Review

The influence of executive functions on spatial biases varies during the lifespan

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ABSTRACT

Many perceptual processes, such as language or face perception, are asymmetrically organised in the hemispheres already in childhood. These asymmetries induce behaviourally observable spatial biases in which the observer perceives stimuli in one of the hemispaces more efficiently or more frequently than in the other one. Another source for spatial biases is spatial attention which is also asymmetrically organised in the hemispheres. The bias induced by attention is directed towards the right side, which is clearly demonstrated by patients with neglect but also in lesser degree by healthy observers in cognitively loading situations. Recent findings indicate that children and older adults show stronger spatial biases than young adults. We discuss how the development of executive functions might contribute to the manifestation of spatial biases during the lifespan. We present a model in which the interaction between the asymmetrical perceptual processes, the age-related development of the lateralised spatial attention and the development of the executive functions influence spatial perceptual performance and in which the development and decline of the executive processes during the lifespan modify the spatial biases.

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1. Introduction

Many perceptual processes such as language or face perception are lateralised predominantly either to the left or to the right hemisphere, inducing rightward or leftward spatial biases. However, regardless of the numerous behavioural and neuroimaging studies carried out to understand the development and the nature of the spatial biases other than those induced by language, the evidence and empirical support for many such biases are still diverse (e.g. see Takio and Hämäläinen, 2012). One of the possible but often neglected confounding processes influencing the performance in perceptual tasks is attention. Results from neglect patient studies (e.g. Corbetta et al., 2008; Corbetta and Shulman, 2002; Heilman et al., 1987; Proverbio et al., 1994), and healthy humans (Posner, 2008; Posner and Raichle, 1994) suggest that the hemispheres are asymmetrical also in attentional mechanisms. Furthermore, research on lateralisation has shown that the hemispheric asymmetries and spatial biases change during the lifespan presumably resulting from a complex interaction of biological and environmental factors. For example, language lateralisation (e.g., Andersson and Hugdahl, 1987; Hiscock and Kinsbourne, 1977, 1980; Sexton and Geffen, 1979) as well as the lateralisation of visuospatial functions (Everts et al., 2009) increase during childhood, and age-related changes in human structural and functional hemispheric asymmetry continue into old age (e.g. Dolcos et al., 2002). Regardless of the large body of lateralisation studies (for review see e.g. Boles et al., 2008), the variable results of the development of the asymmetries in literature make it difficult to determine the exact timing of lateralisation of different processes. Behind such inconsistency of the findings may be the development of executive functions that modulates perceptual performance and asymmetry differently across the lifespan (e.g. Hiscock and Kinsbourne, 1977; Hugdahl and Andersson, 1986). In the present paper, we introduce a theoretical model of the role and the interaction of asymmetrical bottom-up perceptual and attention mechanisms and of the age-related changes in executive functions in spatial biases. The spatial biases refer here to more efficient or frequent perception of stimuli in one side of the hemispace than in the other side.

2. Asymmetrical perceptual mechanisms and confounding processes

Left-hemisphere dominance in language processing is an essential source of the rightward spatial bias for auditory and visual linguistic perception in healthy adults (e.g. Calvo and Nummenmaa, 2009; Corballis, 2009; Koivisto, 1997). Such a rightward bias for language processing in the auditory modality is observable already at a very early age (Andersson and Hugdahl, 1987; Boles et al., 2008; Dehaene-Lambertz et al., 2002; Telkemeyer et al., 2009). Thanks to the proliferated expansion of functional neuroimaging studies, the findings of lateralisation and hemispheric asymmetry have extended to concern more elaborated and sophisticated aspects of perceptual processes. For example, the left hemisphere has been found to be specialised in the processing of local information and categorical spatial relationships of visual stimuli, while the right hemisphere is superior in the processing of global aspects and coordinate spatial relationships (Hellige et al., 2010; Ivry and Robertson, 1998). Nevertheless, still existing constraints of neuroimaging methods create uncertainty about determining whether the activated regions are truly associated with the processes in focus. For example, Martin and co-workers (2008) found right-hemisphere activation in both coordinate and categorical spatial tasks. They proposed that the right-hemisphere activation was indeed related to the lateralisation of spatial attention mechanisms rather than to the lateralisation of spatial coding mechanisms. Thus, the complexity of cognitive processing together with the yet existing limitations of behavioural and neuroimaging methods have raised questions of the confounding processes that put the earlier interpretations of lateralisation studies into a new light. Furthermore, while attention and memory functions are proposed to be such confounding factors in spatial biases (e.g. Callaert et al., 2011; Hiscock and Kinsbourne, 2011), they themselves are asymmetrically distributed in the brain (e.g. Kalpouzos and Nyberg, 2010).

