assumption that the results of sex differences may be task- and/or sample-size-related (e.g. Plante, Schmithorst, Holland, & Byars, 2006; Sommer, Aleman, Somers, Boks, & Kahn, 2008). The most recent meta-analysis of the auditory modality in adults (Sommer et al., 2008) revealed a significant sex difference for handedness with more right-handedness in females,

whereas no sex differences were found in the asymmetry of the planum temporale (a highly lateralized brain structure involved in language processing), or in language lateralization as measured with auditory DL, or in language lateralization as assessed with functional imaging. In a meta-analysis of the magnitude of laterality effects in different modalities and sex differences in functional lateralization, Voyer (1996) concluded that even though sex differences are present in the visual and auditory modality favouring men with stronger functional asymmetries, it is possible that the differences are offset by a much larger number of unpublished negative findings. Against this, Hiscock and co-workers (1999) justified their meta-analyses by arguing that “laterality studies typically are mostly designed to address questions other than sex differences and hence are likely to be published irrespective of whether sex differences are found” (p.17). According to their meta-analyses of sex differences in the brain lateralization separately in auditory (Hiscock, Inch, Jacek, Hiscock-Kalil, & Kalil, 1994), visual (Hiscock, Israelian, Inch, Jacek, & Hiscock-Kalil, 1995) and tactile modalities (Hiscock, Inch, Haweyluk, Lyon, & Perachio, 1999), Hiscock et al. concluded that even though sex differences are infrequent in all modalities, there is a weak population-level sex difference favouring the hypothesis of greater functional specialization of the cerebral hemispheres in males. Both child and adult population studies were included in these meta-analyses, and several significant sex effects interacted with other factors, such as age. As a matter of fact, sex differences in lateralization have been found to be age-dependent for some tasks (Plante et al., 2006), raising the question of whether there are different developmental trajectories of lateralization in females and males.

1.2. Cognitive neuroscience of attention

Attention is probably the most studied phenomenon in cognitive neuroscience since its influence on human everyday performance is, undoubtedly, remarkable and necessary. Throughout life, humans constantly face a variety of stimuli but the brain can analyse and react to only a proportion of the incoming information simultaneously. Attention is the ability to orient to, to shift between, and to maintain focus on events, objects, tasks, and problems. Neuropsychological and -physiological research has shown that the two cerebral hemispheres differ in the control of spatial attention (e.g. Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta, Kincade, Ollinger, McAvoy, & Shuman, 2000; Posner, 2008), and that the asymmetric distribution of the attention

mechanisms contributes to the magnitude and direction of any perceptual asymmetries (Mondor & Bryden, 1992a, 1992b).

Posner and co-workers (Posner, 2008; Posner & Petersen, 1990; Posner & Raichle, 1994) have introduced a rather widely studied neuropsychological model of the attention development during the entire lifespan. Associated with separable but partially overlapping brain regions in cortical and mid-brain structures (e.g. Brodeur & Enns, 1997; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Posner, 2008), three interconnected attention networks can be distinguished: *orienting* to sensory events, *alerting* or maintaining a vigilant state, and *executive control*. Functionally these attentional networks overlap and interact (for review, see Callejas, Lupiañez, Funes, & Tudela, 2005). For example, a single event often simultaneously provides information both on when (alerting) and where (orienting) the target appears (Posner, 2008). Moreover, the alerting network is proposed to inhibit the executive control network to ensure that the attentional system can concentrate on the detection of external signals. The alerting system is also proposed to influence the orienting system so that orienting to the salient stimulus would become faster (Callejas et al., 2005). The orienting system, in turn, is suggested to enhance the efficiency of the executive control network so that it may resolve a conflict situation sooner (Callejas et al., 2005).

1.2.1. Alerting and orienting

Alerting, a mechanism that is localized to the brainstem and later in development to the right frontal lobe (Posner, 2008; van de Weijer-Bergsma, Wijnroks, & Jongmans, 2007), refers to achieving and maintaining an alert state of arousal and a high state of sensitivity to incoming stimuli (Posner, 2008). In other words, alerting is needed to produce and maintain optimal vigilance and performance during tasks. Results from tasks where participants need to focus and sustain attention have shown that the alerting system affects the rate at which a participant directs attention and responds to a target stimulus, regardless of whether the quality of information is sufficient to make correct responses (van de Weijer-Bergsma et al., 2007). Developmentally, the alerting network starts to develop already early in life, but is proposed to develop rather slowly since children even at the age of 10 years have significantly more difficulties in maintaining internal alertness than adults (Rueda et al., 2004). Similar difficulties have been proposed to involve also patients suffering from right-parietal stroke (Posner, 2008) and probably also patients with attention deficit hyperactivity disorder (ADHD) (Rueda et al., 2004). Moreover, the

ability to maintain an alert state seems to develop until adulthood, and decrease as a function of ageing (Posner, 2008; Fernandez-Duque & Black, 2006).

The orienting system, the selection of information from sensory input and orientation or directing attention to specific locations, seems to involve a spatial orienting network in the parietal cortex (also called the dorsal/"where" pathway) and an object recognition pathway in the temporal cortex (also called the ventral/"what" pathway) (van de Weijer-Bergsma et al., 2007; Waszak, Li, & Hommel, 2010, see also Madden et al., 2005). More precisely, the orienting network is proposed to involve areas in the posterior parietal lobe (disengagement of attention), the superior colliculus (shifting of attention to a different location), and the pulvinar nucleus of the thalamus (enhances stimulus processing at the new location) (for review, see Callejas et al., 2005). Orienting can be stimulus-driven or exogenous (involuntary shift of attention to a location), more controlled endogenous (voluntary shift of attention/ directing attention), covert (without eye movement) or overt (shifting the gaze to the attended space). The orienting network is needed, for example, in attention shifts between the left and right space in the visual modality (e.g. Posner, 2008).

Regardless of the existence of several studies on orienting abilities in different age groups, it is rather difficult to get a coherent picture of the development of the orienting system since the applied tasks vary between the studies. Furthermore, only few studies covering the age-related changes during the lifespan have been conducted (Waszak et al., 2010; Brodeur & Enns, 1997). The orienting system shows rapid development already early in life (van de Weijer-Bergsma et al., 2007; see also Johnson & Tucker, 1996). In childhood, the development of goal-directed motor systems interacts with the development of the attentional orienting system (Smith & Chatterjee, 2008) and the stimulus-based orienting reflex has been found to be stronger for both children and old adults than young adults (Brodeur & Enns, 1997). According to Rueda et al. (2004), in childhood between the ages of 6 to 10 years, the ability to orient to visual locations and shift attention to peripheral exogenous cues seems to show minor developmental changes, while the speed of directing attention voluntarily, the accuracy of its termination, and the ability to disengage attention improve with age. Moreover, the maturation of the mechanisms underlying involuntary, stimulus-driven covert orienting, as measured behaviourally, is proposed to be completed by the age of 10 to 11 years (Waszak et al., 2010), and remain relatively unchanged across the lifespan, not being subject to much decline during ageing (Brodeur & Enns, 1997; Posner, 2008).

1.2.2. Asymmetry of attentional mechanisms

Based on the evidence from patient studies, it has been suggested that the hemispheres differ and are asymmetrical in attentional mechanisms (e.g. Luck, Hillyard, Mangun, & Gazzaniga, 1989; 1994). The most severe examples of the asymmetry of perceptual/attentional/awareness systems are observed in the studies of neurological patients with unilateral neglect (Corbetta, Patel, & Shulman, 2008; Deouell, Hämäläinen & Bentin, 2000; Heilman, Bowers, Valenstein, & Watson, 1987; Kinsbourne, 1987; Oliveri et al., 1999), ADHD (Chan et al., 2009; Hale, Zaidel, McGough, Phillips, & McCracken, 2006), and callosotomy (split-brain) (Luck et al., 1989, 1994; Mangun et al., 1994; Proverbio, Zani, Cazzaniga, & Mangun, 1994). According to the definition of neglect by Heilman and co-workers (2000), it is “a failure to report, respond, or orient to meaningful or novel stimuli. This failure is primarily for stimuli or actions that occur on the side contralateral to a hemispheric lesion” (p.463), and cannot be attributed to either an elemental sensory or motor defect. In other words, many symptoms of neglect are related to attentional deficits (Heilman, Valenstein, & Watson, 2000). The nature of the neglect symptom can also be related to memory, motor, or sensory functions (Swan, 2001). Unilateral spatial neglect may occur at least as a result of damage to the posterior parietal cortex, frontal lobe, cingulate gyrus, striatum, thalamus, or brainstem nuclei (e.g. Swan, 2001; Posner & Petersen, 1990). Since the neural damage that produces spatial neglect has been observed at different levels of the neural system, these areas are suggested to constitute a neural network for attention.

In adult neglect patients suffering from a unilateral right hemisphere injury, a strong attentional bias towards the right hemispace is observed, whereas a leftward attentional bias after a unilateral left hemisphere injury is prominently less frequently detected. Here the hemispace refers to the right or left side of the trunk starting at the midline of the body and extending laterally either to the left or right (Swan, 2001). Visuospatial and motor neglect have also been described in children after brain damage similar to adults. Even though it is less clear whether early spatial neglect before the age of three years is more common after left or right hemisphere damage (Smith & Chatterjee, 2008), most of the child patients with neglect show left spatial neglect after right hemisphere damage at the age of three years or above (Laurent-Vannier, Pradat-Diehl, Chevignard, Abada, & De Agostini, 2003). The variation in the very early findings of spatial neglect could be related to the disparate distribution of spatial

attention in the developing precocious brain as compared with the mature brain (Trauner, 2003).

Related to the neglect syndrome, a particular deficit observed during bilateral simultaneous stimulation is called extinction. Here the patient may be able to detect a single left-sided event in isolation, but in a stimulus condition where two stimuli are presented either to the same or different hemifields simultaneously, the left-sided event is missed (see Driver & Vuilleumier, 2001). Thus, the spatial attentional bias appears when multiple events compete for attention at the same time.

Similarly to the neglect patients, both children and adults suffering from ADHD have poorer ability to attend to the stimuli in the left than in the right visual field (for review, see Chan et al., 2009). According to the traditional view, ADHD is a deficiency in executive functions (e.g. Barkley, 1997; Brown, 2006), especially in inhibitory control. However, a deficiency in executive functioning does not always occur along with ADHD and seems not to be specific to it (e.g. Loo et al., 2007). For example, ADHD patients and normal participants performed equally well under conditions of focused attention in a DL study (Hale et al., 2006). Thus, the traditional view has been complemented with more specific and detailed explanations (e.g. Boles, Adair, & Joubert, 2009; Floet, Scheiner, & Grossman, 2010; Furman, 2008). Based on a study of spatial selective attention, it has been proposed that some ADHD subtypes involve atypical cerebral asymmetries in attentional mechanisms: for example, dysregulation and over-activation of the right hemisphere lateralized arousal and attention mechanisms have been proposed to explain ADHD symptoms (for review, see Chan et al., 2009; Hale et al., 2006). As the ADHD is multifactorial and heterogeneous in its etiology and results from dysfunctions in distributed brain network organizations inducing a wide range of ADHD subtypes, it is a good example of the complexity of the interaction of different attentional and cognitive mechanisms (Konrad & Eickhoff, 2010).

The functional imbalance between the two hemispheres after unilateral brain injury or brain dysfunction has evoked diverse theoretical models of hemispheric asymmetry in attentional mechanisms. According to the Kinsbourne's model (Kinsbourne, 1987), both hemispheres orient attention towards the contralateral hemispace, but the left hemisphere has stronger directional bias than the right hemisphere. Heilman et al. (1987) proposed that the right hemisphere has bilateral spatial attentional control over the whole visual field, while the left hemisphere's

attentional control is only contralateral (see also Driver & Vuilleumier, 2001; Kinsbourne, 1987; Proverbio et al., 1994; Swan, 2001). In other words, according to both views, attention is more strongly biased toward the right hemispace than toward the left hemispace. As a matter of fact, Teshiba et al. (2012) in their recent fMRI study proposed that the evidence for each view of attentional asymmetries is not mutually exclusive, and that the functional evidence of the attentional asymmetries depends on the attentional states that were induced (e.g. automatic orienting of attention vs. more controlled orienting of attention). It has also been suggested that the rightward bias and left spatial inattention in (left) unilateral neglect (Corbetta et al., 2008; Deouell et al., 2000; Heilman et al., 1987; Kinsbourne, 1987; Oliveri et al., 1999; Proverbio et al., 1994) and in ADHD (Chan et al., 2009; Hale et al., 2006) result from a dysfunction of the right parieto-temporo-frontal stimulus-driven attention mechanisms which allows involuntary attention to focus on the alerting events in the environment (Corbetta & Shulman, 2002; Corbetta et al., 2008; Driver & Vuilleumier, 2001) or from right-hemisphere impairments in sustained attention and alertness (Boles et al., 2009; Doblér, Manly, Verity, Woolrych, & Robertson, 2002; Posner, 2008). In neglect studies, the right temporoparietal junction has also been shown to be activated in tasks measuring vigilance and arousal (Corbetta et al., 2000; Robertson, Mattingley, Rorden, & Driver, 1998). In terms of the neuropsychological model of attention development (Posner & Petersen, 1990), neglect derived from damage in the right posterior parietal lobe has been related both to the right lateralized alerting system and to an inability to engage as well as disengage from an attentional focus to a target located in the direction opposite to the side of the lesion (Siéroff, Decaix, Chokron, & Bartolomeo, 2007). Thus, deficits in both the alerting and orienting attention networks have been associated with the neglect symptoms (see also Boles et al., 2009).

According to Proverbio and co-workers (1994), the models of the unbalanced attentional bias of the two hemispheres (Heilman et al., 1987; Kinsbourne, 1987) are supported by the findings from an ERP study with a callosotomy (split-brain) patient who had undergone surgical resection of the corpus callosum (see also Mangun et al., 1994): the reaction times to the LVF stimulus were longer than the reaction times to the RVF stimulus. The reaction times increased especially for the leftmost location, whereas such an eccentricity effect for stimuli in the RVF did not exist. The ERP data complemented and extended the reaction time results, together indicating a rightward bias of attention by the left hemisphere and bilateral control by the right hemisphere

over orienting in space. Moreover, Mangun et al. (1994) found in their split-brain patient study using a spatial cuing paradigm that the two hemispheres are asymmetrical in the control over attentional orienting in such a way that the right hemisphere is sensitive to events throughout the visual space (bilateral control), while the left hemisphere is biased toward events in the contralateral right hemisphere.

Evidence for right-lateralized mechanisms of visuospatial attention has also been found in studies on healthy participants (e.g. Posner, 2008; Thiebaut de Schotten et al., 2011). Corbetta and co-workers (1993) found evidence in their PET studies in normal healthy participants that the right superior parietal cortex was active during shifts of visuospatial attention either contralaterally and ipsilaterally, whereas the left hemisphere was active only when attention was shifted toward the contralateral (right) direction. In other words, attention to the left visual field is controlled by the right parietal cortex, while attention to the right visual field is controlled by both parietal cortices. Moreover, Corbetta et al. (2000) in their event-related functional magnetic resonance study found that in healthy adults the activation in the right temporoparietal cortical junction was stronger when the target occurred at an unattended location than at an attended location, which they proposed to indicate that the area involved in the processes of visual spatial reorienting is right-lateralized (see also Posner, 2008; Posner & Raichle, 1994). Furthermore, also the alerting system has been proposed to be right hemisphere lateralized in healthy humans (Callejas et al., 2005; Posner & Petersen, 1990).

In contrast to previous findings of rightward attentional spatial bias in patients with left unilateral neglect, split-brain or ADHD, there are observations of a small leftward spatial bias in line bisection tasks among healthy participants (Boles et al., 2009; Bowers & Heilman, 1980; Chan et al., 2009; McCourt & Jewell, 1999; Nicholls, Mattingley, & Bradshaw, 2005; Sosa, Teder-Sälejärvi, & McCourt, 2010) that has been explained to originate from the same attentional mechanisms as neglect, but is toward the opposite direction from the bias of the neglect patients (McCourt & Jewell, 1999). More precisely, this leftward spatial bias is proposed to originate from the right-lateralized attentional mechanisms, which deploy visuospatial attention into the left hemisphere (Boles et al., 2009; McCourt & Jewell, 1999; Sosa et al., 2010). However, there is yet no unifying quantitative theory of this phenomenon known as pseudoneglect, and there is considerable between-study variability in the theoretical explanations, with inconsistency characterizing the literature (for review, see Jewell & McCourt, 2000). For example, participants misbisect lines in the direction towards the hand used to

perform the bisections, bisection errors are made in the direction toward the hemisphere in which the stimulus is presented, and the direction of visual scanning has often been found to influence the perceived line midpoint in such a way that left-to-right scanning was associated with significantly larger leftward bisection errors than right-to-left scanning (for review, see Jewell & McCourt, 2000; Sosa et al., 2010). Moreover, it seems to be modality-specific: a leftward bias has been found in the visual and tactile modalities, but in the auditory modality a rightward bias was observed (Sosa et al., 2010).

1.2.3. Executive functions

In adult participants, in tasks where attentional control has been required, the perceptual-cognitive asymmetries have been less frequently observed than in child participants, and the asymmetries in adults seem to be more restricted to specific stimulus conditions, such as dichotic listening (e.g. Hugdahl et al., 2009) and visual half-field technique (Bowers & Heilman, 1980; Koivisto, 1997; McCourt & Jewell, 1999; Nicholls et al., 2005). This has led to the hypothesis that young adults are capable of modulating the magnitude of the asymmetries, presumably with the help of the advanced executive functions (e.g. Hugdahl et al., 2009).