3. Asymmetrical spatial attention mechanisms

3.1. Evidence from neurological patients

Neurophysiological and neuropsychological research has shown that the two cerebral hemispheres differ in the control of spatial attention (Corbetta et al., 2008; Driver and Vuilleumier, 2001; Heilman et al., 1987; Proverbio et al., 1994; Posner and Raichle, 1994). The clearest examples of the asymmetry of attentional behaviour are observed in neurological patients with unilateral neglect (Corbetta et al., 2008; Deouell et al., 2000; Heilman et al., 1987; Kinsbourne, 1987; Oliveri et al., 1999), callosotomy (split-brain) (Luck et al., 1989, 1994; Mangun et al., 1994; Proverbio et al., 1994) and attention deficit hyperactivity disorder (ADHD) (Chan et al., 2009; Hale et al., 2006).

According to the definition by Heilman and his co-workers (2000), neglect 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 (see also Swan, 2001). In adult neglect patients suffering from unilateral right hemisphere injury, often a strong attentional bias towards the right hemispace is observed, whereas a leftward attentional bias after left unilateral hemisphere injury is considerably less often observed. Neural damages producing this kind of neglect behaviour can be localised at both cortical and sub-cortical areas and different levels of the neural system in right hemisphere, such as the posterior parietal cortex, frontal lobe, cingulate gyrus, striatum, thalamus, or brainstem nuclei (e.g. Swan, 2001; Posner and Petersen, 1990), suggesting that neglect can be explained by the physiological dysfunction of distributed cortical networks (Corbetta and Shulman, 2011; see also Corbetta et al., 2008). Visuospatial and motor neglect after

brain damage similar to what has been found in adults has also been described in children (Laurent-Vannier et al., 2003).

As in the neglect syndrome, both children and adults suffering from ADHD have shown a poorer ability to attend to the stimuli in the left than in the right visual field under certain circumstances (for review, see Chan et al., 2009). According to the traditional view, ADHD originates from a deficiency in executive functions (e.g. Barkley, 1997; Brown, 2006), especially in inhibitory control. However, recently the deficiency in executive functioning as a unique cause of ADHD has been questioned (e.g. see Loo et al., 2007), and the traditional view has been complemented with more specific and detailed explanations (e.g. see Boles et al., 2009; Floet et al., 2010; Furman, 2008), such as atypical cerebral asymmetries in attentional mechanisms. For example, in a spatial selective attention test, the dysregulation and over-activation of the right-hemisphere lateralised arousal and attention mechanisms have shown to be connected to ADHD symptoms (Chan et al., 2009; Hale et al., 2006).

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. Kinsbourne (e.g. 1987) suggested that both hemispheres orient attention towards the contralateral hemispace, but the left hemisphere has a 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, but the left hemisphere's attentional control is only contralateral (see also Driver and Vuilleumier, 2001; Proverbio et al., 1994; Swan, 2001). Thus, according to both views, attention is more strongly biased to the right. However, these models of asymmetrical attentional gradients, although theoretically elegant, remain speculation. It has been suggested that the rightward spatial bias and left spatial inattention in neglect patients (Corbetta et al., 2008; Deouell et al., 2000; Heilman et al., 1987; Kinsbourne, 1987; Oliveri et al., 1999; Proverbio et al., 1994) and persons with ADHD (Chan et al., 2009; Hale et al., 2006) result from right-hemisphere impairments in sustained attention and alertness (Boles et al., 2009; Dobler et al., 2003; Posner, 2008) or from the dysfunction of the exogenous orienting mechanisms located in the right parieto-temporo-frontal network. This results in deficits in involuntary attention to focus on the alerting events in the environment (Corbetta and Shulman, 2002; Corbetta et al., 2008; Driver and Vuilleumier, 2001). According to the neuropsychological model of attention (Posner and Petersen, 1990), neglect due to damage in the right posterior parietal lobe is related to the right-lateralised alerting system and to an inability to engage as well as disengage from an attentional focus to a target located in a direction opposite to the side of the lesion (Siéroff et al., 2007). Thus, deficits in stimulus-driven alerting and orienting attention networks have been associated with the neglect symptoms (see also Boles et al., 2009). Furthermore, it is proposed that endogenous processes (strategy-driven orienting of attention) are instead relatively preserved in left unilateral neglect (Bartolomeo and Chokron, 2002).

Corbetta and Shulman (2011) argue in their review that the functions of dorsal attention network (involving intraparietal sulcus, superior parietal lobule and frontal eye field) are not lateralised, whereas the ventral attention network (involving temporoparietal junction and ventral frontal cortex) is right lateralised. According to them "The anatomy and right hemisphere dominance of neglect follows from the anatomy and laterality of the ventral regions that interact with the dorsal attention network." (Corbetta and Shulman, 2011).