In the scientific literature, the term executive functions lacks a clear definition (for review, see Jurado & Rosselli, 2007). However, it could be understood as skills necessary for high-level perceptual and cognitive goal-directed behaviour, such as attentional control and cognitive flexibility (see also Hugdahl et al., 2009; Luria, 1973; Posner & Raichle, 1994). Engle (2002) introduced the concept of “executive attention” as an ability to stay focused on a task in the context of distracting or interfering stimuli. In the neuropsychological perspective of attention development, Posner and co-workers proposed that the term “executive control” represents the attentional network that specializes in control processes, such as conflict resolution or detection of errors (see Posner, 2008; Posner & Raichle, 1994). Other concepts associated with the executive functions are set shifting, inhibition and working memory, to mention some (e.g. Garon, Bryson, & Smith, 2008). Efficient executive functioning needs memory functions, such as sensory memory, short-term memory, and long-term memory functions. Working memory is a capacity-limited temporary storage where information for different executive functions, such as language comprehension, learning, and reasoning, are manipulated (Baddeley, 1986). In Baddeley’s model (1986, 2000), working memory is

divided into four independent but interactive components: the visuospatial sketch pad (manipulation of visual images), the phonological loop (manipulation of speech-based information), the episodic buffer (multimodal temporary storage of information, where information from other components can be integrated with long-term episodic memory information), and the central executive, which is assumed to control the other components, control attentional functions, and influence the content of the conscious awareness. In the present work, the terms executive functions and executive control (Posner, 2008; Posner & Raichle, 1994) are used as synonyms, and they can also be considered to be close to Baddeley's (1986, 2000) definition of the central executive and Engle's (2002) definition of executive attention. Although executive functions may encompass many cognitive processes, in the present work, the executive functions are considered to include processes related to goal-directed behaviour, including processes such as manipulating and integrating information (*sensory* and *memory* functions) and conflict resolution (*attentional* focusing and inhibition of irrelevant stimuli or action).

Neuroanatomically, executive functions are assumed to be mediated by slowly developing frontal networks including subcortical structures and thalamic pathways (e.g. Anderson, Anderson, Northam, Jacobs, & Catroppa, 2001; Boles et al., 2008; Garon et al., 2008; Jurado & Rosselli, 2007; Posner & Raichle, 1994; Tsujimoto, 2008). For example, in infants, the frontal cortex is the last brain area to show an increase in glucose metabolism as a signal for the nervous system's connectivity (Chugani, 1998). Frontal lobes are also believed to be more sensitive to age-related changes during the lifespan compared to other parts of the brain (Span et al., 2004).

Development of attention, which is proposed to be one of the main component of executive functions (e.g. Garon et al., 2008), is accompanied by a gradual shift from subcortical processing to increasing cortical control (for review, see van de Weijer-Bergsma et al., 2007). The individual components of executive functions presumably start to develop already in early life and gradually combine into more complex executive function abilities (Garon et al., 2008; Jurado & Rosselli, 2007). For example, Dehaene-Lambertz et al. (2002) proposed that the activity in the prefrontal cortex of the infants aged 2-3 months during the speech perception task is related to the early engagement of active memory-retrieval mechanisms. Furthermore, the infant's ability to control visuospatial orienting and direct attention to peripheral objects is proposed to start to develop between 3 and 6 months of age (Smith & Chatterjee, 2008), whereas efficiency in voluntary covert orienting seems to reach adult-like ability between the

ages of 8 and 10 years (Goldberg, Maurer, & Lewis, 2001; Waszak et al., 2010). The ability to shift attention following an endogenous cue is proposed to be developed by the age of 10 years, whereas the ability to suppress information and actions that are inappropriate in the current context (inhibitory control), and to deal with conflicts during information processing, do not reach maturity until the age of 8 to 10 years or even later in adolescence (Goldberg et al., 2001; Hale, Bronik, & Fry, 1997; for review, see Crone, 2009; Jurado & Rosselli, 2007; Tsujimoto, 2008; Waszak et al., 2010). Thus, different executive functions follow different rates of development.

In older adults, the age-related decline in performance tends to be largest on tasks that heavily rely on executive control (e.g. Madden et al., 2005), but as in children, also in old age it has been rather difficult to assess how ageing influences specific executive functions due to great individual variability (for review, see Jurado & Rosselli, 2007). Older adults have a particular difficulty with divided and selective attention and in tasks that rely on working memory (for review, see Reuter-Lorenz & Sylvester, 2005), thus being more vulnerable to interference of irrelevant stimuli. Inhibition of irrelevant information seems to decline earlier than many other executive functions due to ageing (Jurado & Rosselli, 2007; Ridderinkhof & van der Molen, 1997; see also Waszak et al., 2010). Furthermore, the generalized slowing of information processing may underlie many of the observed age-related changes in perceptual and cognitive performance observed among the elderly (Madden et al., 2005). For example, when the influence of the slowed processing speed is controlled for, the allocation of attention to spatial locations and the shift of attention exhibit some degree of constancy during adulthood (Madden et al., 2005). Since it is difficult to distinguish the age-related changes in executive control processes from the generalized slowing of information processing, both frontal lobe and deep grey matter regions, such as the basal ganglia and thalamus, may all be important in age-related cognitive changes (Madden et al., 2005). For example, an inability to control perceptual biases has been associated with a decline in the efficiency of interhemispheric transfer of information in DL (Martin & Jerger, 2005). This has led to the proposal that an increase in task-non-specific activation of the prefrontal cortex may in fact represent a compensatory mechanism in response to a decline in the efficiency of the neural systems mediated by other brain regions (for review, see Madden et al., 2005; Reuter-Lorenz & Sylvester, 2005).

Sex differences in specific executive functions are also difficult to assess and no unanimous support for gender differences has yet been found. Also, not many studies

addressing sex differences in executive functions have been conducted, and rather often in different studies, males and females have been found to be quite similar with regard to many intellectual abilities. However, it has been proposed that in the adult population on average, females are better at tasks that require fast linguistic processing, fine motor skills, and perceptual speed, while males seem to be better at tasks that require visuospatial, spatiotemporal and mathematical skills, to mention just a few (for a review, see Halpern, 1997). In a study performed in a Finnish sample of adolescents between the ages of 16 and 18, with and without ADHD, indicated that females performed better than males in tasks that tested verbal fluency, fine motor control, reading fluency, set-shifting, and processing speed, whereas males outperformed females in tasks measuring visual orienting, interference control, verbal working memory, and computational skill (Loo et al., 2007). According to recent visuospatial and audiospatial working memory studies applied to Finnish children, boys between the ages of 6 and 10 years made more errors, were less accurate, and had shorter reaction times than girls, but such gender differences were no longer found in children between 11 and 13 years of age (Vuontela et al., 2003). Thus, the maturation of executive functions might take longer for boys than for girls (Vuontela et al., 2003). To summarize, the maturation of different executive functions may vary as a function of both gender and age.

1.2.4. Perceptual asymmetry and executive functions: Dichotic listening (DL) paradigm

The DL procedure with both non-forced and forced-attention paradigms has been used to investigate the possible interaction of the executive functions and the stimulus-driven asymmetries (e.g. Hugdahl, 2003; Hugdahl & Andersson, 1986; Hugdahl et al., 2009; Mondor & Bryden, 1992b). In the DL forced-attention paradigm, the participants are instructed to attend only to the right- or the left-ear stimulus. Several studies have shown that young adults can modify the stimulus-driven REA with the control of attention. By voluntarily attending to the right-ear linguistic stimuli in DL (forced-right attention condition, FR), the REA can be strengthened, and by voluntarily attending to the left-ear linguistic stimuli (forced-left attention condition, FL), the REA can be reduced and even occasionally switched to a left-ear advantage (LEA) (e.g. Andersson & Hugdahl, 1987; Hugdahl & Andersson, 1986; Asbjørnsen & Hugdahl, 1995; Hugdahl, 2003; Hugdahl et al., 2003).

The ability to modify the REA is proposed to result from the interaction of the linguistic right-side perceptual bias (bottom-up, stimulus-driven attention) and the executive functions (top-down control of attention) (Corbetta & Shulman, 2002; Hugdahl et al., 2003; Hugdahl et al., 2009; Tallus, Hugdahl, Alho, Medvedev, & Hämäläinen, 2007; Westerhausen et al., 2011; Westerhausen et al., 2010). Top-down processes, as a component of executive functions, represent knowledge-driven mechanisms designed to facilitate the discrimination between stimulus and noise, to enhance the processing of a relevant sensory input, and to direct the person toward particular spatial locations in which signals may appear. Hugdahl (Hugdahl, 2003; Hugdahl et al., 2003; see also Mondor & Bryden, 1991; Sætrevik & Hugdahl, 2007) proposed that in the forced-attention paradigm, the inherent structural processing advantage of the right-ear linguistic stimulus is controlled with the top-down control of attention. To enhance the REA in the FR attention condition, and to produce the LEA in the FL attention condition, suppression of intrusion from the nonattended ear and facilitation of recognition from the attended ear are probably needed (Asbjørnsen & Hugdahl, 1995; Engle, 2002). The interaction of the bottom-up and top-down processes in the FR and FL attention conditions is assumed to be different. In the FR attention condition, the bottom-up and top-down processes work synergistically, both pushing towards the right-ear response, while in the FL attention condition these two processes are in conflict (Hugdahl et al., 2009). This explains why the LEA is never as strong as the REA.

Sexton and Geffen (1979) proposed that the ability to focus and divide attention to dichotically presented linguistic stimuli is established already before the age of seven years, whereas Hugdahl and Andersson (1987) demonstrated increasing LEA in FL attention condition in eight-year-old children. In addition, Hiscock and Beckie (1993) propose that children at the age of 7 to 10 years were able to modify REA, while Hugdahl et al. (2001) showed that the REA can not be shifted into a significant LEA until the age of 10 to 15 years (Hugdahl, Carlsson, & Eichele, 2001). Thus, the results of the development of language laterality and executive functions in children in DL have been diverse since often, in earlier studies, the age ranges have been rather wide. Thus, the exact timing for when children learn to modify REA with the help of executive functions remains unclear (Andersson & Hugdahl, 1987; Hiscock & Beckie, 1993; Hugdahl & Andersson, 1986; Hugdahl et al., 2001; Sexton & Geffen, 1979). Variations in children's ability to attend to either ear have also been associated with the

development of the ability to read and with language comprehension (Asbjørnsen & Helland, 2006; Asbjørnsen, Helland, Obrzut, & Boliek, 2003; Hiscock & Beckie, 1993; Hugdahl & Andersson, 1987; Kershner & Morton, 1990; Obrzut, Obrzut, Bryden, & Bartels, 1985), but the results have again been contradictory.

Recently, ageing and the decline of top-down attentional control (executive functions) have been reported to weaken the ability to direct attention in the DL procedure (Beaton et al., 2000; Hugdahl, 2003; Hugdahl et al., 2001; Passow et al., 2012; Thomsen et al., 2004). Older participants over 50 years of age have been reported to be unable to direct their attention especially towards the left ear and to show LEA (Hugdahl, 2003; Hugdahl et al., 2001; Thomsen et al., 2004).

1.2.5. Modification of executive functions by training

Personal habits and special circumstances may lead to the development of the executive control towards an even superior level. For example, individuals who practised music regularly showed superior left-ear monitoring skills in linguistic DL when compared to the individuals who did not practise music or were non-musical (Milovanov, Tervaniemi, Takio, & Hämäläinen, 2007). In other words, individuals who practised music regularly were better at overcoming the conflict induced by inherent speech processing asymmetry favouring the right-ear stimuli and focusing on left-ear linguistic stimuli in DL. Furthermore, individuals with sensory deficits have been shown to be more efficient than healthy adults in directing attention and processing the spatial information with their intact modalities (Collignon, Voss, Lassonde, & Lepore, 2009; Lewald, 2002; Kujala, Alho, & Näätänen, 2000). For example, enhanced performance and different brain activation in blind individuals, compared with sighted participants, have been found in higher order cognitive and perceptual abilities, such as in speech discrimination (Niemeyer & Starlinger, 1981), localization of sounds (Lessard, Paré, Lepore, & Lassonde, 1998; Lewald, 2002; Röder et al., 1999; Weeks et al., 2000), and in memory functions (Röder & Rösler, 2003; Röder, Rösler, & Neville, 2001). Moreover, Röder et al. (1999) showed that blind individuals displayed superior localization abilities to peripheral auditory stimuli than sighted individuals (see also Fieger, Röder, Teder-Sälejärvi, Hillyard, & Neville, 2006). It has also been suggested that blind individuals are better especially at suppressing the stimuli presented in the task-irrelevant modality at the attended location in space (Hötting, Rösler, & Röder, 2004). The enhanced performance in blind individuals in many cognitive tasks has been

proposed to be related to the neuronal plasticity and cross-modal reorganization (Bavelier & Neville, 2002; Kujala et al., 2000; Röder et al., 1999), and to the blind individuals' enhanced ability in executive functioning: for example, blindness enhances the ability to respond and to switch and divide attention between two signal sources (Kujala, Alho, Paavilainen, Summala, & Näätänen, 1992; Kujala, Lehtokoski, Alho, Kekoni, & Näätänen, 1997; Röder et al., 1999).

2 Aims

The main goal of the present work was twofold. First of all, the aim was to study whether or not the spatial perceptual/attentional bias, observed in several DL studies (e.g. Andersson & Hugdahl, 1987; Asbjørnsen & Helland, 2006; Hiscock & Decter, 1988; Hiscock & Kinsbourne, 1977; Hugdahl, 2003), is related to the linguistic nature of the stimuli and to the modality. Second, the goal was to investigate whether or not the spatial perceptual bias observed with lateralized stimuli change as a function of age and praxis due to a sensory deficit.

More specifically, in Study I, the goal was to investigate with a cross-sectional experiment from a lifespan perspective, whether the auditory REA in DL with forced-attention paradigm changes as a function of age among healthy participants aged between 5 and 79 years, presumably due to the development of executive functioning. Furthermore, in this study, the possible relationship between the REA and the development of phonological awareness or learning a second language in children was also examined. In Study II, the aim was to determine whether the REA is stimulus-specific or not (linguistic vs. non-linguistic), and whether the lifespan changes observed in DL in ear advantages would also be found in auditory spatial attention tasks that put load on attention. Based on earlier results of dichotic listening and language development, it was predicted, that the spatial bias should vary as a function of age and early development of phonological awareness. In Study III, the aim was to investigate further with visual spatial attention tasks, mimicking the auditory tasks applied in Study II, whether the spatial bias is modality (auditory vs. visual) specific and/or influenced by stimulus type (linguistic vs. non-linguistic). It was expected in Study III that the perceptual asymmetries would be more intensive among the child and old adult participants than among the young adults whose executive functioning can be assumed to be at the most advanced level. Finally, as it has been suggested that sensory deficit enhances the executive functioning in intact modalities through their greater utilization, the aim in Study IV was to determine, whether blindness modifies the ear advantages in DL with forced-attention paradigm, which requires both sensory and attentional level of information processing in the auditory sensory modality.

3 Methods

3.1. Dichotic listening test

In Studies I and IV, the Finnish version of the DL test [the original “DLCV-108” dichotic listening test by Hugdahl and Andersson (1986)] with consonant-vowel (CV) syllables was applied. The dichotic stimuli consisted of six stop consonants paired with the vowel /a/ to form the CV syllables /ba/, /da/, /ga/, /pa/, /ta/ and /ka/. Each CV syllable was approximately 350-400 ms in duration and the inter-trial interval was approximately four seconds. The six CV syllables were combined in pairs in all possible combinations, thus forming a total of 36 different pairs of syllables, including six homonyms. In each trial, one CV syllable was presented to the left ear and another to the right ear with simultaneous onset. The 36 dichotic pairs were presented three times with three different randomizations resulting in three attentional conditions which differed with regard to the instructions on how to focus attention. In the NF attention condition, no specific instruction regarding attention was given and the participants were told to report, after each trial, the single syllable which they subjectively perceived most clearly of the six possible syllables. In the FR attention condition, participants were told to attend to the right-ear stimulus only, and to report the CV syllable presented to this ear only. In the FL attention condition, participants were told to attend to the left-ear stimulus only, and to report the syllables presented to this ear only.

3.2. Auditory Go/No-Go Spatial Attention test (AGSA)

In the Auditory Go/No-Go Spatial Attention test (AGSA), the digits 1-9 for adult participants or the names of nine different animals for child participants were presented in a randomized order into the left, right or both ears with simultaneous onset (Study II). The AGSA test consisted of subtasks, each including a total of 240 trials. In each subtask, 60 of the 240 trials included the targets. Of the 60 targets, 20 were presented in randomised order unilaterally to the right, 20 to the left, and 20 bilaterally to both ears with simultaneous onset. The participant’s task was to discriminate the targets and the non-targets from the left and/or right side and to respond by pressing buttons on the computer keyboard as fast and accurately as she/he could with the left and/or right forefinger when a target was perceived. The difficulty level of the subtasks was manipulated by the duration of the inter-stimulus interval (ISI = 200-1000 ms or 150-

650 ms) and/or the number of targets (2 targets (2T) or 4 targets (4T)).

3.3. Auditory Divided Spatial Attention test (ADSA)

In the Auditory Divided Spatial Attention test (ADSA), 550 Hz sinusoidal tones of 100 ms duration were presented into the left, right, or both ears with simultaneous onset (Study II). The ADSA test consisted of subtasks which differed in the duration of the inter-stimulus interval (ISI = 1000 ms or 500 ms). In the subtasks, 50 sinusoidal tones of the total of 150 tones were presented in randomised order to the right, 50 to the left, and 50 binaurally to both ears with simultaneous onset. The participant's task was to press the buttons on the computer keyboard as fast and accurately as she/he could with the left and/or right forefinger when a sinusoidal tone was perceived.

3.4. Visual Go/No-Go Spatial Attention test (VGSA)

In the Visual Go/No-Go Spatial Attention test (VGSA), pictures of the digits 1-9 for adults and of nine different animals for children (Figure 2) were presented into the LVF or/and RVF in a horizontal visual angle of 30° to the right and/or left from the fixation point (Study III). The VGSA test consisted of several subtasks. In each subtask, 60 trials of the total of 240 trials included targets. Of the 60 target trials, 20 were presented in a randomised order unilaterally to the LVF, 20 to the RVF, and 20 bilaterally to both visual fields (BVF) with simultaneous onset. The participant's task was to fixate her/his eyes to the fixation point and to discriminate the targets and the non-targets from the left and/or right side and to respond by pressing buttons on the computer keyboard as fast and accurately as she/he could with the left and/or right forefinger when a target was perceived. The difficulty level of the subtasks was manipulated with the duration of the stimulus-onset asynchrony time (SOA = 500-1500 ms or 300-800 ms) and/or the number of targets (2T or 4T).

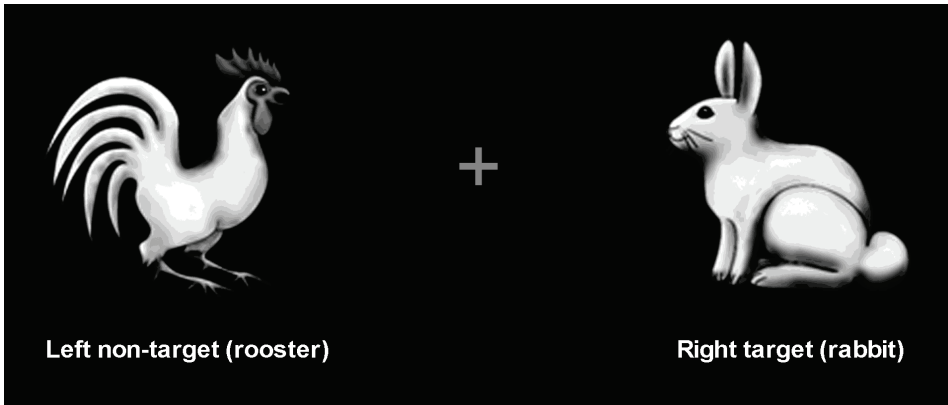


Figure 2. An example of the non-target (rooster) and the target (rabbit) pictures of the animals presented to child participants in the Visual Go/No-Go Spatial Attention test (VGSA). (Copyright of the original drawings is owned by Tuominen, T., LearnLab/ University of Oulu).

3.5. Visual Divided Spatial Attention test (VDSA)

In the Visual Divided Spatial Attention test (VDSA), dots of light were presented into the LVF or/and RVF visual fields in a horizontal visual angle of 30° to the right and/or left from the fixation point (Study III). The VDSA test consisted of subtasks which differed in the stimulus-onset asynchrony time (SOA = 1500 ms or 750 ms). In both subtasks, from the total of the 150 trials, 50 were presented in a randomised order to the LVF, 50 to the RVF and 50 bilaterally to the BVF with simultaneous onset. The participant's task was to fixate her/his eyes on the fixation point and to press the buttons on the computer keyboard as fast as she/he could with the right and/or left forefinger whenever a dot of light was perceived.

3.6. Other cognitive tests

All adult participants' numeric short-term memory was tested with the Wechsler Memory Scale- Revised (WMS-R, Digit Span). To take the possibility of mild cognitive impairment (MCI) into account, the older adults were also tested with the Wordlist learning test and the Wordlist delayed recall (the Finnish version of the Consortium to Establish a Registry for Alzheimer's Disease (CERAD)), since the Wordlist learning test is relatively sensitive to MCI (e.g. Karrasch, Sinervä, Grönholm, Rinne, & Laine, 2005). The 5-9-year-old children's ability to read was tested with a short sentence and their phonological awareness with parts of the Phonological Awareness Test (Poskiparta, Niemi, & Lepola, 1994; Silvén, Poskiparta, Niemi, & Voeten, 2007): Rhyme task (*Riimit*), Alliteration task (*Alkusointu*), and Phoneme-isolation task (*Alkuäänne*).

4 Summary of the Studies

4.1. Description of participants

Table 1. The groups and gender distributions in Studies I-IV

	<i>Group</i>	<i>N</i>	<i>Females</i>	<i>Males</i>	<i>Mean Age (SD)</i>
Study I	5-7 years	30	17	13	6.1 (0.1)
	8-9 years	41	19	22	8.6 (0.5)
	10-11 years	25	12	13	10.8 (0.3)
	19-32 years	50	30	20	24.6 (3.0)
	59-79 years	40	18	22	69.0 (4.8)
Study II*	5-7 years	18-26	12-14	6-12	6.5-6.8 (0.5-0.7)
	8-9 years	38-39	19	19-20	9.2 (0.5)
	10-11 years	27-28	13-14	14	10.8 (0.3-0.4)
	19-32 years	40-47	21-27	19-20	24.7 (3.0)
	59-79 years	38-40	16-18	22	69.0 (4.9)
Study III*	5-7 years	29	16	13	6.4 (0.7)
	8-9 years	42	20	22	9.1 (0.5)
	10-11 years	24-29	13-14	11-15	10.8 (0.3)
	19-32 years	38-50	20-30	18-20	24.6-24.8 (3.0-3.2)
	59-79 years	33-40	11-18	22	69.0-69.5 (4.8-5.0)
Study IV	Blind	14	10	4	48.6 (9.2)
	17-59 years	129	92	37	26.5 (9.3)

* The data from some of the participants had to be excluded due to either technical problems or the participant's inability or refusal to perform the test. Therefore, the number of participants in different participant groups varies between the tests applied in the Studies II and III.

4.2. The effect of age on attentional modulation in Dichotic listening (Study I)

Study I was designed to get an overall picture of the age-related changes across the lifespan in top-down control of bottom-up processes in DL with the forced-attention paradigm (Hugdahl & Andersson, 1986). Another aim was to investigate whether the development of phonological awareness and the beginning to acquire a second language in children interact with the language lateralization and the ability to use top-down control of attention in DL. A total of 186 right-handed healthy participants between the

ages of 5 and 79 years (divided into groups of 5-7-year-olds, 8-9-year-olds, 10-11-year-olds, 19-32-year-olds and 59-79-year-olds) were tested with CV- syllables presented dichotically under three attention instructions (NF, FR, FL) (Hugdahl & Andersson, 1986).

All age groups showed a REA in recognition of syllables in the NF attention condition (Figure 3A). Thus, the stimulus-driven rightward asymmetry in language processing is present already in the 5-7-year-old children and is maintained throughout the lifetime. Furthermore, in the 5-7- and 8-9-year-old children, the development of phonological awareness, more precisely, the development of recognition of phonemes correlated with the increase in rightward asymmetry: the better the child was at recognizing the phonemes from the beginning of the word, the more she or he was biased towards the right, independent of the attention instructions. This is thought to reflect the left hemisphere specialization for phonological processing, in particular for deriving phonetic features from auditory traces (see Tartter, 1988). Furthermore, among the 10–11-year-old children, the learning of a second language (English) covaried with the asymmetrical ability to recognise the phonemes: the better the English grade of the participant, the stronger was the REA in the FR attention condition.

The ability to modify the stimulus-driven REA in the FR and FL attention conditions changed as a function of age (Figure 3A). Only the young adults from the 19 to 32 years of age were able to fully modify the stimulus-driven REA effect with executive functions in both forced-attention conditions. Children under the age of nine years were not able to modify the REA, while the 10-11-year-old children began to show an ability to do so with top-down control of attention. Throughout the DL task, the performance of the 59–79-year-old adults was inferior to the performance of any other age group, mostly due to reduced performance for the left-ear stimuli. Like children, the old adults were unable to reverse the REA into a no-ear-advantage or into a LEA in the FL attention condition. However, the older participants showed a tendency to be able to partially suppress the intrusion from the nonattended right ear during the FL attention condition.

4.3. Auditory rightward spatial bias varies as a function of age (Study II)

Based on the earlier findings from DL studies (e.g. Hugdahl et al., 2003; Hugdahl et al., 2009), the aim of Study II was to investigate asymmetry and age-related changes in auditory spatial detection of linguistic and non-linguistic stimuli with selective and divided spatial attention tasks. It was predicted that the rightward spatial bias would be observed for linguistic stimuli in the AGSA task, and that the bias would vary as a function of age (development of executive functions) and as a function of development of phonological awareness. By analysing the data according to the Signal detection theory (SDT; Stanislaw & Todorov, 1999), it was possible to find out whether the expected rightward bias is perceptual by nature (sensitivity value d') or whether it also involves other cognitive processes (decision criterion value c). High sensitivity value d' refers to a good ability to discriminate the targets and the non-targets, whereas low d' refers to a poor ability to do so. With the decision value c it is possible to determine the participant's tendency to respond, irrespective of whether the stimulus is a target or a non-target. Furthermore, based on earlier studies of pure tones (e.g. Efron et al., 1983; Galbraith & Arroyo, 1993; Murray, 1986), there was no reason to presume that the processing of pure tones is lateralized to either hemisphere as is the processing of linguistic stimuli. By applying the ADSA test with non-linguistic stimuli (sinusoidal tones), the aim was to study whether the rightward spatial bias, observed previously in DL with linguistic stimuli, is specifically related to the linguistic nature of the stimuli or not. If any spatial bias is observed with non-linguistic stimuli, the bias is probably related to the hemispheric asymmetry in other than linguistic mechanisms. A total of 180 right-handed healthy participants between the ages of 5 and 79 years (divided into groups of 5-7-year-olds, 8-9-year-olds, 10-11-year-olds, 19-32-year-olds and 59-79-year-olds) were tested.

The speed and efficiency of the performance in the AGSA and ADSA tests increased in childhood, were best developed in young adulthood, and decreased in old age. The 5-7-year-old children's performance level was significantly inferior to that of the older children, while the performance level of 59-79-year-olds dropped in some of the conditions to the same level as the 10-11-year-old children. All age groups were biased to discriminate better the linguistic targets and non-targets from the right side than from the left side. In addition, the rightward perceptual bias in linguistic bilateral (dichotic) stimulus condition was observed throughout the lifespan. However, compared

to all the other age groups, the old adults made the most right side unilateral responses to the bilateral targets, indicating that bilateral (dichotic) targets were more difficult for them to perceive than for the others. Interestingly, also other rightward spatial asymmetries were observed in linguistic as well as in non-linguistic tests, and these asymmetries were more common in the children between 5 and 9 years of age and in the old adults than in the 10-11-year-old children or in the young adults. The 5-7-year-old children and the old adult participants detected the right-side stimuli better than the left-side stimuli in the non-linguistic binaural stimulus conditions. Furthermore, the 5-7-year-olds made more responses to the right side than to the left side, irrespective of the presence or absence of the non-linguistic stimuli. Moreover, the 8-9-year-old children responded more often to the right side than to the left side, irrespective of whether the stimuli were targets or non-targets. In other words, their decision criterion was more lax towards the right side than towards the left side. In conclusion, the auditory rightward spatial bias observed under attentional load in Study II was not specific to the linguistic nature of the stimuli and the nature and the incidence of the rightward spatial bias changed as a function of age (Table 2).

In the 5-9-year-old children, the correlation analyses between the phonological awareness and laterality indices revealed that the better the child performed in the rhyme task (recognized that two out of the three words named by the examiner ended with a similar sound pattern), the less he/she was biased toward the right side relative to the left side in discriminating the linguistic targets and the non-targets. This suggests that the present rightward perceptual bias in children cannot exclusively be explained by the development of linguistic abilities such as phonological awareness.

In old adults between the ages of 59 and 79 years the correlation analyses indicated that the more the old adult had difficulties in the numeric short-term memory test, the more he/she was biased to discriminate better the linguistic targets and the non-targets presented to the right side relative to the left side. Also, the more the old adult had difficulties in the numeric short-term memory test, the more he/she was biased to respond toward the right side than toward the left side, irrespective of the presence or the absence of the target. Moreover, the more the old adult participant made extra responses as errors toward the right side relative to the left side in the non-linguistic divided attention test, the less he/she was able to learn the CERAD wordlist. These results can be interpreted to reflect a relationship between age-related cognitive decline and the ability to voluntarily resist the rightward spatial biases.

Table 2. Summary of the results from Studies II and III. **R** stands for significant rightward spatial bias, **L** stands for significant leftward spatial bias, and **n** stands for no significant difference between the left and right.

	<i>Age group</i>				
	5-7	8-9	10-11	19-32	59-79
Study II					
<i>Auditory Go/No-Go Spatial attention test</i>					
d'	R	R	R	R	R
c	n	R	n	n	n
bilateral targets	R	R	R	R	R
<i>Auditory Divided Spatial attention test</i>					
correct responses	n	n	n	n	n
extra responses	R	n	n	n	n
binaural stimuli	R	n	n	n	R
Study III					
<i>Visual Go/No-Go Spatial attention test</i>					
d'	n	n	n	n	n
c	R	R	n	n	n
bilateral targets	n	n	n	R	R
<i>Visual Divided Spatial attention test</i>					
correct responses	n	n	R	n	R
extra responses	R	n	n	n	n
bilateral stimuli	R	R	R	R	R

4.4. Visual rightward spatial bias varies as a function of age (Study III)

The purpose of Study III was to examine with visual tests mimicking the auditory tests of Study II whether the rightward spatial bias observed in the auditory modality is a multimodal phenomenon, hence occurring also in the visual modality. Based on earlier findings that linguistic material is often better perceived and recognized from the right than from the left hemispace, it was hypothesised that in the VGSA test with linguistic stimuli, perceptual right hemispace asymmetries would be observed. Again, the data were analysed according to the Signal detection theory (Stanislaw & Todorov, 1999). Moreover, since no unequivocal hemispheric advantages have been documented in the processing of dots, it was assumed that if any spatial asymmetries in the detection of non-linguistic visual stimuli (such as dots) under attentional load are to be observed, they must be due to a hemispheric functional asymmetry in other than linguistic mechanisms. For this, the non-linguistic VDSA test with dots of light as stimuli was applied. Finally, if the hemispace asymmetries change as a function of age in a similar

manner as in the auditory modality, asymmetries should be more intensive in the child and the old adult participants than in the young adults. A total of 190 right-handed healthy participants between the ages of 5 and 79 years in five age groups (5-7-year-olds, 8-9-year-olds, 10-11-year-olds, 19-32-year-olds and 59-79-year-olds) were tested.

Similar to the results of Study II in the auditory modality, the speed and efficiency of the performance increased in childhood, were best developed in young adulthood, and decreased in old age. Also as in the auditory modality, in the visual modality, the 5-7-year-olds' performance level was inferior to that of the older children, and the performance level of the 59-79-year-olds dropped occasionally to the same level as the 10-11-year-old children. Moreover, the main findings of Study II were replicated, but now in the visual modality: solely rightward spatial bias was observed for linguistic and non-linguistic stimuli in unilateral and/or bilateral presentation conditions. The incidence of the rightward spatial biases changed as a function of age: they were more common in the children and the old adult participants than in the young adults. Nevertheless, the nature of the rightward spatial bias was somewhat distinct in different age groups. With linguistic stimuli the children between the ages of 5 and 9 years responded more often towards the right side than towards the left side, irrespective of whether the stimulus was a target or a non-target. In other words, their decision criterion was more lax towards the right hemispace than towards the left hemispace, similarly as was seen in the auditory modality among the 8-9-year-olds. Again, as in the auditory modality, with non-linguistic stimuli, the 5-7-year-olds responded more often toward the right side than toward the left side, even irrespective of whether any visual stimulus was presented on that side or not. Such rightward asymmetries observed in the younger children (5-9-year-olds) were not observed in the children between 10 and 11 years or in the adult participants. However, the children between the ages of 10 and 11 years and the old adults detected the unilateral non-verbal stimuli (dots) more often in the right than in the left visual field, thus showing rightward spatial bias. When the dot was presented bilaterally, a rightward spatial bias was observed in all age groups, whereas only the adult participants showed a rightward spatial bias also for bilateral linguistic (digit) stimuli. It is noteworthy that the old adults more frequently made right unilateral responses to bilateral linguistic targets than did the young adults. Thus, the cognitively more demanding bilateral stimulus condition induced stronger rightward spatial bias in the old adult participants than in the other participants. Finally, increasing the presentation speed decreased the old adults' performance more than that of the other age

groups. In conclusion, the results showed that the visual spatial bias observed in Study III occurred under attentional load, was towards the right hemispace, and was not specific to the linguistic nature of the stimuli. The incidence and nature of the rightward spatial bias changed as a function of age (Table 2).