Finally, Ptak and Schnider (2011) measured directly neglect patients' and control subjects' activations to various spatial attention tasks. According to Corbetta et al. (2005) neglect touches primarily the ventral network, but though structurally intact, the dorsal fronto-parietal network is nevertheless functionally impaired in the acute phase of neglect. According to the voxel-based-lesion-symptom mapping (Ptak and Schnider, 2011), temporo-parietal junction is critical for the occurrence of spatial neglect. Neglect was also associated with damage to the intraparietal sulcus, which is one of the central nodes of the attention network in the brain. The third region predicting impairments of attention in spatial neglect was the dorsal premotor cortex, the middle frontal gyrus being a global predictor of the occurrence of spatial neglect. The middle frontal gyrus constitutes a link between the dorsal (including intraparietal sulcus and frontal eye fields) and the ventral (including temporo-parietal junction and ventral prefrontal cortex) attention network (Corbetta et al., 2008). The authors conclude that the intraparietal sulcus, dorsal premotor cortex and temporo-parietal junction are associated with neglect, and that interactions within a network formed by these regions predict the performance of neglect patients in a task measuring dynamic aspects of spatial attention.

3.2. Evidence from normal observers

Evidence for right-lateralised mechanisms of spatial attention has also been found in studies on healthy participants. Pollmann (1996) demonstrated an extinction-like phenomenon in neurologically intact subjects with tachistoscopically presented stimuli: highly salient distracter stimuli interfered more strongly with the search of contralateral low-salience targets when the distracters were presented to the right visual field than when presented to the left field. Pollmann (2000) suggested that this phenomenon is related to hemispheric asymmetries in the disengagement component of attention. Corbetta and co-workers (1993) found in their PET studies among healthy adult participants that the left superior parietal cortex was active during shifts of visuospatial attention towards contralateral (right) direction, whereas the right hemisphere was active when attention was shifted both contralaterally and ipsilaterally. They concluded that the right parietal cortex controls attention to the left visual field while attention to the right visual field is controlled by both parietal cortices. Moreover, in their event-related functional magnetic resonance imaging (fMRI) study on healthy adults (Corbetta et al., 2000), the activation in the right temporoparietal cortical junction was stronger when the target

occurred at an unattended location than at an attended location. This was proposed to indicate that the area involved in the processes of visual spatial reorienting is right-lateralised (see also Posner, 2008; Posner and Raichle, 1994). Finally, in a study on healthy participants, stronger white matter connectivity of the temporoparietal junction in the right hemisphere was related to right-lateralised stimulus-driven attention and sensory awareness (Kucyi et al., 2012).

Thiebaut de Schotten et al. (2011) describe a larger parieto-frontal network in the right than in the left hemisphere, and a significant correlation between the degree of anatomical lateralisation and asymmetry of visuospatial perception. Parieto-frontal connections are organised in three (dorsal, middle, ventral) longitudinal fasciculi (SLF). Dorsal SLF is symmetrically distributed between the hemispheres, the middle SLF shows a trend of right lateralisation, and the ventral SLF is right lateralised. The lateralisation of the middle SLF correlates with behavioural measures of laterality (line bisection and detection time). The cortical projections of the dorsal SLF overlap with the dorsal network related to voluntary goal-directed visual spatial attention, whereas the ventral SLF overlaps with the ventral network activated by automatic capture of spatial attention by visual targets. This network is damaged in patients with visuospatial neglect. The middle SLF overlaps with the parietal component of the ventral network and the prefrontal component of the dorsal network (Thiebaut de Schotten et al., 2011).

Recently the spatial biases in perceptual performance have been studied in both the auditory and visual modalities. Measurements in right-handed participants revealed that under an intensive attentional load, only rightward spatial biases for linguistic as well as for non-linguistic stimuli (sinusoidal tones and dots of light) were observed in both auditory and visual modalities (Takio et al., 2011, 2013). As the processing of linguistic stimuli is strongly left-hemisphere lateralised, the observed multimodal rightward spatial bias for linguistic stimuli reflects, first of all, left-hemisphere processing advantage of linguistic stimuli (Takio et al., 2011, 2013; see also Dehaene-Lambertz et al., 2002; Della Penna et al., 2007; Kimura, 1967; Takio et al., 2009). Since the processing of non-linguistic stimuli is not as clearly lateralised as the processing of linguistic stimuli (Boles et al., 2008; Efron et al., 1983; Galbraith and Arroyo, 1993; Gregory et al., 1983; Murray, 1986; Obrzut et al., 1989), we proposed that the asymmetrical attention mechanisms induced the observed behavioural rightward spatial biases for both linguistic and non-linguistic stimuli under a sufficiently intensive attentional load (Takio et al., 2011, 2013; see also Martin et al., 2008) (see also Fig. 2a). It is noteworthy that this bias was evident only in conditions with a sufficient attentional load, either in fast-paced stimulus sequences or when several target items had to be kept in working memory and monitored in the left, right, or both sides. Thus, when spatial attention and/or executive functions are strongly burdened, attention is more readily drawn to the right hemispace irrespective of the stimulus type, and the right-side stimuli are more readily processed and responded to than the left side stimuli independent of the modality (Takio et al., 2011, 2013). Although

these rightward attention shifts occurred more frequently in children and old adults and for bilateral stimuli, they were detectable also for unilateral stimuli in young adults. Because unilateral stimuli cause an exogenous capture of attention, the ventral attention network should be involved in generating the bias. In line with Corbetta and Shulman's (2011) model, we can assume that an increased demand on the right-lateralised ventral network induced a global overload in the right hemisphere attention networks, causing a hemispheric imbalance favouring the left dorsal network and thus biasing attention rightward. A similar mechanism may also explain the rightward shift in attention that is produced by a decrease in alertness (Newman et al., 2013): decreased activation in the right ventral network may cause a more global decrease in right hemisphere activation, giving the left dorsal network an advantage over the right one, thus biasing attention rightwards. Finally, asymmetrical attention mechanisms can plausibly explain the findings that visual exogenous cueing or preparation to make an eye movement towards the peripheral verbal stimuli (e.g. in a word recognition task) improves the recognition accuracy of linguistic stimuli more when presented to the left visual field than to the right visual field (Hyönä and Koivisto, 2006; Mondor and Bryden, 1992): the asymmetrical attention mechanisms are more readily allocated to the right hemispace, and therefore cueing has a stronger impact on orienting attention to the left-side stimuli than to the right-side stimuli.

The multimodal spatial biases towards right side in *bilateral* stimulus conditions (Hämäläinen and Takio, 2010; Takio and Hämäläinen, 2012; Takio et al., 2011, 2013) can be explained in terms of limited attention capacity. They resemble the neurological deficit called 'extinction' which can be observed in right-hemisphere damaged patients during bilateral simultaneous stimulation: the patient may be able to detect a single left-sided event in isolation, but in a bilateral stimulus condition, the left-sided event is missed (for review, see Driver and Vuilleumier, 2001). According to one view, visual extinction is a pathological limitation of attention capacity, and the possible reason why difficulties in becoming immediately aware of multiple targets are under some circumstances observed even in normal healthy humans (Driver and Vuilleumier, 2001). Thus, the spatial bias appears when multiple events compete for attention at the same time. In line with this view, in a fast-paced task requiring the detection of the appearance of visual dots, rightward asymmetries in a bilateral stimulus condition were found in children between the ages of 5 and 11 years, in young adults, as well as in the elderly (Takio et al., 2013). Moreover, the elderly participants made right unilateral responses to the bilateral targets more frequently and showed a stronger rightward bias than the children or the young adults in a linguistic task that required discrimination between target and non-target stimuli (Takio et al., 2013). In the auditory modality, the 5–7-year-old children and the elderly participants detected the right side sinusoidal tones better than the left side sinusoidal tones in the binaural stimulus conditions (Takio et al., 2011). A plausible explanation for the rightward bias in bilateral stimulus conditions is that a mild extinction-like phenomenon is present throughout the lifespan also

in healthy humans, but is more evident in young children and in the elderly than in young adults. The results also show that the ability to distribute attention to multiple targets simultaneously decreases in the course of ageing.

To summarise, the evidence from neurological patients shows that neural damages or dysfunctions of the neural systems in the right hemisphere induce more severe attentional deficits than damages in left hemisphere. In addition, structural and functional brain imaging in normal observers suggests right hemisphere dominance in visual spatial attention. The damages in the right hemisphere typically bias attention towards the right side (e.g., in neglect), but also neurologically normal observers, particularly children and elderly people, sometimes show multimodal rightward biases.

4. Effect of age as indicator for the modifying role of executive functions in spatial perceptual asymmetries

The review above identified two components which produce behaviourally detectable spatial biases: perceptual bottom-up processes (e.g., the left hemisphere dominance in language perception produces a right-side bias) and attentional processes (e.g., in neglect and extinction as well as in normal observers under loading conditions attention is biased towards the right side). In attention, the right-lateralised ventral attention network is most likely the primary source of the rightward bias, but it interacts with the dorsal attention network so that top-down attention is biased towards the right side. Although there is strong evidence that the hemispheres differ in the functional dominance for e.g. language and attention processes, then, why are the spatial biases less frequently observed among adult participants than in children and elderly participants? We propose that the age-dependent differences in spatial biases reflect the developmental changes in executive functions.

4.1. Development of executive functions

Executive functions consist of skills necessary for goal-directed behaviour, such as attentional control and cognitive flexibility (Engle, 2002; Hugdahl et al., 2009; Luria, 1973; Posner and Raichle, 1994). Thus, executive functions encompass a large range of cognitive functions such as manipulating and integrating information with memory functions (Miyake et al., 2000) and conflict resolution with attentional focusing and inhibition (Posner and Raichle, 1994).