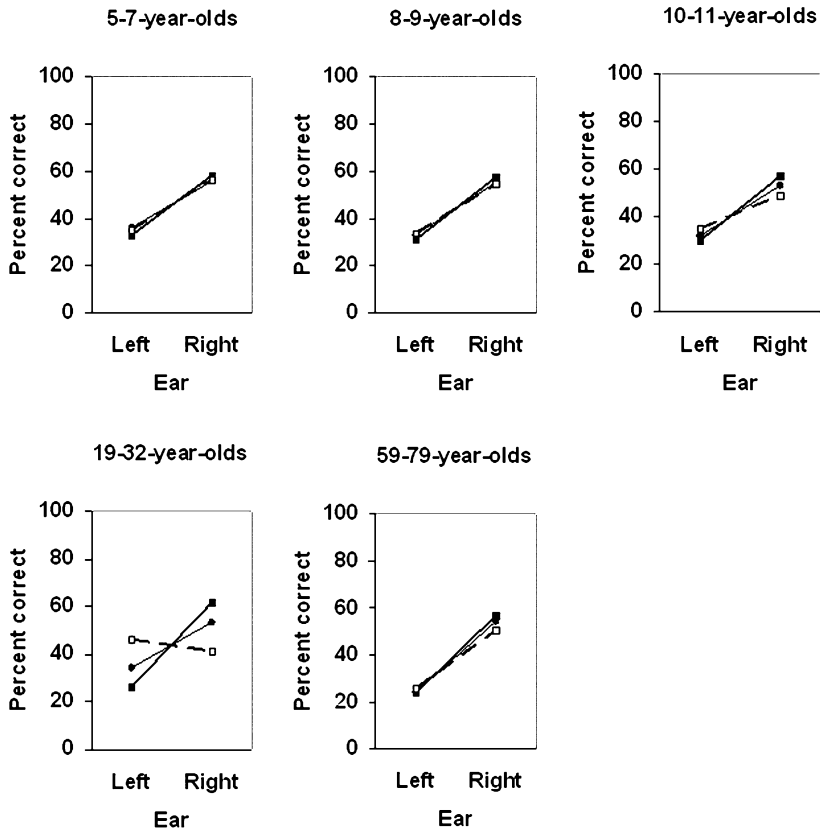
Although the correlation analyses between the laterality indices in the visual tests and other cognitive tests are not reported in the original paper, similarly to the auditory tests, in the VGSA test, the laterality indices for d' and c were calculated with the formula $(RVF-LVF)$, while the laterality indices for correct responses and extra responses for the VDSA test were calculated with the formula $[(RVF-LVF)/(RVF+LVF)]*100$. To test the possible influence of the development of phonological awareness on spatial bias in VGSA with linguistic stimuli, the correlations between the laterality indices from the VGSA subtasks and Phonological awareness tasks (Rhyme task, Alliteration task and Phoneme-isolation task) were analysed with Pearson correlation coefficient. In the 5-9-year-old children, the correlation analyses between the phonological awareness and laterality indices revealed that the better the child was at recognizing the sound patterns from the beginning of the word, the less he/she was biased to respond to the right side, irrespective of the presence or absence of the target ($r = .269, p = .027$). Also, the better the child was at recognizing and producing the first sound in a word, the less he/she was biased to respond to the right side, irrespective of the presence or absence of the target ($r = .238, p = .05$). Moreover, it has been suggested that the decline in executive functions might influence the observed spatial bias (Hugdahl, 2003; Hugdahl et al., 2001; Thomsen et al., 2004). To test for this, the correlations between the laterality indices from all visual subtasks and WMS-R digit span and CERAD (Wordlist learning test, Wordlist delayed recall and Wordlist savings) were analysed with Pearson correlation coefficient. In the young adult participants, the larger the participant's working memory -span was, the less he/she was biased to discriminate the right visual field targets better than the left visual field targets ($r = -.45, p = .007$).

4.5. Blind individuals show enhanced perceptual and attentional sensitivity for identification of speech sounds (Study IV)

The aim in Study IV was to determine the influence of the loss of sight on the auditory laterality, phonetic processing, and on the attentional control of laterality effect with the DL forced-attention paradigm (Hugdahl & Andersson, 1986). The main goal was to investigate whether blind individuals have increased sensitivity for detection of CV syllables (Niemeyer & Starlinger, 1981), and whether they would be better at directing attention than sighted individuals. The performance of 14 blind individuals (age range 29-60) was compared with that of 129 normally sighted individuals (age range 17-59).

The results showed that the blind participants perceived the linguistic stimuli significantly more accurately than did the sighted participants (Figure 3B). Both groups (sighted, blind) showed a REA in NF and in FR attention conditions, and a LEA in the FL attention condition. Most importantly, the blind participants were better than the sighted participants at focusing attention to enhance reporting the stimuli from the attended ear and in inhibiting processing of the irrelevant stimuli in the non-attended ear, especially in the FL attention condition.

A) Study I



B) Study IV

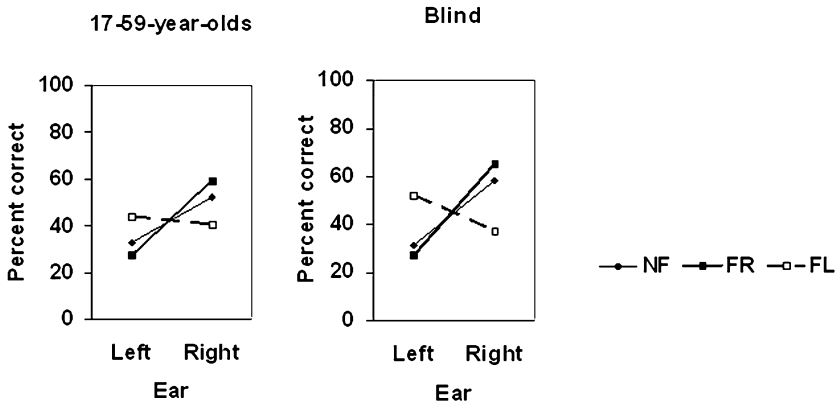


Figure 3. Percentage of correct reports for the left and the right ear stimuli in Non-Forced (NF), Forced-Right (FR), and Forced-Left (FL) attention conditions in Study I (A) and in Study IV (B).

5 Discussion

The main goal of the present work was to investigate whether spatial perceptual/attentional bias, observed in DL studies (e.g. Andersson & Hugdahl, 1987; Asbjørnsen & Helland, 2006; Hiscock & Decter, 1988; Hiscock & Kinsbourne, 1977; Hugdahl, 2003), is related to the nature of the stimuli and modality, and to study whether the possible spatial asymmetries change as a function of age and praxis due to a sensory deficit. The salient findings in the present work are as follows. In the tasks with cognitive load on spatial attention, only rightward spatial bias was observed, independent of the nature of the stimuli (linguistic vs. non-linguistic) in both the auditory and the visual modalities (see also Mondor & Bryden, 1992a, 1992b). The strength, incidence, and nature of the rightward spatial bias changed as a function of age and due to a sensory deficit via praxis. Such findings of a multimodal rightward spatial bias under attentional load and its' changes due to age and praxis are unique and unprecedented.

5.1. The role of age and praxis in perceptual tasks: summary of the results

In both auditory and visual spatial attention tasks, the efficiency of the performance increased in childhood between 5 and 11 years of age, was at its best in the young adults and decreased again in the elderly (see also Ridderinkhof & van der Stelt, 2000; Span et al., 2004) (Studies I-III). In equivalent auditory and visual spatial attention tests (Studies II and III), the 5-7-year-olds' performance level was inferior to that of the older children, and the performance level of the 59-79-year-olds dropped occasionally to the same level as that of the 10-11-year-old children. The nature, incidence, and strength of the rightward spatial bias varied between the age groups. Moreover, long-term blindness enhanced both the processing of auditory linguistic stimuli and attention modulation compared with the normally sighted adults (Study IV).

5.1.1. Children

Finnish children between the ages of 5 and 11 years showed a stimulus-driven REA in the DL NF attention condition (Study I), as well as a rightward perceptual bias in the bilateral (dichotic) stimulus conditions in the fast-paced auditory linguistic spatial attention test (Study II). In addition, the children between the ages of 5 and 11 years

were biased to discriminate the linguistic targets and the non-targets better from the right ear than from the left ear (Study II), and they showed a rightward perceptual bias in the visual non-linguistic bilateral stimulus conditions (Study III). Furthermore, in most of the auditory and visual linguistic and non-linguistic experimental setups, where manual responses were required, the children between the ages of 5 and 11 years had significantly faster RTs to the right side than to the left side (Studies II and III).

In contrast to what was observed in the 10-11-year-olds, a rightward spatial bias was observed in the children between the ages of 5 to 9 years, independent of the stimulus type, the sensory modality or the cognitive load of the task (Studies I, II and III). More precisely, in DL, the children between the ages of 5 and 9 years showed a stimulus-driven REA in all attention conditions, and they were not able to modify the REA with the top-down control of attention (Study I). Furthermore, the children between the ages of 5 and 7 years showed a rightward perceptual bias in the auditory non-linguistic bilateral stimulus conditions (Study II). In addition, the children between the ages of 5 and 9 years were more biased to respond with their right hand, or to respond to the stimuli presented in the right hemispace, irrespective of whether the stimuli were targets or non-targets, and independent of the modality where the stimuli were presented (Studies II and III). This functional rightward spatial bias was even more frequently observed in the 5-7-year-olds than in the 8-9-year-olds. Thus, especially the children under the age of eight years responded more readily to the right than to the left side, independent of the correctness of such responses or irrespective of the modality or the stimulus type.

Such functional rightward spatial asymmetries observed in the children under the age of 10 years were not observed in the children at the age of 10 to 11 years (Studies II and III). The 10-11-year-old children were also the youngest age group in the present work which in DL started to show some influence of the top-down attentional control over the stimulus-driven REA, either by facilitating the recognition of the right ear stimuli in the FR attention condition or by suppressing the right ear response tendency and facilitating recognition of the left ear stimuli in the FL attention condition (Study I). Nonetheless, the 10-11-year-old children still showed a rightward spatial bias in both the linguistic and non-linguistic stimulus conditions: in DL, the REA was observed throughout the test (Study I), and similar to the old adults, the 10-11-year-old children detected the unilateral dots more often in the right than in the left visual field (Study III).

5.1.2. Young and middle-aged adults

In DL, in a similar way to the other age groups, the young and middle-aged adults showed a stimulus-driven REA in the NF attention condition (Studies I and IV). However, only the young and middle-aged adults among the normally sighted participants in the present work were able to increase the REA by focusing on the right ear stimulus in the FR attention condition, as well as to overcome the REA and at least numerically recall more syllables from the left ear than from the right ear in the FL attention condition. As the result was observed in two separate DL studies with a reasonable sample of sighted adult participants (Studies I and IV), the result is rather reliable among the Finnish adult population. More detailed analyses in Study I showed that the performance of the young adults was due to suppression of intrusion from the non-attended ear, and facilitation of the corresponding attended ear during the forced-attention conditions. In Studies II and III, strong asymmetries were not observed in the young adults, and the few mild perceptual-cognitive asymmetries, which were mostly observed among all age groups, were predominantly observed in bilateral and/or linguistic stimulus conditions and were all towards the right hemispace: the young adults showed a rightward perceptual bias in the auditory and visual linguistic, and in the visual non-linguistic bilateral stimulus conditions (Study II and III), were biased to discriminate the linguistic targets and non-targets better from the right ear than from the left ear (Study II), and had significantly faster RTs to the right side than to the left side (Studies II and III).

5.1.3. Old adults

Like the other age groups, the elderly adults showed a stimulus-driven REA in the dichotic listening NF attention condition (Study I). They also showed a rightward perceptual bias in the auditory and visual linguistic, and in the visual non-linguistic bilateral stimulus conditions (Studies II and III). They were also biased to discriminate the linguistic targets and non-targets better from the right ear than from the left ear (Study II), and in those experimental setups where manual responses were required, had significantly faster RTs to the right side than to the left side (Studies II and III). In general, the older adults' performance was not only inferior to that of the young adults, but they also showed stronger rightward spatial bias in both auditory and visual modalities (Studies I, II and III), mostly resembling the bias observed in the children. For example, similarly to the 10-11-year-old children, the elderly detected the unilateral

non-verbal visual stimuli (dots) more often in the right than in the left visual field (Study III). Also, like the 5-7-year-old children, the elderly detected the right side non-linguistic stimuli better than the left side non-linguistic stimuli in the auditory binaural stimulus conditions (Study II).

Especially the cognitively demanding bilateral stimulus conditions induced stronger multimodal rightward spatial bias in the elderly than in any other age group. In DL (Study I), more detailed analyses suggested that the top-down inhibitory control of the stimulus-driven laterality effect related to speech sound perception in the FL condition may be maintained in older adults but not to such an extent that they would be able to overcome the REA. Thus, the results from all applied tests together indicated that older adults were inferior to young adults especially in directing their attention towards the left side in cognitively more demanding bilateral stimulus conditions.

5.1.4. Blind participants

Blindness was found to influence the performance in the dichotic listening test. Compared with the sighted adult participants, the blind individuals were better at processing and detecting linguistic auditory stimuli. The blind individuals were also better than the sighted adult participants at overcoming the stimulus-driven laterality effect related to speech sound perception, and at directing their attention to the appropriate spatial location (Study IV).

5.2. Multimodal rightward spatial bias – underlying mechanisms

To summarise, in all participant groups, the right-ear linguistic stimuli were detected better than the left-ear linguistic stimuli in DL (Studies I and IV). Furthermore, in all healthy participant groups, the linguistic targets and the non-targets were discriminated better when presented to the right than to the left ear in the linguistic auditory spatial attention test (Study II). In the visual modality, adult participants showed a rightward spatial bias for bilateral linguistic stimuli (Study III). Such a rightward spatial bias for linguistic stimuli could reflect a left-hemisphere processing advantage for the right-side linguistic stimuli, commonly observed in bilateral stimulus conditions (e.g. Boles et al., 2008; Dehaene-Lambertz et al., 2002; Della Penna et al., 2007; Kimura, 1966, 1967). The perceptual asymmetry in language processing, assessed on the basis of the NF attention condition in DL, was present already in the children

between the ages of 5 and 7 years, was maintained throughout the lifespan, and was also found in the blind individuals (Studies I and IV). In the children between the ages of 5 and 9 years, development of the identification of phonemes was associated with the asymmetry favouring the right ear CV syllables, probably reflecting the linguistic development and the early left hemisphere's specialization for phonological processing (see also Carroll et al., 2003). Thus, the present findings support the proposal that the linguistic development has an important connection with the children's asymmetrical performance in the DL task (e.g. Hugdahl & Andersson, 1987; Kershner & Morton, 1990). In turn, a negative correlation between the phonological awareness and the rightward spatial bias in the fast-paced linguistic spatial tasks with an attentional load, as well as a positive correlation between the English grade and the FR laterality index probably reflect the general level of cognitive development. This cognitive development affects both the development of the linguistic processes and executive functions that modify the behaviourally observable perceptual asymmetry.

The disparate response requirements in different studies may have influenced dissimilarly the observed rightward spatial bias. In the DL task (Studies I and IV), a verbal report was required, adding even more linguistic demands to the DL tasks compared to the other tasks. In the studies where manual responses were required (Studies II and III), the reaction times for correct responses were mostly faster to the right side than to the left side in all healthy participants, independent of the modality or the nature of the stimuli. All the participants were right-handed, so the rightward motor asymmetry might partly explain the reaction time results and the rightward response bias observed as extra responses or as a more lax response criterion toward the right-side stimuli than towards the left-side stimuli in the 5-7-year-olds and/or in the 8-9-year-olds in the auditory and visual modalities.

However, handedness and motor asymmetry cannot explain the observed rightward spatial biases which were due to the better detection of the right-side stimuli relative to the left-side stimuli. Since the rightward spatial bias was observed also in stimulus conditions in which processing is not assumed to be lateralized in the same manner as the linguistic processes, an alternative, but not necessary exclusive explanation for the present multimodal, stimulus-non-specific rightward spatial bias might be that under attentional load the right-side stimuli are more readily processed and/or responded to than the left-side stimuli, independent of the modality (auditory, visual) or the stimulus type (verbal, non-verbal). Therefore, the asymmetrical attentional

mechanisms (Driver & Vuilleumier, 2001; Heilman et al., 1987; Martin et al., 2008; Proverbio et al., 1994; Posner & Raichle, 1994) may play a substantial role in the present rightward spatial bias, and may interact with asymmetrical perceptual and/or motor processes (see Mondor and Bryden, 1992b). Heilman et al. (1987) proposed that the right hemisphere has bilateral spatial attentional control toward the left and right hemispaces, while the left hemisphere only directs attention contralaterally. In other words, there is redundant control of right space by both hemispheres, whereas the left space is only controlled by the right hemisphere. It has also been suggested that the left hemisphere has stronger directional bias than the right hemisphere (e.g. Kinsbourne, 1987). As the attentional mechanisms, such as alerting and orienting, are right-hemisphere lateralized also in the healthy brain (e.g. Posner, 2008; Posner & Raichle, 1994), it is possible that in a situation where the cognitive load is high, attentional resources are more readily allocated to stimuli in the right than the left hemisphere, irrespective of the stimulus type, since both hemispheres have attentional control over the right hemisphere (see also Mondor and Bryden, 1992b). Thus, the present multimodal rightward spatial bias may be contributed to by the hemispheric asymmetry of spatial attentional mechanisms, producing supramodal spatial right hemisphere preference in tasks under difficult discrimination conditions with attentional load.