Executive functions are mediated by frontal networks and additional subcortical structures and thalamic pathways (e.g. Anderson et al., 2001; Boles et al., 2008; Dehaene-Lambertz et al., 2002; Garon et al., 2008; Jurado and Rosselli, 2007; Posner and Raichle, 1994; Tsujimoto, 2008). They develop slowly during childhood and adolescence, are best advanced in adulthood and decline as a function of ageing (e.g. Baddeley, 1986, 2000; Burke and Barnes, 2006; Chugani, 1998; Engle, 2002; Jurado and Rosselli, 2007; Luria, 1973; Madden et al., 2005; Posner, 2008; Posner and Raichle, 1994; Span et al., 2004;

Tsujimoto, 2008). The development of attention in childhood is associated with a gradual shift from subcortical processing to increasing cortical control over attention (for review, see van de Weijer-Bergsma et al., 2007). For example, infants' ability to control visuospatial orienting and to direct attention to peripheral objects starts to develop already between 3 and 6 months of age (Smith and Chatterjee, 2008), while the ability to suppress inappropriate information and actions (inhibition), and to deal with conflicts in information processing seems to reach maturity rather late in adolescence (Goldberg et al., 2001; Hale et al., 1997; Jurado and Rosselli, 2007; Takio et al., 2009; Tsujimoto, 2008; Waszak et al., 2010). Moreover, the efficiency of voluntary covert orienting increases as a function of age during childhood, reaching the adult-like ability somewhere between the ages of 8 and 10 years, and the ability to shift attention following an endogenous cue is well developed around the age of 10 years (Goldberg et al., 2001; Waszak et al., 2010).

Frontal lobes are more sensitive to age-related changes in the lifespan compared to other parts of the brain (Span et al., 2004). The declines in performance due to ageing tend to be largest on tasks that rely on executive control (e.g., Madden et al., 2005) and especially on the inhibitory control of irrelevant stimuli, as the inhibitory control seems to decline earlier than other components of executive functions (Jurado and Rosselli, 2007; Ridderinkhof and van der Molen, 1997; see also Waszak et al., 2010). For example, older adults have particular difficulties with divided and selective attention and in tasks that rely on working memory (for review, see Reuter-Lorenz and Sylvester, 2005), thus being more vulnerable to interference by irrelevant stimuli. In addition, a generalised slowing of information processing is one of the factors that explain age-related changes in cognitive processing among the elderly (Madden et al., 2005).

4.2. Spatial biases are modified by executive functions

The age-related changes in executive functions reviewed above modify the occurrence of spatial biases during the lifespan. This can be directly shown by asking the participants voluntarily to attend to the stimuli presented either to the left ear or the right ear during dichotic listening (DL) (e.g., Andersson and Hugdahl, 1987; Asbjørnsen and Helland, 2006; Hiscock and Decter, 1988; Hiscock and Kinsbourne, 1977; Hugdahl, 2003). DL refers to an experimental arrangement in which the two ears simultaneously receive distinct acoustic inputs. With linguistic stimuli (e.g. spoken words, syllables, digits), a typical finding in a normal right-handed participant when attention is not voluntarily directed to either ear is a right-ear advantage (REA) in recognizing the stimuli. Despite the multiple models explaining the possible mechanisms behind the REA (for review, see Hiscock and Kinsbourne, 2011), several studies affirm that young adults can modify the stimulus-driven REA for speech perception in DL by directing attention to the right ear (forced-right attention condition, FR) or to the left ear (forced-left attention condition, FL); the FR attention condition strengthens the REA, and the FL attention condition
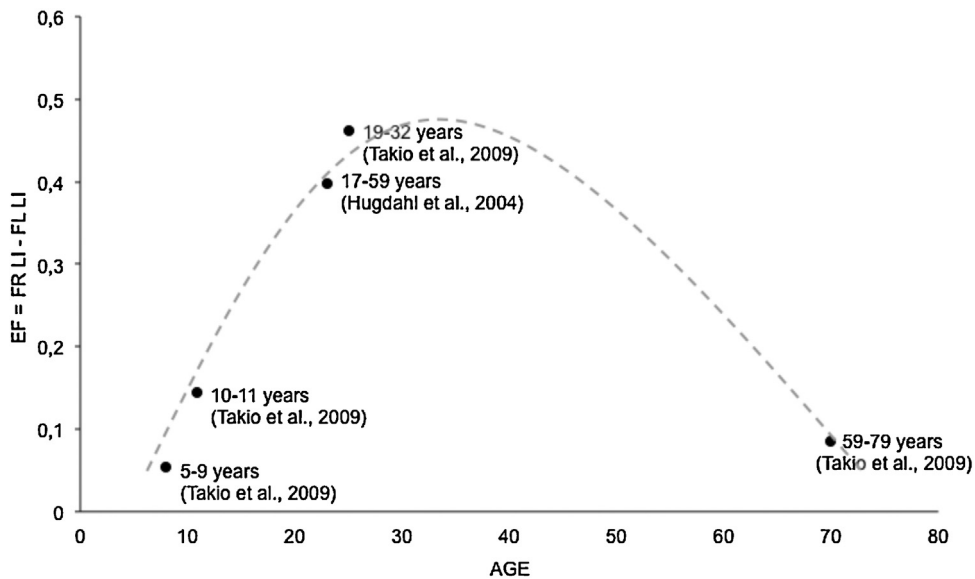
Fig. 1. The efficiency of executive functions (EF) during a dichotic listening forced attention paradigm (Hugdahl et al., 2004; Takio et al., 2009) was calculated by subtracting the dichotic listening forced-left lateralisation index (FL LI) from the forced-right lateralisation index (FR LI) in each participant group. The difference score describes how efficiently the participants were able to modify the ear advantage under the forced-attention conditions in dichotic listening: the higher the different score is, the better the participant group was able to modify the ear advantage.