5.3. Effect of age and praxis as evidence for the role of executive functions in perceptual asymmetries

What could explain the age-related and the sensory deficit -related changes observed in the strength of the rightward spatial bias? Based on findings from DL studies, Hugdahl (2003; see also Hugdahl et al., 2009) has suggested that adults can modify the stimulus-driven hemispheric processing advantage of the right-ear linguistic stimulus in DL with top-down control of attention. This volitional top-down control of attention influences the localization of the stimuli, is time-consuming, capacity-limited and highly participant-regulated (Hiscock, Inch, & Ewing, 2005). In the present experimental conditions, the participants' task was to direct their attention either to the left or right hemisphere or to monitor the whole hemisphere while the stimuli were presented randomly either to the left and/or the right hemisphere. A good level of performance required the ability to divide attention between the left and right hemisphere, in some tasks to filter the relevant stimuli from the irrelevant stimuli, and to suppress the perceptual-cognitive rightward spatial bias to prevent an inappropriate response or a

response to irrelevant stimuli with the help of the executive functions (see also Corbetta et al., 2008). Executive functions show slow early development in childhood and late decline among the elderly (e.g. Burke & Barnes, 2006; Jurado & Rosselli, 2007; Posner, 2008; Posner & Petersen, 1990; Posner & Raichle, 1994; Span et al., 2004; Tsujimoto, 2008). Therefore, it is proposed that the present rightward spatial bias, which was more pronounced in childhood and in old age than in young adulthood, was modulated by the executive functions (Baddeley, 1986; Engle, 2002; Posner, 2008; Posner & Petersen, 1990; Posner & Raichle, 1994), that is, functions responsible for goal-directed behaviour, such as resolution of conflict with attentional focusing, inhibitory functions and integration and manipulation of information with memory functions. Since especially the children and the elderly responded more readily to the right side stimuli and their attention was more readily drawn to the right hemispace, the age-related changes in the results indicate that the executive functions undergo significant developmental changes and are best utilized in adulthood. Young and middle-aged healthy adults, as well as adult blind participants, were, at least partly, able to overcome the conflict between the rightward spatial bias and the test demands. Praxis, normal development, age-related decline, and the interaction of different underlying asymmetrical mechanisms might then explain the observed group differences in the strength of the rightward spatial bias.

The present results among children between the ages of 5 and 11 years showed that the older the child was, the fewer right-side errors he/she made, presumably due to maturation of the executive functions. Moreover, the lack of attentional effects in the children between the ages of 5 and 9 years in DL (Study I) suggests that in children under the age of 10 years, the top-down attention control has not yet developed to the stage needed to suppress or inhibit the stimulus-driven bottom-up laterality effect for speech perception favouring the right ear. This result does not agree with previous dichotic listening studies indicating that children at the age of nine years and below are able to overcome REA and show significant LEA in the FL attention condition (e.g. Hugdahl & Andersson, 1987; Sexton & Geffen, 1979), but is in line with the findings of Hugdahl et al. (2001) who also demonstrated that children under the age of 10 were not able to modify the REA with top-down control of attention. Furthermore, the functional rightward bias observed in younger counterparts in fast-paced spatial attention tests was not found in older children at the age of 10 to 11 years. Thus, the present findings together indicate that the movement and impulse control and ability to inhibit the

response tendency develop first. The abilities to resist distractions, suppress information and actions, disengage attention, as well as impulse control, improve with age, some abilities being rather well developed around the age of 10 to 11 years (for review, see Hale et al., 1997; Jurado & Rosselli, 2007; Rueda et al., 2004). The findings indicate a gradual development of the executive functions in childhood and are in line with the earlier findings of Finnish children showing that 5-9-year-olds are behaviourally more impulsive than older children (Vuontela et al., 2003). However, in contrast to previous findings (e.g. Hugdahl et al., 2001), even children between the ages of 10 and 11 years were not able to fully modify the stimulus-driven REA and shift it into a significant LEA in DL. In other words, the present findings, together with the previous findings (e.g. Hugdahl et al., 2001), indicate that the adult level of cognitive control needed in the present tasks does not reach maturity earlier than in adolescence, presumably after the age of 11 years.

In old age, the inability to control perceptual asymmetries has been associated with a decline in cognitive abilities, and with a decline in the efficiency of interhemispheric transfer of information (Martin & Jerger, 2005). For example, the inability to correctly respond to a left-ear stimulus in a DL task has been shown to correlate with left prefrontal structural and functional changes (Thomsen et al., 2004), presumably reflecting failure in executive functions. An explanation for the decreased performance and the inability to change the REA into LEA in DL among the old adults in the present study might be similar to the one that Hugdahl et al. (2003) offered for schizophrenia patients. According to Hugdahl et al. (2003), the results indicate that due to changes in cognitive and especially executive inhibitory functions, the conflict in the FL attention condition between the linguistic bottom-up processes and the top-down control is too great for older people to change the REA into a LEA. As a matter of fact, a recent DL study (Passow et al., 2012) showed that the greater the conflict between the top-down attention control and the stimuli's perceptual saliency, the more perceptually driven behaviour and the less efficient attentional control were observed in older adults compared to younger adults.

A decline in executive functions might also explain the observed overall decline in the performance of older people. Even though no correlations between the old participants' laterality indices in DL and CERAD or WMS-R digit span were found, ageing did enhance the rightward spatial bias, especially in bilateral stimulus conditions, independent of the stimulus type. This multimodal rightward spatial bias especially

observed in bilateral stimulus conditions could be explained in terms of limited attention capacity. According to one view, visual extinction is a pathological exaggeration of the limited attention capacity, and therefore difficulties in becoming immediately aware of multiple targets are, in some circumstances, observed even in normal healthy humans (for review, see Driver and Vuilleumier, 2001). The present findings suggest that a mild extinction-like phenomenon can be observed throughout the lifespan, but the ability to distribute attention to multiple targets simultaneously decreases especially due to ageing. Moreover, in the speeded linguistic and non-linguistic auditory spatial attention tests, a relationship between age-related cognitive decline and the ability to voluntarily resist the rightward spatial bias was found: the less the old participants were able to learn the CERAD wordlist, or the more difficulties they had in numeric short-term memory, the stronger the rightward perceptual spatial bias observed. To conclude, in old age, the asymmetrical perceptual and cognitive processes become visible especially in fast-based, cognitively demanding perceptual tasks and bilateral stimulus conditions, perhaps due to the generalized slowing of processing speed and the decline of executive functions.

In a superior way to the sighted young and middle-aged adults, the blind individuals perceived more correct syllables and they were better at modifying the right-ear advantage with the control of attention (Study IV). The present results support previous findings showing that blind individuals are superior to sighted participants especially in speech sound discrimination tasks (Niemeyer & Starlinger, 1981). Blindness has been proposed to enhance involuntary orienting and stimulus discrimination (Alho, Kujala, Paavilainen, Summala, & Näätänen, 1993; Kujala et al., 1995; Röder, Rösler, Hemminghausen, & Näcker, 1996, Kujala et al., 1997). Furthermore, Röder and colleagues (1996) proposed that the enhanced brain activation during auditory tasks in the more posterior area of the occipital cortex in blind than in sighted participants is related to the multimodal attentional mechanisms (see also Alho et al., 1993). Praxis in the utilization of intact modalities compared to sighted individuals, and mechanisms such as brain plasticity and reorganization, are believed to enable the blind individuals' superior performance in their intact modalities: activation of the visual cortex in response to auditory and tactile stimulation and probably also attentional functions support the conclusion that the brain can reorganize itself after the loss of sight (for review, see Collignon et al., 2009). The present finding suggests that blindness enhances the ability to focus, divide or switch attention between two auditory

signal sources, especially in the task where localization of a sound within auditory space is required (Lewald, 2002; Röder et al., 1999).

In Study IV, the group of blind participants consisted of both congenitally and late blind individuals. Recently, it has been shown that independent of the time when the sight has been lost, both congenitally and late blind individuals are behaviourally more precise than sighted individuals at localizing and focusing attention on sounds in the periphery (Collignon et al., 2009; Fieger et al., 2006; Röder et al., 1999). In Study IV, a comparison of congenitally blind ($N = 7$) and late blind ($N = 7$) participants suggests that behaviourally the congenitally and late blind individuals performed equally well. However, based on ERP studies it has been proposed that the superior behaviour of blind individuals is mediated via different mechanisms depending of the timing of their sight loss (Fieger et al., 2006; Röder et al., 1999), which, in turn, has been proposed to indicate that in the developing brain, there is a limited time period when early attentional filtering processes can be altered by experience, whereas late attentional processes are modifiable throughout the lifetime (Fieger et al., 2006). In Study IV, the blind participants were probably better than the sighted participants at suppressing intrusion from the non-attended ear and facilitating of recognition from the attended ear. Thus, even though it is not possible to separate the underlying mechanisms behind the superior performance of the blind participants in the present work, it can still be concluded that blind individuals' abilities to process bilateral linguistic auditory stimuli and to control attention in the auditory modality are both enhanced.

Dichotic listening with the forced-attention paradigm was applied to all participant groups in the present work. By subtracting the DL Forced-left lateralization index (FL LI) from the Forced-right lateralization index (FR LI), the strength of the executive functions (EF) in the performance of each participant group can be nicely demonstrated (see Figure 4). The Post Hoc multiple comparisons showed that the strength of executive functions ($F_{6,328} = 13,76, p < .001$) was significantly stronger in the young and middle aged adults and in the blind participants than in the children or in the older adults (All p -values $\leq .001$). The age-related changes in the strength of the executive functions followed an inverted U curve: it increased in childhood, was well developed in young adulthood and decreased in old age (see Figure 4). The strength of the executive functions was numerically highest in the blind group. Moreover, all the observed significant correlations between the strength of the executive functions and the laterality indices from the applied tests exclusively supported the conclusion that the

stronger the strength of the executive functions, the less the participant was biased toward the right hemisphere. More precisely, in the children, a negative correlation between the laterality index for d' in the AGSA 2T subtask and the strength of the executive functions ($N = 83$, $r = -.24$, $p = .029$) was found, as well as a positive correlation between the laterality index for c in the AGSA 4T subtask and the strength of the executive functions ($N = 82$, $r = .27$, $p = .015$). The lack of significant correlations between the effect of the executive functions and all laterality indices from all subtasks could result from the small variations in the results within the age groups.

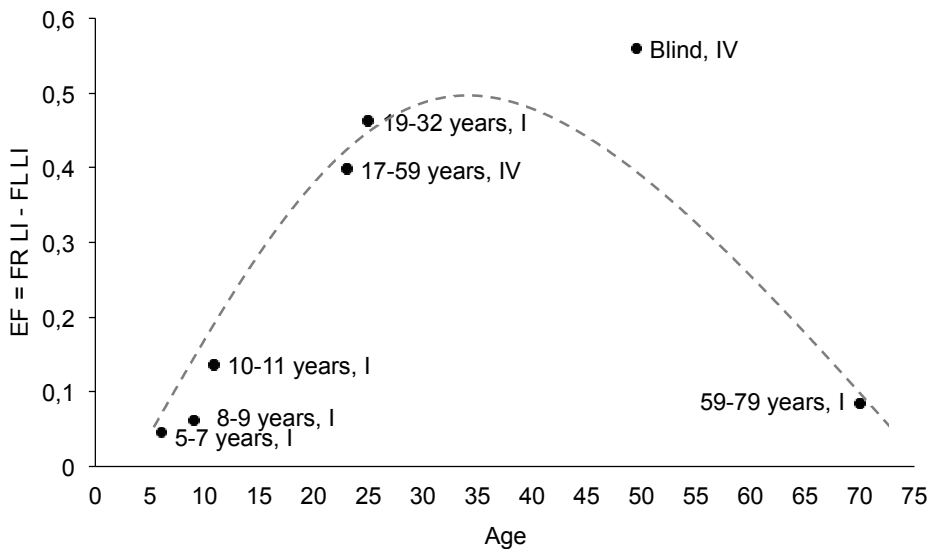


Figure 4. The strength of the executive functions (EF) is calculated by subtracting the DL Forced-left lateralization index (FL LI) from the Forced-right lateralization index (FR LI) in each participant group separately (Studies I and IV).

Although the enhanced rightward spatial bias was observed in the children and in the older adults, dissimilarities in the performances between these age groups were also observed. It is well known that old adults use different strategies in executive tasks than children (e.g. Span et al., 2004). It has been proposed that in normal ageing the ability to sustain attention remains, but that old adults tend to adopt rather conservative response criteria (Fernandez-Duque & Black, 2006). The latter was observed also in the present studies: the old adults used a more conservative response strategy than the children, who showed rightward response tendency irrespective of the presence or absence of the stimuli/target. Additionally, in some experimental setups, increasing the presentation

speed increased the reaction times in children but slowed the reaction times in adults, which might imply that children focus more on speed than on accuracy, while adults may focus more on accuracy than on speed (see also Jurado & Rosselli, 2007).

The present interpretation of a complex interaction of asymmetrical perceptual and cognitive processes and executive functions in perceptual asymmetries also agrees with the earlier findings related to the visual spatial attention. It has been shown that visual attentional exogenous cueing or preparation to make an eye movement toward the peripheral verbal stimuli (e.g. word recognition task) has a significant impact on verbal visual field asymmetry (Hyönä & Koivisto, 2006; Mondor and Bryder, 1992a): with preparation to make an eye movement or with exogenous cueing, the processing of the LVF stimuli benefits more from attentional cueing than the processing of the RVF stimuli, and the RVF advantage for verbal stimuli disappears. Mondor and Bryder, (1992a) suggest that the left hemisphere/RVF advantage for processing linguistic stimuli appears in situations where only few attentional resources are allocated to the linguistic discrimination task. However, in situations where attention is exogenously or endogenously oriented to the left hemispace well prior to the stimulus presentation, the attentional orienting attenuates inherent bottom-up rightward asymmetry and improves the recognition accuracy of linguistic stimuli presented to the LVF more than to the RVF (Mondor & Bryden, 1992a; see also Calvo & Nummenmaa, 2009; Hyönä & Koivisto, 2006). On the basis of the present findings of a rightward spatial bias for both linguistic and non-linguistic stimuli in a task with attentional load, an alternative cause of such an asymmetrical cuing effect could be the asymmetrical attentional mechanisms, which are more readily allocated to the right hemispace, and therefore exogenous cuing would affect orienting more to the stimuli in the left hemispace.

5.4. The model of interaction of cognitive functions underlying the age- and praxis-related change in rightward spatial bias

The key finding of the present work is a multimodal, stimulus-non-specific rightward spatial bias which was more often observed in the children and in the elderly than in the young adults. According to the present and earlier findings (e.g. Dehaene-Lambertz et al., 2002; Della Penna et al., 2007; Kimura, 1967), it can be concluded that the observed multimodal rightward spatial bias with linguistic stimuli reflects, at least

partly, a left-hemisphere processing advantage of linguistic stimuli. Since the processing of dots of light or sinusoidal tones is perhaps lateralized but not as clearly as the processing of linguistic stimuli (e.g. Boles et al., 2008; Efron et al., 1983; Galbraith & Arroyo, 1993; Gregory et al., 1983; Murray, 1986; Obrzut et al., 1989), it is proposed that the asymmetrical attention mechanisms (Heilman et al., 1987; Kinsbourne, 1987) interact with the perceptual processes, together inducing the multimodal, stimulus-non-specific rightward spatial bias which becomes visible under an adequately intensive attentional load. In other words, the multimodal perceptual rightward spatial bias in right-handed individuals results from a complex interaction of asymmetrical perceptual and cognitive processes that in the present work are related to language and attentional mechanisms. The effect of age and praxis due to a sensory deficit can be seen as evidence for the role of executive functions in modulating behaviourally observable left-right asymmetries.

The following model (Figure 5) integrates the mechanisms inducing the rightward spatial bias (linguistic/left hemisphere dominance and attentional/right hemisphere dominance; Figure 5a) and executive functions (prefrontal areas; Figure 5a) that modify this bias. The effects induced by these mechanisms on spatial cognitive processing and their synergistic functioning are depicted in Figure 5a, where the arrows show the direction of the influence of the mechanisms. According to this model it is possible to separate the effects of the different mechanisms by applying linguistic or non-linguistic stimulus conditions: in linguistic tasks the rightward spatial bias is induced by a combination of language and attentional mechanisms, whereas in such non-linguistic tasks which are not associated with perceptual hemispheric asymmetries, the attentional mechanisms presumably have a more dominant impact. Figure 5b summarizes the interaction of these different mechanisms at different age levels and in blind participants. As shown by the leftmost figurine in Figure 5b, children exhibit strong rightward spatial bias due to the biasing mechanisms not being balanced by the yet undeveloped executive functions. The next figurine on the right shows the balancing effect of fully developed executive functions on the biasing mechanisms in young adults, who are capable of modulating the rightward spatial bias and of directing their attention either to the left or right hemispace, or of monitoring the whole perceptual space. In elderly participants (next figurine to the right in Figure 5b), under attentional load, the decline in executive functions discloses the rightward spatial bias. And finally, as shown in the rightmost figurine in Figure 5b, blind participants have an enhanced ability to divide

spatial attention and to resist rightward spatial bias, which is presumably due to the extra praxis of processing linguistic auditory spatial information.