weakens the REA or occasionally even switches it into a left-ear advantage (e.g. Andersson and Hugdahl, 1987; Asbjørnsen and Hugdahl, 1995; Hiscock and Kinsbourne, 2011; Hugdahl and Andersson, 1986; Hugdahl, 2003; Hugdahl et al., 2003). This can be explained with an ability to control attention or, for example, with a more effective strategy that meets the task demands (context effects; see Hiscock and Kinsbourne, 2011, for a review).

Support for the role of the executive functions in spatial biases is provided by the results showing that personal skills and training influence the ability to modify spatial biases in the DL paradigm. Both young and old bilingual adults are better at focusing attention and ignoring task-irrelevant stimuli than monolingual adults in a dichotic forced-attention paradigm (Soveri et al., 2011). Young adults who practiced choir singing regularly showed superior left-side monitoring skills in a dichotic forced attention paradigm compared to young adults without such practice (Milovanov et al., 2007). Furthermore, Soveri et al. (2013) showed that the training of top-down attentional control in a dichotic listening test modulates the allocation of attention in the auditory space: after 4-week training, young adults were better at directing attention to the left-ear linguistic stimuli in the forced-left attention condition than the adults who did not undergo such training. A transfer effect to an auditory spatial go/no-go task was also observed. As a conclusion, systematic training seems to enhance the efficiency of executive functions in controlling the effects of spatial biases.

4.3. Development and decline of executive functions during the lifespan modify spatial biases

Our explanation to the age dependent spatial bias is a "two-component model" (named by Hiscock and Kinsbourne, 2011), consisting of bottom-up versus top-down processing, formulated by Hugdahl et al. (2009). The components in our model are the bottom-up spatial perceptual/attentional asymmetry and the executive functions. The ability to modify the stimulus-driven spatial biases changes as a function of age (e.g. Takio et al., 2009). This reflects the changes in executive functions during the lifespan: the ability to use executive functions efficiently (i.e. to modify the REA) increases during childhood and decreases as a function of ageing. These changes coincide well with the estimated efficiency of executive functions (EF, see Fig. 1) based on the ability to resist the REA and to attend to the left-ear stimuli at different age levels. For example in our dichotic listening study, children under the age of 9 were unable to modify the stimulus-driven REA by voluntary attention (Takio et al., 2009; see also Hugdahl, 2003; Hugdahl et al., 2001) whereas the 10–11-year-old children started to show this ability (Takio et al., 2009). Moreover, ageing and the decline of (top-down) attentional control (executive functions) have been reported to weaken the ability to direct attention in the dichotic listening procedure especially towards the left-ear linguistic stimuli (Beaton et al., 2000; Hugdahl, 2003; Hugdahl et al., 2001; Takio et al., 2009; Thomsen et al., 2004).

Besides the DL studies, our studies of auditory and visual perceptual asymmetries with linguistic and non-linguistic stimuli have shown that the magnitude and the incidence of the rightward spatial bias change in spatial attention tests as a function of age. The rightward bias is more intensive in children and in the elderly than in young adults (Takio et al., 2011, 2013). For example, we found that children under the age of 9 years were more biased to respond towards the right side or to respond to the linguistic stimuli presented in the right hemispace in linguistic target detection tasks, irrespective of whether the stimuli were targets

or non-targets and independent of the auditory and visual modality of the stimuli (Takio et al., 2011, 2013). Also, our results for 5- to 11-year-old children from visual and auditory stimulus/target detection tasks showed that the older the child was, the less right-side biased errors he/she made (Takio et al., 2011, 2013). As the 5–9-year-old children are behaviourally more impulsive than older children due to a larger degree of immaturity of executive functions (Vuontela et al., 2003), the decrease in the right-side response bias can be interpreted to result from the gradual development of the executive functions in childhood (Hämäläinen and Takio, 2010).

It has been suggested that the top-down inhibitory control of the stimulus-driven laterality effect related to speech sound perception in a selective attention condition may be maintained in the elderly, but not to such an extent that the elderly would be able to overcome the stimulus-driven laterality effect (REA) with executive functions in dichotic stimulus conditions (Takio et al., 2009). In our studies of selective and divided attention in the auditory (Takio et al., 2011) and visual (Takio et al., 2013) modalities, the 59–79-year-old adults' performance was not only inferior to that of young adults, but they also showed a stronger multimodal rightward spatial bias. The inability to control the perceptual spatial asymmetries to the same extent as young adults are able to may be related to the decline in the efficiency of interhemispheric transfer of information, to the changes in executive functions and to the generalised ageing-related slowing of processing speed (e.g. Martin and Jerger, 2005; Takio et al., 2011, 2013; see also Madden et al., 2005). For example, it has been suggested that increasing task-non-specific activation of 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 and Reuter-Lorenz and Sylvester, 2005). Thus, the generalised slowing of information processing alongside with the decreasing executive functioning may underlie many of the observed age-related changes in perceptual and cognitive asymmetries in the elderly (see also Madden et al., 2005).