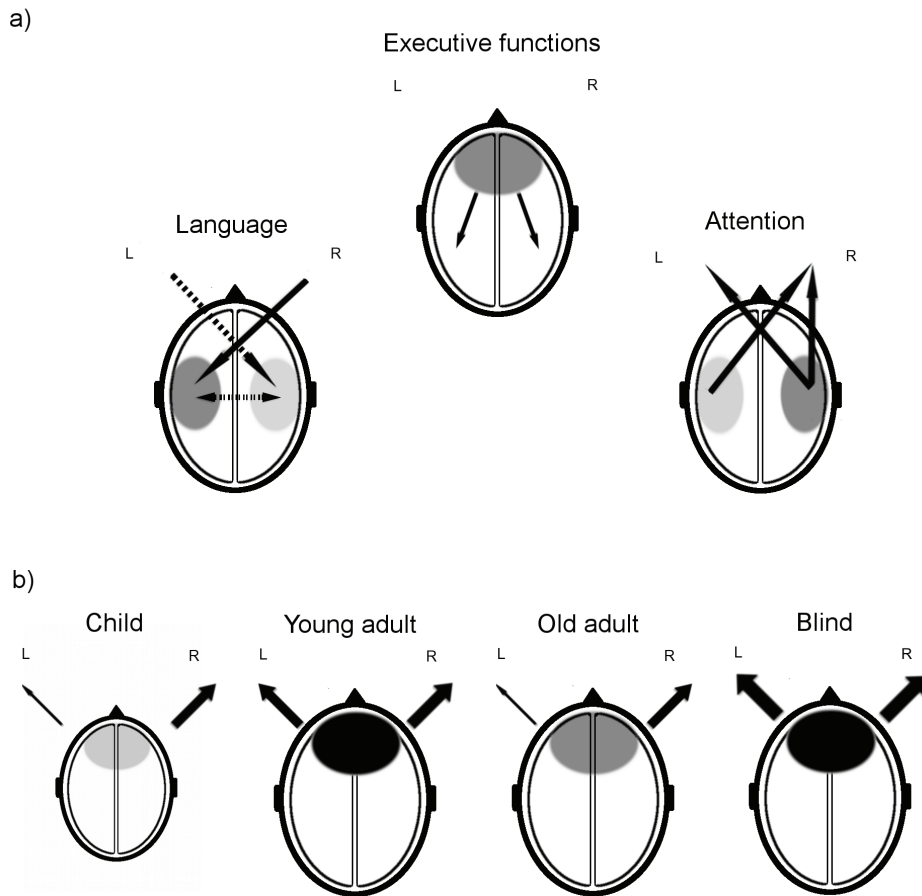


Figure 5. Simplified schematic presentation of the underlying mechanisms (a) and of the age and sensory deficit related changes (b) in rightward spatial bias in situations with attentional load. In Figure 5a and b, R stands for right hemisphere and L stands for left hemisphere.

In conclusion, the efficiency of the performance in spatial attention tasks and the ability to overcome the rightward spatial bias with executive functions increases as a function of childhood development, is at its best in young adulthood, and decreases as a function of ageing. Independent of the time when the sight has been lost, due to praxis, blindness enhances the ability to direct attention to an appropriate spatial location with executive functions.

The proposal of the existence of a multimodal rightward spatial bias related to the asymmetrical perceptual and cognitive processes is consistent with brain imaging

studies indicating that there are supramodal stimulus-driven and voluntary attention mechanisms (Macaluso, 2010; Teshiba et al., 2012). According to Macaluso (2010) attention mechanisms are structurally divided into two interactive brain networks: the dorsal fronto-parietal regions (dFP) are proposed to regulate endogenous (voluntary) control of attention, while the ventral fronto-parietal network (vFP) is primarily involved in stimulus-driven control of attention. Task-irrelevant auditory stimuli (vFP) can affect the reorienting processes and the endogenous attention control system (dFP) in visuo-spatial detection task, suggesting an interaction between the stimulus-driven and voluntary attention control in a multisensory context (Santangelo, Belardinelli, Spence, & Macaluso, 2009). Other recent studies (fMRI, PET) indicate that voluntary spatial attentional allocation or orienting activates the same neural systems irrespective of modality (Krumbholz, Nobis, Weatheritt, & Fink, 2009; Macaluso, Frith, & Driver, 2002). Also modality-specific subregions for attentional control exist (for review, see Krumbholz et al., 2009): e.g. modality-specific control is supported by distinct visual and auditory activations (Salmi, Rinne, Degerman, Salonen, & Alho, 2007) and distinct visual and tactile activations (Macaluso et al., 2002) in the parietal cortex during spatial attention tasks. Thus, it is possible that the behaviourally observed multimodal rightward spatial bias is related to the supramodal attention mechanisms, and the modality specific differences in the results in the present experiment could be associated with the modality-specific attention mechanisms.

5.5. Gender differences

In the original study papers, only in Study I were the gender differences reported even though in the statistical analysis in Studies II and III, gender was included as a variable. This was done because no unequivocal results for gender differences were found in a separate analysis. When inspecting all the results of gender differences from all the experimental setups among the age groups in parallel, the prominent absence of gender differences in most of the variables indicates that, throughout the lifetime, gender differences in the performances of spatial attention tasks are not preponderant (see e.g. Sommer et al., 2008). However, a few gender differences were found in the original analyses in Studies I, II and III enabling cautious interpretations to be made.

In the 5-11-year-old children, sporadically observed gender differences showed that in the linguistic dichotic listening task (Study I), the 5-7-year-old girls had stronger rightward spatial bias than the boys ($F_{1,28} = 8.14, p = .008$). Similar results were also

found in the non-linguistic VDSA test in the 10-11-year-olds ($F_{1,27} = 5.05, p = .033$). In other words, in both tests, the girls had stronger rightward spatial bias than the boys in bilateral stimulus conditions. In the linguistic VGSA test, independent of the age, the girls had overall a more conservative response criterion than the boys ($F_{1,89} = 7.98, p = .006$). This result is in line with previous findings from audiospatial and visuospatial working memory tasks, where Finnish boys between the ages of 6 and 10 years made more multiple responses as errors than girls (Vuontela et al., 2003). Additionally, a more careful analysis of the significant interactions between Age group, Difficulty level and Gender ($F_{2,89} = 3.28, p = .042$) indicated that unlike for other child participants, for the 10-11-year-old girls increasing the targets from two to four in the VGSA test did not influence their ability to discriminate the targets from the non-targets. However, separate analyses for each age group did not reveal any significant interactions between Difficulty level and Gender. In the non-linguistic ADSA test, increasing the difficulty level decreased the 10-11-year-old girls' performance more than that of the boys ($F_{1,26} = 5.79, p = .024$), while the 8-9-year-old girls ($F_{1,37} = 16.35, p < .001$) and the 10-11-year-old girls ($F_{1,26} = 6.72, p = .015$) responded overall more quickly than the boys. Finally, in dichotic listening, the 8-9-year-old girls' ($F_{1,39} = 5.58, p = .023$) and the 10-11-year-old girls' ($F_{1,23} = 5.22, p = .032$) performance was overall inferior to that of the boys.

Among the young adult participants, in the non-linguistic ADSA test, the males made overall more correct responses than the females ($F_{1,44} = 13.67, p = .001$), and increasing the difficulty level of the test decreased the young adult females' performance more than that of the males ($F_{1,44} = 10.81, p = .002$). Moreover, in the linguistic AGSA, the males were better at discriminating the targets from the non-targets than the females ($F_{1,38} = 4.56, p = .039$). In the old age group, the results were somewhat conflicting: in DL, the females' performance was overall better than that of the males' ($F_{1,38} = 4.47, p = .041$), while in the non-linguistic VDSA tests the significant interaction between Gender and Visual field ($F_{2,76} = 3.73, p = .038$) revealed that the bilateral stimuli were more difficult than the unilateral stimuli for the females than the males to detect. In the linguistic VGSA tests with a longer SOA, increasing the targets from two to four increased the unilateral responses for the bilateral targets more in females than in males, while with a shorter SOA the effect was the reverse ($F_{1,31} = 6.56, p = .016$). Also in old age, in the non-linguistic ADSA test, the significant interaction between gender and response side ($F_{1,36} = 5.97, p = .020$) showed a rightward bias in reaction times for the females but not for the males.

In conclusion, throughout the lifetime, gender differences in the performances of spatial attention tasks are not preponderant. However, the results cautiously suggest that since the results of the observed gender differences are age-dependent, there might be different developmental trajectories of the lateralization or the executive functioning in females and males.

5.6. Conclusions

The general goal of this work was to investigate with auditory and visual spatial attention tests, whether spatial perceptual asymmetries are related to the nature of the stimuli and modality, and whether they change as a function of age and praxis via a sensory deficit. The following conclusions can be drawn from the results of Studies I-IV:

1. Independent of the modality or the type of stimuli, under sufficiently intensive attentional load only rightward spatial bias was observed (Studies I-III). This multimodal, stimulus-non-specific rightward spatial bias in right-handed individuals probably results from a complex interaction of asymmetrical perceptual and cognitive processes that are related to language, attentional, and/or motor mechanisms. The nature and the strength of the interaction of the underlying mechanisms probably depend on the type of stimuli, on the response requirements of the experimental setup, and on the cognitive demands on behaviour.
2. The strength of the multimodal rightward spatial bias changed as a function of age and as a function of sensory deficit. In the right-handed individuals, the ability to voluntarily suppress and inhibit the multimodal rightward spatial bias probably reflects the developmental level of executive functions (see Figure 5 for schematic presentation).
 - a. The efficiency of the performance in spatial attention tasks and the ability to modulate and overcome the rightward spatial bias increased as a function of age in childhood, was at its best in young adulthood, and decreased as a function of ageing (Studies I-III). In childhood between the ages of 5 to 11 years probably movement and impulse control develop first, followed by the gradual development of the abilities to inhibit distractions and disengage attention. However, the adult level of cognitive control needed in the present tasks does not reach maturity until adolescence. The errors especially in bilateral

stimulus conditions suggest that a mild extinction-like phenomenon can be observed throughout the lifespan, but the ability to distribute attention to multiple targets simultaneously decreases especially in the course of ageing.

- b. Independent of the time when the sight has been lost, via praxis, blindness enhances the processing of bilateral linguistic auditory stimuli, the ability to overcome a stimulus-driven laterality effect related to speech sound perception, and the ability to direct attention to the appropriate spatial location (Study IV).

5.7. Limitations and suggestions for future research

Generalization of the present interpretations should be made with some caution, since a cross-sectional instead of a longitudinal design was used. However, the sample sizes of the healthy participants in the present work were considerable which makes the conclusions more comprehensive. As in most executive function studies, the generalization of the present results on age-related changes in specific executive function is difficult, since successful performance in the auditory and visual tests depended on a wide range of abilities. The wide age range, which is one of the strengths of the present study, produced the disadvantage that some of the tests and procedures needed modification when they were applied to the children. For example, the detection of numbers might have been more automatic in the adults than the detection of the applied pictures of animals in the children (e.g. Fischer, Castel, Dodd, & Pratt, 2003). Furthermore, it was assumed that both pictures of animals and pictures of numbers were processed as linguistic stimuli. However, it is possible that the processing mechanisms of these different visual stimuli might have been distinct: for example, it has been proposed that the processing of complex and coordinate spatial stimuli such as drawings of animals (e.g. Laeng & Peters, 1995) might require a variable set of processing of both categorical and coordinate spatial relations (Hellige et al., 2010). Finally, the test procedures needed modifications when applied to different participant groups, which might have had the effect that the tests or the test situations for all participants were not directly comparable.

To my knowledge, this is the first time that multimodal perceptual-cognitive asymmetries and their possible changes as a function of age and praxis have been studied, thus making the findings unique, and the theoretical interpretations tentative. In

future, it would be recommendable to apply the AGSA and VGSA with names or pictures of animals as stimuli also for adult participants, so that the results from the adults and the children would become better comparable. To investigate what, if any, role is played by handedness and possible motor asymmetry in the present results (Studies II and III), responses could be carried out in a different way than was done in the present study: for example, in 50% of the test-trials, participants should respond only with the right hand, and in 50 % only with the left hand.

Although comprehensive screening methods for executive functioning have not yet been developed, it is recommendable to study whether clinical neuropsychological assessments of executive functioning support the present interpretations of the age- and sensory deficit-related changes in executive functions. Moreover, it would be interesting to study whether training of the performance, for example, in the DL forced attention task influences the ability to focus attention to the left-ear stimuli. In addition, the experimental setups should be taken into more ecologically valid surroundings; for example, the young and old adults should be tested with the driving simulator to see whether rightward spatial bias is a phenomenon influencing our everyday life competence.

Only few studies focusing on the lifelong changes in the development of spatial asymmetries have been conducted (e.g. Boles et al., 2008), and most of the studies applied to children have focused on the early developmental stages. However, it has been suggested (e.g. Hugdahl et al., 2003) that most of the executive functions may reach an adult-like level during adolescence, so it is important to conduct more detailed analyses of participants between the ages of 12 and 18. The present studies investigated the functional asymmetries, which are presumably related to the lateralization of the brain. It has been demonstrated that behavioural visual half-field experiments can accurately measure hemispheric asymmetries and correlate with the hemodynamic response (Hunter & Brysbaert, 2008). However, behavioural results from manual tasks cannot be compared directly with the results from brain-imaging studies of the hemispheric asymmetries. Thus, neuroimaging studies are needed to further investigate the observed functional rightward spatial bias with spatial attention tasks (e.g. Westerhausen et al., 2010). Also, if the enhanced executive functioning is behind the better performance of the blind participants, neuroimaging studies that compare frontal activity during cognitively demanding tasks between blind and sighted individuals would give more support to this interpretation. Finally, as mentioned in the introduction,

the developmental timing for lateralization may vary in different domains, some processes lateralizing earlier than others (Boles et al., 2008). Most of the earlier studies have focused on asymmetries either in the motor, visual, auditory, or tactile modality separately. To my knowledge, the present work is one of the first studies in which the developmental timing of asymmetries in both auditory and visual modalities has been studied during the lifespan.

Acknowledgements

First I wish to thank my supervisors, Professor Heikki Hämäläinen and Docent Mika Koivisto who both helped me to distinguish the essential from the unessential and walked with me through this fascinating journey. Heikki, your enthusiasm for the research field, your innovative way of thinking “outside the box” and your ability to put appropriate pressure on the project made me work hard throughout this challenging project. Mika, thank you for your highly proficient and professional support, advice, and for your patience to immerse yourself in the research problems we have been dealing with, and especially, thank you Mika for always having time for my questions.

I also wish to thank Professor Teija Kujala and Professor Synnöve Carlson for agreeing to review this work, and for the valuable advice you have given me.

I am especially grateful to my co-author Assistant Professor Seppo J. Laukka for allowing me to carry out this research in collaboration with the University of Oulu, MA Tuulikki Tuominen for intensive practical assistance and for creating wonderful pictures and figures with endless enthusiasm, MA Laura Viljanen, MA Faramosh Rashid, MA Johanna Puolakanaho, MA Ville Penttilä, MA Mika Rekilä, MA Päivi Klemola and MA Niina Salo for practical assistance, data collection and priceless help.

Special thanks are due to MSc Teemu Laine for programming, MSc Maria Ek for continuous encouragement and practical and emotional support in moments of stalemate, MA Christian Haarala Björnberg and Docent Lauri Nummenmaa for helping with statistical analyses and Professor Maarit Silvén for helping me with the challenges and possible pitfalls when applying experimental setups for child participants. I also want to thank Docent Timo Ruusuvirta for asking me the right questions in time when the direction of my journey was temporarily lost. Furthermore, I wish to thank all my colleagues at the Centre for Cognitive Neuroscience and Department of Behavioural Sciences and Philosophy for friendship and support. MA Jacqueline Välimäki is greatly acknowledged for revising the English language of the original articles and this work.

Special thanks are due to the participants for taking part in the study, for being so cooperative.

Acknowledgements

I would like to express my gratitude to all my friends who never put pressure on me but still seemed to tenaciously believe that a Karonkka will eventually be held.

Finally I wish to thank my mother Ritva Takio for love and for always encouraging me to invest in myself, my brothers Teemu Takio and Totti Takio for friendship, for being my personal IT administrators, and for being the best brothers one could hope for, my father Tapani Takio and his wife Helena Virta for all the support you have given me, Paula Takio for her friendship and for helping me out with the English language, and my favourite aunt Kaija Jyllilä and favourite “uncle” Leo Mikkola for encouraging me to achieve more in life. I also wish to thank my other families, the Ahola and Kaustara families, for their support. And of course, my endearing nephew Martti, and our godchildren Pietari, Laura, Arttu, Tuure, Eero and Ilona, for frequently astonishing and surprising me with your increasing abilities and talents.

My biggest and most heartfelt thanks go to my loveable husband Teemu who never stopped to believe in me and my work.

This work was supported financially by the Nordic Centre of Excellence in Cognitive Control, the Finnish Graduate School in Psychology and the Finnish Cultural Foundation.

Turku, 16.5.2012

Fiia Takio

References

- Alho, K., Kujala, T., Paavilainen, P., Summala, H., & Näätänen, R. (1993). Auditory processing in visual brain areas of the early blind: evidence from event-related potentials. *Electroencephalography and clinical neurophysiology*, *86*, 418-427.
- Alivisatos, B., & Petrides, M. (1997). Functional activation of the human brain during mental rotation. *Neuropsychologia*, *35*, 111-118.
- Anderson, V. A., Anderson, P., Northam, E., Jacobs, R., & Catroppa, C. (2001). Development of executive functions through late childhood and adolescence in an Australian sample. *Developmental Neuropsychology*, *20*, 385-406.
- Andersson, B., & Hugdahl, K. (1987). Effects of sex, age, and forced attention on dichotic listening in children: a longitudinal study. *Developmental Neuropsychology*, *3*, 191-206.
- Asbjørnsen, A. E., & Helland, T. (2006). Dichotic listening performance predicts language comprehension. *Laterality*, *11*, 251-262.
- Asbjørnsen, A. E., Helland, T., Obrzut, J. E., & Boliek, C. A. (2003). The role of dichotic listening performance and tasks of executive functions in reading impairment: a discriminant function analysis. *Child Neuropsychology*, *9*, 277-288.
- Asbjørnsen, A. E., & Hugdahl, K. (1995). Attentional effects in dichotic listening. *Brain and Language*, *49*, 189-201.
- Baddeley, A. D. (1986). *Working memory*. Oxford: Oxford University Press.
- Baddeley, A. D. (2000). The episodic buffer: a new component of working memory?. *Trends in Cognitive Science*, *4*, 417-423.
- Barkley, R. A. (1997). Behavioral inhibition, sustained attention, and executive functions: constructing a unifying theory of ADHD. *Psychological Bulletin*, *121*, 65-94.
- Bavelier, D., & Neville, H. J. (2002). Cross-modal plasticity: where and how? *Nature Review Neuroscience*, *3*, 443-452.
- Beaton, A. A., Hugdahl, K., & Ray, P. (2000). Lateral asymmetries and interhemispheric transfer in aging: a review and some new data. In M. Mandal, M. Mulman-Fleming, & G. Tiwari (Eds.), *Side bias: A Neuropsychological perspective* (pp. 101-152). Netherlands: Kluwer Academic Publisher.
- Boles, D. B. (1986). Hemispheric differences in the judgement of number. *Neuropsychologia*, *24*, 511-519.
- Boles, D. B., Adair, L. P., & Joubert, A-M. (2009). A preliminary study of lateralized processing in attention-deficit/hyperactivity disorder. *The Journal of General Psychology*, *136*, 243-258.
- Boles, D. B., Barth, J. M., & Merrill, E. C. (2008). Asymmetry and performance: toward a neurodevelopmental theory. *Brain and Cognition*, *66*, 124-139.
- Bowers, D., & Heilman, K. M. (1980). Pseudoneglect: effect of hemispace on a tactile line bisection task. *Neuropsychologia*, *18*, 491-498.
- Brodeur, D. A., & Enns, J. T. (1997). Covert visual orienting across the lifespan. *Canadian Journal of Experimental Psychology*, *51*, 20-35.
- Brown, T. E. (2006). Executive functions and attention deficit hyperactivity disorder: implications of two conflicting views. *International Journal of Disability, Development and Education*, *53*, 35-46.
- Bryden, M. P. (1988). An overview of the dichotic listening procedure and its relation to cerebral organization. In K. Hugdahl (Ed.), *Handbook of Dichotic Listening: Theory, Methods and Research* (pp. 1- 43). Chichester: John Wiley & Sons Ltd.
- Burke, S. N., & Barnes, C. A. (2006). Neural plasticity in the ageing brain. *Nature Reviews, Neuroscience*, *7*, 30-40.
- Callejas, A., Lupiañez, J., Funes, M. J., & Tudela, P. (2005). Modulations among the alerting, orienting and executive control networks. *Experimental Brain Research*, *167*, 27-37.
- Calvo, M. G., & Nummenmaa, L. (2009). Lateralised covert attention in word identification. *Laterality*, *14*, 178-195.
- Carroll, J. M., Snowling, M. J., Hulme, C., & Stevenson, J. (2003). The development of phonological awareness in preschool children. *Developmental Psychology*, *39*, 913-923.
- Chan, E., Mattingley, J. B., Huang-Pollock, C., English, T., Hester, R., Vance, A., & Bellgrove, M. A. (2009). Abnormal spatial asymmetry of

References

- selective attention in ADHD. *Journal of Child Psychology and Psychiatry*, 50, 1064-1072.
- Chiang, C. H., Ballantyne, A. O., & Trauner, D. A. (2000). Development of perceptual asymmetry for free viewing of chimeric stimuli. *Brain and Cognition*, 44, 415-424.
- Chugani, H. T. (1998). A critical period of brain development: studies of cerebral glucose utilization with PET. *Preventive Medicine*, 27, 184-188.
- Collignon, O., Voss, P., Lassonde, M., & Lepore, F. (2009). Cross-modal plasticity for the spatial processing of sounds in visual deprived subjects. *Experimental Brain Research*, 192, 343-358.
- Corballis, M. C. (2009). The evolution and genetics of cerebral asymmetry. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 364, 867-879.
- Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, 3, 292-297.
- Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1993). A PET study of visuospatial attention. *The Journal of Neuroscience*, 13, 1202-1226.
- Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron*, 58, 306-324.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews, Neuroscience*, 3, 201-215.
- Corbetta, D., & Thelen, E. (1996). The developmental origins of bimanual coordination: a dynamic perspective. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 502-522.
- Corbetta, D., & Thelen, E. (1999). Lateral biases and fluctuations in infants' spontaneous arm movements and reaching. *Developmental Psychobiology*, 34, 237-255.
- Crone, E. A. (2009). Executive functions in adolescence: inferences from brain and behavior. *Developmental Science*, 12, 825-830.
- Daselaar, S., & Cabeza, R. (2005). Age-related changes in hemispheric organization. In R. Cabeza, L. Nyberg, & D. Park (Eds.), *Cognitive Neuroscience of Aging: Linking Cognitive and Cerebral Aging* (pp. 325-353). New York: Oxford university press.
- Dehaene-Lambertz, G., Dehaene, S., & Hertz-Pannier, L. (2002). Functional neuroimaging of speech perception in infants. *Science*, 298, 2013-2015.
- Della Penna, S., Brancucci, A., Babiloni, C., Franciotti, R., Pizzella, V., Rossi, D., ... Luca Romani, G. (2007). Lateralization of dichotic speech stimuli is based on specific auditory pathway interactions: neuromagnetic evidence. *Cerebral Cortex*, 17, 2303-2311.
- Deouell, L. Y., Hämäläinen, H., & Bentin, S. (2000). Unilateral neglect after right-hemisphere damage: contributions from event-related potentials. *Audiology & Neuro-otology*, 5, 225-234.
- Dien, J. (2009). A tale of two recognition systems: implications of the fusiform face area and the visual word form area for lateralized object recognition models. *Neuropsychologia*, 47, 1-16.
- Dobler, V. B., Manly, T., Verity, C., Woolrych, J., & Robertson, I. H. (2003). Modulation of spatial attention in a child with developmental unilateral neglect. *Developmental Medicine & Child Neurology*, 45, 282-288.
- Dolcos, F., Rice, H. J., & Cabeza, R. (2002). Hemispheric asymmetry and aging: right hemisphere decline or asymmetry reduction. *Neuroscience and Biobehavioral Reviews*, 26, 819-825.
- Domellöf, E., Rönnqvist, L., & Hopkins, B. (2007). Functional asymmetries in the stepping response of the human newborn: a kinematic approach. *Experimental Brain Research*, 177, 324-335.
- Driver, J., & Vuilleumier, P. (2001). Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*, 79, 39-88.
- Efron, R., Koss, B., & Yund, E. W. (1983). Central auditory processing. IV. Ear dominance – spatial and temporal complexity. *Brain and Language*, 19, 264-282.
- Engle, R.W. (2002). Working memory capacity as executive attention. *Current Directions in Psychological Science*, 11, 19-23.
- Everts, R., Lidzba, K., Wilke, M., Kiefer, C., Mordasini, M., Schroth, G., ... Steinlin, M. (2009). Strengthening of laterality of verbal and visuospatial functions during childhood and adolescence. *Human Brain Mapping*, 30, 473-483.

References

- Fagard, J., Spelke, E., & von Hofsten, C. (2009). Reaching and grasping a moving object in 6-, 8-, and 10-month-old infants: laterality and performance. *Infant Behavior and Development*, *32*, 137-146.
- Fan, J., McCandliss, B. D., Fossella, J., Flombaum, J. I., & Posner, M. I. (2005). The activation of attentional networks. *NeuroImage*, *26*, 471-479.
- Fernandez-Duque, D., & Black, S. E. (2006). Attentional networks in normal aging and Alzheimer's disease. *Neuropsychology*, *20*, 133-143.
- Fieger, A. L., Röder, B., Teder-Sälejärvi, W., Hillyard, S. A., & Neville, H. J. (2006). Auditory spatial tuning in late-onset blindness in humans. *Journal of Cognitive Neuroscience*, *18*, 149-157.
- Fischer, M. H., Castel, A. D., Dodd, M. D., & Pratt, J. (2003). Perceiving numbers causes spatial shift of attention. *Nature Neuroscience*, *6*, 555-556.
- Floet, A. M. W., Scheiner, C., & Grossman, L. (2010). Attention-deficit/hyperactivity disorder. *Pediatrics in Review*, *31*, 56-69.
- Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psychology*, *66*, 39-52.
- Furman, L. M. (2008). Attention-deficit hyperactivity disorder (ADHD): does new research support old concepts?. *Journal of Child Neurology*, *23*, 775-784.
- Galbraith, G. C., & Arroyo, C. (1993). Selective attention and brainstem frequency-following responses. *Biological Psychology*, *37*, 3-22.
- Garon, N., Bryson, S. E., & Smith, I. M. (2008). Executive function in preschoolers: a review using an integrative framework. *Psychological Bulletin*, *134*, 31-60.
- Ginsburg, H. J., Fling, S., Hope, M. L., Musgrove, D., & Andrews, D. (1979). Maternal holding preferences: a consequence of newborn head-turning response. *Child Development*, *50*, 280-281.
- Goble, D. J., & Brown, S. H. (2008). The biological and behavioural basis of upper limb asymmetries in sensorimotor performance. *Neuroscience and Biobehavioral Reviews*, *32*, 598-610.
- Goldberg, M. C., Maurer, D., & Lewis, T. L. (2001). Developmental changes in attention: the effects of endogenous cueing and of distractors. *Developmental Science*, *4*, 209-219.
- Gregory, A. H., Efron, R., Divenyi, P. L., & Yund, E. W. (1983). Central auditory processing. I. Ear dominance - a perceptual or an attentional asymmetry. *Brain and Language*, *19*, 225-236.
- Haaland, K. Y. (2006). Left hemisphere dominance for movement. *The Clinical Neuropsychologia*, *20*, 609-622.
- Haaland, K. Y., & Harrington, D. L. (1996). Hemispheric asymmetry of movement. *Current Opinion in Neurobiology*, *6*, 796-800.
- Hale, S., Bronik, M. D., & Fry, A. F. (1997). Verbal and spatial working memory in school-age children: developmental differences in susceptibility to interference. *Developmental Psychology*, *33*, 364-371.
- Hale, T. S., Zaidel, E., McGough, J. J., Phillips, J. M., & McCracken, J. T. (2006). Atypical brain laterality in adults with ADHD during dichotic listening for emotional intonation and words. *Neuropsychologia*, *44*, 896-904.
- Halpern, D. F. (1997). Sex difference in intelligence. Implications for education. *American Psychological Association*, *52*, 1091-1102.
- Harris, I. M., Egan, G. F., Sonkkila, C., Tochon-Danguy, H. J., Paxinos, G., & Watson, J. D. G. (2000). Selective right parietal lobe activation during mental rotation. A parametric PET study. *Brain*, *123*, 65-73.
- Heilman, K. M., Valenstein, E., & Watson, R. T. (2000). Neglect and related disorders. *Seminars in neurology*, *20*, 463-470.
- Heilman, K. M., Bowers, D., Valenstein, E., & Watson, R. T. (1987). Hemispace and hemispatial neglect. In M. Jeannerod (Ed.), *Neurophysiological and Neuropsychological Aspects of Spatial Neglect* (pp. 115-150). North-Holland: Elsevier Science Publishers B.V.
- Helland, T., & Asbjørnsen, A. (2001). Brain asymmetry for language in dyslexic children. *Laterality*, *6*, 289-301.
- Hellige, J. B., Laeng, B., & Michimata, C. (2010). Processing asymmetries in the visual system. In K. Hugdahl & R. Westerhausen (Eds.), *The two halves of the brain: Information processing in the cerebral hemispheres* (pp. 379-415). Cambridge, MA: The MIT Press.
- Hepper, P. G., McCartney, G. R., & Shannon, E. A. (1998). Lateralised behaviour in first trimester human foetuses. *Neuropsychologia*, *36*, 531-534.
- Hirnstein, M., Leask, S., Rose, J., & Hausmann, M. (2010). Disentangling the relationship between

References

- hemispheric asymmetry and cognitive performance. *Brain and Cognition*, 73, 119-127.
- Hiscock, M., & Beckie, J. L. (1993). Overcoming the right-ear advantage: a study of focused attention in children. *Journal of Clinical and Experimental Neuropsychology*, 15, 754-772.
- Hiscock, M., & Decter, M. (1988). Dichotic listening in children. In K. Hugdahl (Ed.), *Handbook of Dichotic Listening: Theory, Methods and Research* (pp. 431- 473). Chichester: John Wiley & Sons Ltd.
- Hiscock, M., Inch, R., & Ewing, C. T. (2005). Constant and variable aspects of the dichotic listening right-ear advantage: a comparison of standard and signal detection tasks. *Laterality*, 10, 517-534.
- Hiscock, M., Inch, R., Hawryluk, J., Lyon, P. J., & Perachio, N. (1999). Is there a sex difference in human laterality? III. An exhaustive survey of tactile laterality studies from six neuropsychology journals. *Journal of Clinical and Experimental Neuropsychology*, 21, 17-28.
- Hiscock, M., Inch, R., Jacek, C., Hiscock-Kalil, C., & Kalil, K. M. (1994). Is there a sex difference in human laterality? I. An exhaustive survey of auditory laterality studies from six neuropsychology journals. *Journal of Clinical and Experimental Neuropsychology*, 16, 423-435.
- Hiscock, M., Israelian, M., Inch, R., Jacek, C., & Hiscock-Kalil, C. (1995). Is there a sex difference in human laterality? II. An exhaustive survey of visual laterality studies from six neuropsychology journals. *Journal of Clinical and Experimental Neuropsychology*, 17, 590-610.
- Hiscock, M., & Kinsbourne, M. (1977). Selective listening asymmetry in preschool children. *Developmental Psychology*, 13, 217-224.
- Hiscock, M., & Kinsbourne, M. (1980). Asymmetries of selective listening and attention switching in children. *Developmental Psychology*, 16, 70-82.
- Hugdahl, K. (2003). Dichotic listening in the study of auditory laterality. In K. Hugdahl & R. Davidson (Eds.), *The Asymmetrical Brain* (pp. 441-476). Cambridge, Massachusetts, London.
- Hugdahl, K., & Andersson, B. (1987). Dichotic listening and reading acquisition in children: a one-year follow-up. *Journal of Clinical and Experimental Neuropsychology*, 9, 631-649.
- Hugdahl, K., & Andersson, L. (1986). The "forced-attention paradigm" in dichotic listening to CV-syllables: a comparison between adults and children. *Cortex*, 22, 417-432.
- Hugdahl, K., Bodner, T., Weiss, E., & Benke, T. (2003). Dichotic listening performance and frontal lobe function. *Cognitive Brain Research*, 16, 58-65.
- Hugdahl, K., Brønnick, K., Kyllingsbæk, S., Law, I., Gade, A., & Paulson, O. B. (1999). Brain activation during dichotic presentations of consonant-vowel and musical instrument stimuli: a ¹⁵O-PET study. *Neuropsychologia*, 37, 431-440.
- Hugdahl, K., Carlsson, G., & Eichele, T. (2001). Age effects in dichotic listening of consonant-vowel syllables: interactions with attention. *Developmental Neuropsychology*, 20, 445-457.
- Hugdahl, K., Helland, T., Færevaaag, M. K., Lyssand, E. T., & Asbjørnsen, A. (1995). Absence of ear advantage on the consonant-vowel dichotic listening test in adolescent and adult dyslexics: specific auditory-phonetic dysfunction. *Journal of Clinical and Experimental Neuropsychology*, 17, 833-840.
- Hugdahl, K., Rund, B. R., Lund, A., Asbjørnsen, A., Egeland, J., Landrø, N. I., ... Sundet, K. (2003). Attentional and executive dysfunctions in schizophrenia and depression: evidence from dichotic listening performance. *Biological Psychiatry*, 53, 609-616.
- Hugdahl, K., Westerhausen, R., Alho, K., Medvedev, S., Laine, M., & Hämäläinen, H. (2009). Attention and cognitive control: unfolding the dichotic listening story. *Scandinavian Journal of Psychology*, 50, 11-22.
- Hunter, Z. R., & Brysbaert, M. (2008). Visual half-field experiments are a good measure of cerebral language dominance if used properly: evidence from fMRI. *Neuropsychologia*, 46, 316-325.
- Hyönä, J., & Koivisto, M. (2006). The role of eye movements in lateralised word recognition. *Laterality*, 11, 155-169.
- Hötting, K., Rösler, F., & Röder, B. (2004). Altered auditory-tactile interactions in congenitally blind humans: an event-related potential study. *Experimental Brain Research*, 159, 370-381.
- Ivry, R. B., & Robertson, L. C. (1998). *The two sides of perception*. Cambridge, Massachusetts, London, England: The MIT Press.
- Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: a review and meta-analysis of