In summary, executive functions mature slowly in childhood and decline in old age. These changes in executive function during the lifespan are paralleled by children's and elderly people's defective ability to voluntarily control their spatial biases.

5. The model of interaction of cognitive functions underlying the age-related changes in spatial asymmetry

Our recent findings showed that under an intensive attentional load, rightward spatial biases for linguistic as well as for non-linguistic stimuli were observed (Takio et al., 2011, 2013). According to these results and earlier findings (e.g. Dehaene-Lambertz et al., 2002; Della Penna et al., 2007; Kimura, 1967) 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 many non-linguistic stimuli (such as dots of light or sinusoidal tones) is not as strongly and clearly lateralised as the processing of
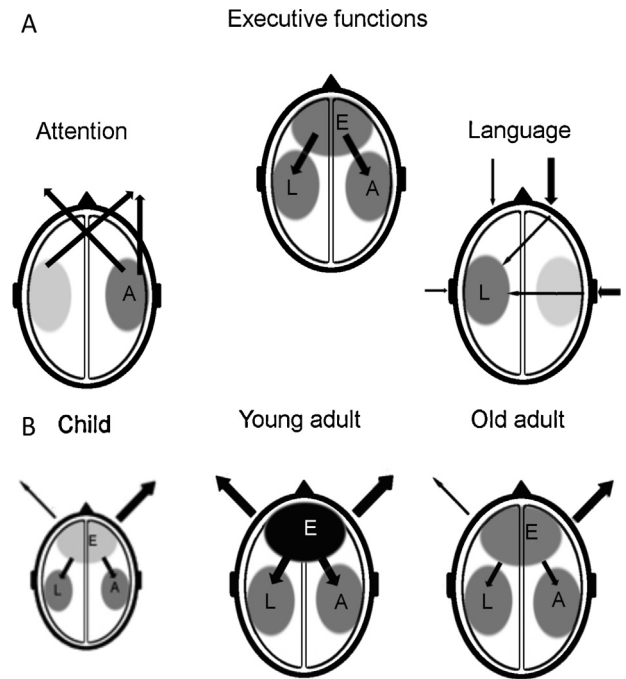
Fig. 2. Simplified schematic presentation of the underlying mechanisms (A) and of the age-related changes (B) in rightward spatial bias in situations with attentional load. In figure A, the mechanisms that induce the spatial rightward bias (language lateralised in the left hemisphere and attention lateralised in the right hemisphere) are presented. This rightward bias is modified by the executive functions located in the prefrontal areas. Black arrows denote a strong influence of the mechanism, narrow arrows denote a light influence. In figure B, the strength and the interactions of these mechanisms during the lifespan are summarised. The thickness of the arrows denotes the strength of the spatial bias. The darkness of the prefrontal areas denotes the efficiency of the executive functions. The E stands for executive functions, the L stands for language and the A stands for attention.

linguistic stimuli (e.g. Boles et al., 2008; Efron et al., 1983; Galbraith and Arroyo, 1993; Gregory et al., 1983; Murray, 1986; Obrzut et al., 1989), we propose that the asymmetrical attention mechanisms (Corbetta and Shulman, 2011; Heilman et al., 1987; Kinsbourne, 1987; Thiebaut de Schotten et al., 2011) influence perceptual processes inducing the multimodal, stimulus-non-specific rightward spatial bias. This attentional bias to the right becomes visible in healthy right-handed participants under an adequately intensive spatial attentional load, either when multiple targets must be kept in memory and attended to in fast-paced spatial attention tasks (Takio et al., 2011, 2013) or when the executive control functions are directly loaded (Takio et al., 2009). In other words, we propose that our findings of the multimodal rightward spatial bias in linguistic and in non-linguistic spatial attention tasks (Takio et al., 2009, 2011, 2013) result from asymmetrical language and attentional bottom-up neural processes. The effect of age on spatial biases can be seen as evidence for the role of executive functions in attentional control and modulation of the behaviourally observable left–right biases.