References

- performance factors in line bisection tasks. *Neuropsychologia*, *38*, 93-110.
- Johnson, M. H., & Tucker, L. A. (1996). The development and temporal dynamics of spatial orienting in infants. *Journal of Experimental Child Psychology*, *63*, 171-188.
- Jurado, M. B., & Rosselli, M. (2007). The elusive nature of executive functions: a review of our current understanding. *Neuropsychology review*, *17*, 213-233.
- Kanwisher, N., & Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society, Serie B*, *361*, 2109-2128.
- Karrasch, M., Sinervä, E., Grönholm, P., Rinne, J., & Laine, M. (2005). CERAD test performances in amnesic mild cognitive impairment and Alzheimer's disease. *Acta Neurologica Scandinavica*, *111*, 172-179.
- Kershner, J. R., & Morton, L. L. (1990). Directed attention dichotic listening in reading disabled children: a test of four models of maladaptive lateralization. *Neuropsychologia*, *28*, 181-198.
- Kimura, D. (1966). Dual functional asymmetry of the brain in visual perception. *Neuropsychologia*, *4*, 275-285.
- Kimura, D. (1967). Functional asymmetry of the brain in dichotic listening. *Cortex*, *3*, 163-178.
- Kinsbourne, M. (1970). The cerebral basis of lateral asymmetries in attention. *Acta Psychologica*, *33*, 193-201.
- Kinsbourne, M. (1987). Mechanisms of unilateral neglect. In M. Jeannerod (Ed.), *Neurophysiological and neuropsychological Aspects of Spatial Neglect* (pp. 69-86). North-Holland: Elsevier Science Publishers B.V.
- Koivisto, M. (1997). Time course of semantic activation in the cerebral hemispheres. *Neuropsychologia*, *35*, 497-504.
- Konrad, K., & Eickhoff, S. B. (2010). Is the ADHD brain wired differently? A review on structural and functional connectivity in attention deficit hyperactivity disorder. *Human Brain Mapping*, *31*, 904-916.
- Krumbholz, K., Nobis, E. A., Weatheritt, R. J., & Fink, G. R. (2009). Executive control of spatial attention shifts in the auditory compared to the visual modality. *Human Brain Mapping*, *30*, 1457-1469.
- Kujala, T., Alho, K., & Näätänen, R. (2000). Cross-modal reorganization of human cortical functions. *Trends in Neurosciences*, *23*, 115-120.
- Kujala, T., Alho, K., Paavilainen, P., Summala, H., & Näätänen, R. (1992). Neural plasticity in processing of sound location by the early blind: an event-related potential study. *Electroencephalography and clinical Neurophysiology*, *84*, 469-472.
- Kujala, T., Alho, K., Kekoni, J., Hämäläinen, H., Reinikainen, K., & Salonen, O., ... Näätänen, R. (1995). Auditory and somatosensory event-related brain potentials in early blind humans. *Experimental Brain Research*, *104*, 519-526.
- Kujala, T., Lehtokoski, A., Alho, K., Kekoni, J., & Näätänen, R. (1997). Faster reaction times in the blind than sighted during bimodal divided attention. *Acta Psychologica*, *96*, 75-82.
- Laeng, B., & Peters, M. (1995). Cerebral lateralization for the processing of spatial coordinates and categories in left- and right-handers. *Neuropsychologia*, *33*, 421-439.
- Laurent-Vannier, A., Pradat-Diehl, P., Chevignard, M., Abada, G., & De Agostini, M. (2003). Spatial and motor neglect in children. *Neurology*, *60*, 202-207.
- Lenneberg, E. H. (1967). *Biological foundations of language*. New York: Wiley.
- Lessard, N., Paré, M., Lepore, F., & Lassonde, M. (1998). Early-blind human subjects localize sound sources better than sighted subjects. *Nature*, *395*, 278-280.
- Lewald, J. (2002). Opposing effects of head position on sound localization in blind and sighted human subjects. *European Journal of Neuroscience*, *15*, 1219-1224.
- Loo, S. K., Humphrey, L. A., Tapio, T., Moilanen, I. K., McGough, J. J., McCracken, J. T., ... Smalley, S. L. (2007). Executive functioning among Finnish adolescents with attention-deficit/hyperactivity disorder. *Journal of American Academy of Child and Adolescent Psychiatry*, *46*, 1594-1604.
- Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1989). Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature*, *342*, 543-545.
- Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1994). Independent attentional scanning in the separated hemispheres of split-brain patients. *Journal of Cognitive Neuroscience*, *6*, 84-91.

References

- Luria, A. R. (1973). *The Working Brain. An introduction to neuropsychology*. England: Penguin Books Ltd.
- Macaluso, E. (2010). Orienting of spatial attention and the interplay between the senses. *Cortex*, *46*, 282-297.
- Macaluso, E., Frith, C. D., & Driver, J. (2002). Directing attention to locations and to sensory modalities: multiple levels of selective processing revealed with PET. *Cerebral Cortex*, *12*, 357-368.
- Madden, D. J., Whiting, W. L., & Huettel, S. A. (2005). Age-related changes in neural activity during visual perception and attention. In R. Cabeza, L. Nyberg, & D. C. Park (Eds.), *Cognitive neuroscience of aging: linking cognitive and cerebral aging* (pp. 157-185). University Press, Oxford.
- Mangun, G. R., Luck, S. J., Plager, R., Loftus, W., Hillyard, S. A., Handy, T., ... Gazzaniga, M. S. (1994). Monitoring the visual world: hemispheric asymmetries and subcortical processes in attention. *Journal of Cognitive Neuroscience*, *6*, 267-275.
- Martin, J. S., & Jerger, J. F. (2005). Some effects of aging on central auditory processing. *Journal of Rehabilitation Research and Development*, *42*, 25-44.
- Martin, R., Houssemand, C., Schiltz, C., Burnod, Y., & Alexandre, F. (2008). Is there continuity between categorical and coordinate spatial relations coding? Evidence from a grid/no-grid working memory paradigm. *Neuropsychologia*, *46*, 576-594.
- McCartney, G., & Hepper, P. (1999). Development of lateralized behaviour in the human fetus from 12 to 27 weeks' gestation. *Developmental Medicine & Child Neurology*, *41*, 83-86.
- McCourt, M. E., & Jewell, G. (1999). Visuospatial attention in line bisection: stimulus modulation of pseudoneglect. *Neuropsychologia*, *37*, 843-855.
- Miller, L. K. (1981). Perceptual independence of the hemifields in children and adults. *Journal of experimental child psychology*, *32*, 298-312.
- Miller, L. K. (1984). Sources of visual field interference in children and adults. *Journal of Experimental Child Psychology*, *37*, 141-157.
- Milovanov, R., Tervaniemi, M., Takio, F., & Hämäläinen, H. (2007). Modification of dichotic listening (DL) performance by musico-linguistic abilities and age. *Brain Research*, *1156*, 168-173.
- Mondor, T. A., & Bryden, M. P. (1991). The influence of attention on the dichotic REA. *Neuropsychologia*, *29*, 1179-1190.
- Mondor, T. A., & Bryden, M. P. (1992a). On the relation between visual spatial attention and visual field asymmetries. *The Quarterly Journal of Experimental Psychology. A, Human experimental psychology*, *44*, 529-555.
- Mondor, T. A., & Bryden, M. P. (1992b). On the relation between auditory spatial attention and auditory perceptual asymmetries. *Perception and Psychophysics*, *52*, 393-402.
- Murray, J. (1986). The role of spatial complexity in the perception of speech and pure tones in dichotic listening. *Brain and Cognition*, *5*, 452-464.
- Nicholls, M. E. R., Mattingley, J. B., & Bradshaw, J. L. (2005). The effect of strategy on pseudoneglect for luminance judgements. *Cognitive Brain Research*, *25*, 71-77.
- Niemeyer, W., & Starlinger, I. (1981). Do the blind hear better? Investigations on auditory processing in congenital or early acquired blindness. II. Central functions. *Audiology*, *20*, 510-515.
- Obrzut, J. E., Obrzut, A., Bryden, M. P., & Bartels, S. G. (1985). Information processing and speech lateralization in learning-disabled children. *Brain and Language*, *25*, 87-101.
- Obrzut, J. E., Conrad, P. F., & Boliiek, C. A. (1989). Verbal and nonverbal auditory processing among left- and right-handed good readers and reading-disabled children. *Neuropsychologia*, *27*, 1357- 1371.
- Oliveri, M., Rossini, P. M., Traversa, R., Cicinelli, P., Filippi, M. M., Pasqualetti, P., Tomaiuolo, F., & Caltagirone, C. (1999). Left frontal transcranial magnetic stimulation reduces contralesional extinction in patients with unilateral right brain damage. *Brain*, *122*, 1731-1739.
- Passow, S., Westerhausen, R., Wartenburger, I., Hugdahl, K., Heekeren, H. R., Lindenberger, U., & Li, S-C. (2012). Human aging compromises attentional control of auditory perception. *Psychology and Aging*, *27*, 99-105.
- Penolazzi, B., Spironelli, C., Vio, C., & Angrilli, A. (2006). Altered hemispheric asymmetry during word processing in dyslexic children: an event-related potential study. *Neuroreport*, *17*, 429-433.
- Plante, E., Schmithorst, V. J., Holland, S. K., & Byars, A. W. (2006). Sex differences in the

- activation of language cortex during childhood. *Neuropsychologia*, *44*, 1210-1221.
- Poskiparta, E., Niemi, P., & Lepola, J. (1994). Diagnostiset testit 1: Lukeminen ja kirjoittaminen. [Diagnostic Tests 1: Reading and writing]. Finland: University of Turku.
- Posner, M. I. (2008). Measuring alertness. *Annals of the New York Academy of Sciences*, *1129*, 193-199.
- Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25-42.
- Posner, M. I., & Raichle, M. E. (1994). *Images of mind*. New York: Scientific American Library.
- Proverbio, A. M., Zani, A., Gazzaniga, M. S., & Mangun, G. R. (1994). ERP and RT signs of a rightward bias for spatial orienting in a split-brain patient. *NeuroReport*, *5*, 2457-2461.
- Reuter-Lorenz, P., & Sylvester, C-Y. C. (2005). The cognitive neuroscience of working memory and aging. In R. Cabeza, L. Nyberg, & D. Park (Eds.), *Cognitive Neuroscience of Aging: Linking Cognitive and Cerebral Aging* (pp. 186-217). New York, NY: Oxford University Press.
- Ridderinkhof, K. R., & van der Molen, M. W. (1997). Mental resources, processing speed, and inhibitory control: a developmental perspective. *Biological Psychology*, *45*, 241-261.
- Ridderinkhof, K. R., & van der Stelt, O. (2000). Attention and selection in the growing child: views derived from developmental psychophysiology. *Biological Psychology*, *54*, 55-106.
- Robertson, I. H., Mattingley, J. B., Rorden, C., & Driver, J. (1998). Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature*, *395*, 169-172.
- Rueda, M. R., Fan, J., McCandliss, B. D., Halparin, J. D., Gruber, D. B., Lercari, L. P., & Posner, M. I. (2004). Development of attentional networks in childhood. *Neuropsychologia*, *42*, 1029-1040.
- Röder, B., Rösler, F., Hennighausen, E., & Näcker, F. (1996). Event-related potentials during auditory and somatosensory discrimination in sighted and blind human subjects. *Cognitive Brain Research*, *4*, 77-93.
- Röder, B., Teder-Sälejärvi, W., Sterr, A., Rösler, F., Hillyard, S. A., & Neville, H. J. (1999). Improved auditory spatial tuning in blind humans. *Nature*, *400*, 162-166.
- Röder, B., & Rösler, F. (2003). Memory for environmental sounds in sighted, congenitally blind and late blind adults: evidence for cross-modal compensation. *International Journal of Psychophysiology*, *50*, 27-39.
- Röder, B., Rösler, F., & Neville, H. J. (2001). Auditory memory in congenitally blind adults: a behavioral-electrophysiological investigation. *Cognitive Brain Research*, *11*, 289-303.
- Rönnqvist, L. (1995). A critical examination of the Moro response in newborn infants – symmetry, state relation, underlying mechanisms. *Neuropsychologia*, *33*, 713-726.
- Rönnqvist, L., & Domellöf, E. (2006). Quantitative assessment of right and left reaching movements in infants: a longitudinal study from 6 to 36 months. *Developmental Psychobiology*, *48*, 444-459.
- Rönnqvist, L., & Hopkins, B. (1998). Head position preference in the human newborn: a new look. *Child Development*, *69*, 13-23.
- Rönnqvist, L., Hopkins, B., van Emmerik, R., & de Groot, L. (1998). Lateral bias in head turning and the Moro response in the human newborn: are they both vestibular in origin?. *Developmental Psychobiology*, *33*, 339-349.
- Salmi, J., Rinne, T., Degerman, A., Salonen, O., & Alho, K. (2007). Orienting and maintenance of spatial attention in audition and vision: multimodal and modality specific brain activations. *Brain Structure and Function*, *212*, 181-194.
- Santangelo, V., Belardinelli, M. O., Spence, C., & Macaluso, E. (2009). Interactions between voluntary and stimulus-driven spatial attention mechanisms across sensory modalities. *Journal of Cognitive Neuroscience*, *21*, 2384-2397.
- Sexton, M., & Geffen, G. (1979). Development of three strategies of attention in dichotic monitoring. *Developmental Psychology*, *15*, 299-310.
- Siéroff, E., Decaix, C., Chokron, S., & Bartolomeo, P. (2007). Impaired orienting of attention in left unilateral neglect: a componential analysis. *Neuropsychology*, *21*, 94-113.
- Silvén, M., Poskiparta, E., Niemi, P., & Voeten, M. (2007). Precursors of reading skill from infancy to first grade in Finnish: continuity and change in a highly inflected language. *Journal of Educational Psychology*, *99*, 516-531.
- Smith, S. E., & Chatterjee, A. (2008). Visuospatial attention in children. *Archives of Neurology*, *65*, 1284-1288.

- Sommer, I. E., Aleman, A., Somers, M., Boks, M. P., & Kahn, R. S. (2008). Sex difference in handedness, asymmetry of the planum temporale and functional language lateralization. *Brain Research, 1206*, 76-88.
- Sosa, Y., Teder-Sälejärvi, W. A., & McCourt, M. E. (2010). Biases of spatial attention in vision and audition. *Brain and Cognition, 73*, 229-235.
- Span, M. M., Ridderinkhof, K. R., & van der Molen, M. W. (2004). Age-related changes in the efficiency of cognitive processing across the life span. *Acta psychologica, 117*, 155-183.
- Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers, 31*, 137-149.
- Swan, L. (2001). Unilateral spatial neglect. *Physical Therapy, 81*, 1572-1580.
- Szaflarski, J. P., Holland, S. K., Schmithorst, V. J., & Byars, A. W. (2006). fMRI study of language lateralization in children and adults. *Human Brain Mapping, 27*, 202-212.
- Sætrevik, B., & Hugdahl, K. (2007). Endogenous and exogenous control of attention in dichotic listening. *Neuropsychology, 21*, 285-290.
- Tallus, J., Hugdahl, K., Alho, K., Medvedev, S., & Hämäläinen, H. (2007). Interaural intensity difference and ear advantage in listening to dichotic consonant-vowel syllable pairs. *Brain Research, 1185*, 195-200.
- Tartter, V. (1988). Acoustic and phonetic feature effects in dichotic listening. In Hugdahl, K. (Ed.), *Handbook of Dichotic Listening: Theory, Methods and Research* (pp. 283-321). Chichester: John Wiley & Sons Ltd.
- Telkemeyer, S., Rossi, S., Koch, S. P., Nierhaus, T., Steinbrink, J., Poeppel, D., ... Wartenburger, I. (2009). Sensitivity of newborn auditory cortex to the temporal structure of sounds. *The Journal of Neuroscience, 29*, 14726-14733.
- Teshiba, T. M., Ling, J., Ruhl, D. A., Bedrick, B. S., Peña, A., & Mayer, A. R. (2012). Evoked and intrinsic asymmetries during auditory attention: implications for the contralateral and neglect models of functioning. *Cerebral Cortex, Advance Access, February 27*, 1-10.
- Thiebaut de Schotten, M., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience, 14*, 1245-1246.
- Thomsen, T., Specht, K., Hammar, Å., Nytingnes, J., Erslund, L., & Hugdahl, K. (2004). Brain localization of attentional control in different age groups by combining functional and structural MRI. *NeuroImage, 22*, 912-919.
- Trauner, D. A. (2003). Hemispatial neglect in young children with early unilateral brain damage. *Developmental Medicine & Child Neurology, 45*, 160-166.
- Tsujimoto, S. (2008). The prefrontal cortex: functional neural development during early childhood. *The Neuroscientist, 14*, 345-358.
- Turkewitz, G., Gordon, E. W., & Birch, H. G. (1965). Head turning in the human neonate: effect of prandial condition and lateral preference. *Journal of Comparative and Psychological Psychology, 59*, 189-192.
- Voyer, D. (1996). On the magnitude of laterality effects and sex differences in functional lateralities. *Laterality, 1*, 51-83.
- Vuontela, V., Steenari, M-R., Carlson, S., Koivisto, J., Fjällberg, M., & Aronen, E. T. (2003). Audiospatial and visuospatial working memory in 6-13 year old school children. *Learning & Memory, 10*, 74-81.
- Waszak, F., Li, S-C., & Hommel, B. (2010). The development of attentional networks: cross-sectional findings from a life span sample. *Developmental Psychology, 46*, 337-349.
- Weeks, R., Horwitz, B., Aziz-Sultan, A., Tian, B., Wessinger, C. M., Cohen, L. G., ... Rauschecker, J. P. (2000). A position emission tomography study of auditory localization in the congenitally blind. *The Journal of Neuroscience, 20*, 2664-2672.
- van de Weijer-Bergsma, E., Wijnroks, L., & Jongmans, M. J. (2007). Attention development in infants and preschool children born preterm: a review. *Infant Behavior & Development, 31*, 333-351.
- Westerhausen, R., & Hugdahl, K. (2008). The corpus callosum in dichotic listening studies of hemispheric asymmetry: a review of clinical and experimental evidence. *Neuroscience and Biobehavioral Reviews, 32*, 1044-1054.
- Westerhausen, R., Luders, E., Specht, K., Ofe, S. H., Toga, A. W., Thompson, P. M., ... Hugdahl, K. (2011). Structural and functional reorganization of the corpus callosum between the age of 6 and 8 years. *Cerebral Cortex, 21*, 1012-1017.
- Westerhausen, R., Moosmann, M., Alho, K., Belsby, S-O., Hämäläinen, H., Medvedev,

References

- S., ... Hugdahl, K. (2010). Identification of attention and cognitive control networks in a parametric auditory fMRI study. *Neuropsychologia*, *48*, 2075-2081.
- Young, A. W., & Bion, P. J. (1979). Hemispheric laterality effects in the enumeration of visually presented collections of dots by children. *Neuropsychologia*, *17*, 99-102.