The following model (Fig. 2) integrates the mechanisms inducing the rightward spatial bias (linguistic/left hemisphere and attentional/right hemisphere; Fig. 2A) and

executive functions (prefrontal areas; Fig. 2A) that modify the rightward spatial bias. These prefrontal executive functions mimic the dorsal fronto-parietal attention network. The effects induced by these mechanisms on spatial cognitive processing and their synergistic functioning are depicted by the arrows showing the direction of the influence. As pointed out by Hiscock and Kinsbourne (2011), it is demanding to differentiate the so-called structural and attentional asymmetries. However, we believe that according to our model, it is possible to separate the effects of the different mechanisms by applying attentionally demanding linguistic or non-linguistic stimulus-conditions: in linguistic tasks, the rightward spatial bias is induced by the interaction of asymmetrical language and attentional mechanisms, whereas in non-linguistic tasks not involving bottom-up language asymmetries, the spatial bias is produced by the asymmetrical attentional mechanisms. Fig. 2B summarises the interaction of these different mechanisms during the lifespan. As shown by the leftmost figurine in 2B, children exhibit a strong rightward bias due to the biasing mechanisms not being balanced by the immature (light grey) executive functions. The next figurine to the right shows the balancing effect of fully developed executive functions (black) 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. And finally, as shown in the rightmost figurine in 2B, in the elderly the decline of the executive functions (dark grey) discloses the rightward spatial bias. As a conclusion, the efficiency of the performance in spatial attention tasks and the ability to overcome the rightward spatial bias with executive functions increase as a function of childhood development, are best in young adulthood, and decrease as a function of ageing.

As relevant for all our results on spatial bias and especially for those on DL, Westerhausen et al. (2010) targeted an elegant study on possible neural correlates for the mechanisms of these biases. They conducted an event-related fMRI study in which they manipulated the relative saliency (inter-aural intensity difference) of the syllables in the DL paradigm. They described a fronto-parietal attention control network and a medial-lateral cognitive control network. The latter one was involved in the processing of a conflict between the attention instruction (FR/FL) and the inter-aural stimulus salience. The conflict during dichotic listening was the strongest in the FL condition when low intensity syllables were presented to the left ear and high intensity syllables to the right ear. Falkenberg et al. (2011) further extended the Westerhausen et al. (2010) study and described in more detail the two attention- related brain networks. The fronto-parietal top-down cognitive control network involved in cognitively demanding conditions was described to consist of the pre-supplementary motor area, anterior cingulate cortex, inferior frontal junction, insula, and inferior parietal lobe. The other network, involved in less demanding cognitive control conditions, included the superior temporal and post-central gyri. Finally, Kompus et al. (2012) described the activations in the three DL-paradigm attention conditions, based on a large database of 113 subjects measured in different studies by the Bergen

group. All conditions (NF, FR, FL) activated the right inferior frontal gyrus and caudate, whereas the FL condition with the strongest cognitive conflict also produced distinct activations in the left inferior prefrontal gyrus and caudate nucleus. The left prefrontal activation coincides well with the findings by Thomsen et al. (2004), and thus it emphasises the role of the left prefrontal areas in control of spatial biases, which is also demonstrated in our model in Fig. 2.

In future research, the model could be tested in neurological patients with a brain damage in prefrontal or any other areas impairing executive functions: they should show stronger spatial biases or be less able to overcome the biases as compared with normal participants. For lifespan studies, the model predicts that in tasks which reveal perceptual "bottom-up" biases, children and older people would show stronger biases than young adults during perceptual tasks that involve a strong load on executive functions or which need to be performed while the executive functions are loaded by another simultaneous task. This prediction follows from the assumption that executive functions are not matured in children and they are deteriorating in older adults so that in these age groups the executive functions cannot be employed to the same degree as in young adults to overcome the biases. In principle the developmentally varying biases could be observed also towards the left hemispace, provided that the perceptual task involves a strong enough leftward perceptual bottom-up bias. However, such tasks will be difficult to find because the attentional component (see Fig. 2A) favours the right side and thus works against any leftward bias. Finally, the relation between rightward spatial bias shown by our studies and the well-documented phenomenon of pseudo-neglect in line-bisection task and their age dependence should be further studied. At least recent evidence (Benwell et al., 2014) suggests that there is a rightward bias in pseudo-neglect in normal ageing.

6. Conclusions

The role of asymmetrical spatial attention mechanisms has recently been recognised as one of the mechanisms of asymmetrical hemispheric activations and asymmetrical perceptual-cognitive performance (e.g. Corbetta et al., 2008; Hämäläinen and Takio, 2010; Martin et al., 2008; Posner, 2008; Takio and Hämäläinen, 2012; Takio et al., 2011, 2013). Together with asymmetrical perceptual processes, they often bias attention towards the right side. Age-related changes in spatial biases indicate that the complex interactions between the lateralised processes (such as spatial attentional and perceptual processes) and the executive functions (see Posner, 2008; Posner and Raichle, 1994; Takio and Hämäläinen, 2012) influence the perceptual and cognitive performance in adult populations (e.g. Hugdahl et al., 2009; Martin et al., 2008). The slow development and decline of the executive functions during the lifespan modify the degree of the spatial biases, making children and older adults less able to compensate the biasing effects of asymmetric perceptual processes and attention.

Conflict of interest

There is no conflict of interest.

Acknowledgements

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