NeuroImage 82 (2013) 531–546

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Age-associated modulations of cerebral oscillatory patterns related to attention control

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ARTICLE INFO

Article history:
Accepted 7 June 2013
Available online 15 June 2013

Keywords:
Visual attention
Orienting
Aging
EEG
Oscillatory activity

ABSTRACT

Visual attention depends on bottom-up sensory activation and top-down attentional guidance. Although aging is known to affect sensory processing, its impact on the top-down control of attention remains a matter of debate. We investigated age-related modulations of brain oscillatory activity during visual attention using a variant of the attention network test (ANT) in 20 young and 28 elderly adults. We examined the EEG oscillatory responses to warning and target signals, and explored the correlates of temporal and spatial orienting as well as conflict resolution at target presentation. Time–frequency analysis was performed between 4 and 30 Hz, and the relationship between behavioral and brain oscillatory responses was analyzed. Whereas temporal cueing and conflict had similar reaction time effects in both age groups, spatial cueing was more beneficial to older than younger subjects. In the absence of cue, posterior alpha activation was drastically reduced in older adults, pointing to an age-related decline in anticipatory attention. Following both cues and targets, older adults displayed pronounced motor-related activation in the low beta frequency range at the expense of attention-related posterior alpha activation prominent in younger adults. These findings support the recruitment of alternative motor-related circuits in the elderly, in line with the dedifferentiation hypothesis. Furthermore, older adults showed reduced midparietal alpha inhibition induced by temporal orienting as well as decreased posterior alpha activation associated with both spatial orienting and conflict resolution. Altogether, the results are consistent with an overall reduction of task-related alpha activity in the elderly, and provide functional evidence that younger and older adults engage distinct brain circuits at different oscillatory frequencies during attentional functions.

Introduction

Selective attention is a complex cognitive process depending on the integrity of a large fronto-parietal network that includes a dorsal part involved in top-down attentional guidance and a ventral part, mainly in the right hemisphere, that mediates bottom-up attention (Corbetta and Shulman, 2002). A decline of selective visual attention is documented in normal aging (Fabiani, 2012; Madden, 2007), partly attributed to the degradation of bottom-up sensory processing affecting the transmission of the visual signal (Schneider and Pichora-Fuller, 2000; Spear, 1993). However, deficits of top-down attentional selection are also present in the course of aging (Pesce et al., 2005), along with the alteration of several cognitive functions (Fabiani, 2012 for review). The main theoretical views underlying cognitive aging include the decline in processing speed (Birren and Fisher, 1995; Salthouse, 1996), the decline in executive control, likely related to age-specific alterations of the prefrontal cortex (Braver and West, 2008; West, 1996), the increase in neural noise, causing enhanced response variability (Hong and Rebec, 2012; Li et al., 2001), and the degradation of inhibitory processes (Hasher and Zacks, 1988), resulting in less efficient filtering of task-irrelevant information and increased distractibility (Fabiani et al., 2006; Gazzaley et al., 2005; McDowd and Filion, 1992).

Warning signals prior to an event can be used to direct attention, and may thus be particularly relevant to improve attention control in older adults. A neutral (task-irrelevant) warning cue prior to a target induces automatically a state of alertness speeding up response performance. According to the cue–target time interval (foreperiod) duration, this effect is referred to as alerting or temporal orienting (Weinbach and Henik, 2012). Alerting is defined as a high state of bottom-up arousal that reaches maximal effect over short foreperiods (<500 ms) (Hackley et al., 2009). Temporal orienting is obtained using longer, regular foreperiods that induce an involuntarily orientation of attentional

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http://dx.doi.org/10.1016/j.neuroimage.2013.06.037

resources (Weinbach and Henik, 2012). In addition to temporal prediction, the cue can provide spatial information about the upcoming target, facilitating the processing of sensory input by selection of location (spatial orienting) (Posner, 1980). Following cue-related preparatory set, the occurrence of the target requires further attentional control relative to executive functions, often studied by tasks involving resolution of conflict in the presence of competing information (Botvinick et al., 2004 for review). The three functions of alerting, spatial orienting and executive control have been formally attributed to three specialized networks of anatomical areas, designed as attentional networks (Posner and Petersen, 1990). The attention network test (ANT) has been specifically designed to test the behavioral efficiency of these networks within a single paradigm combining the cued reaction time and flanker tasks (Fan et al., 2002). While alerting and spatial orienting are triggered by specific warning cues shortly preceding the target (<500 ms), conflict resolution is examined using targets flanked by congruent or incongruent patterns of distractors.

The beneficial effects of attentional cueing essentially manifest by reaction time speeding and concomitant enhancement of cortical preparatory activity and processing of expected stimulus (for review, Carrasco, 2006; Hillyard et al., 1998). A reduction of these beneficial effects would a priori be expected in old age given the decline in bottom-up and top-down attentional processing, but the issue remains actively debated. After adjustment for visual processing speed, known to decrease in elderly adults (Birren and Fisher, 1995; Salthouse, 1996), aging has been associated with a smaller alerting effect, providing that the duration of the warning cue and warning-to-target-interval is kept short and constant (Gamboz et al., 2010; Jennings et al., 2007). Conversely, both spatial orienting, triggered by peripheral cues, and executive control, examined during interference resolution in the flanker task, are marginally affected in elderly individuals (Fernandez-Duque and Black, 2006; Festa-Martino et al., 2004; Gamboz et al., 2010; Ishigami and Klein, 2011; Jennings et al., 2007). However, some studies report inconsistent age-associated findings, such as enhanced alerting effect (Fernandez-Duque and Black, 2006) or decreased interference resolution (Zhou et al., 2011), probably attributable to variations in experimental settings.

Neurophysiological mechanisms underlying signal attentional gating includes the enhancement of the neural responsiveness to an attended signal and concomitant deactivation of irrelevant neural generators (Luck et al., 1997; Moran and Desimone, 1985). These mechanisms are known to modulate the brain oscillatory activities within 8 to 30 Hz EEG frequency bands. Overall, a suppression of alpha oscillatory activity (8–12 Hz) is observed in areas actively engaged in the attentional processing of visual information (Bastiaansen and Brunia, 2001; Pfurtscheller and Lopes da Silva, 1999), in parallel with an enhancement of alpha activity in task-irrelevant regions (Foxe and Snyder, 2011; Jensen and Mazaheri, 2010). Beta oscillations (14–30 Hz) follow similar patterns, with a more specific implication in motor preparation and execution processes engaged in visuomotor attention tasks (Engel and Fries, 2010; Gola et al., 2012; Tzagarakis et al., 2010). These alpha and beta modulations can be observed prior to target occurrence, and constitute reliable markers of the engagement of attentional and executive resources for an expected stimulus and response (Deiber et al., 2010; Foxe and Snyder, 2011; Gola et al., 2012; Jensen and Mazaheri, 2010; Kaiser et al., 2001; Rihs et al., 2007; Thut et al., 2006; Tzagarakis et al., 2010).

The aim of the present study was to examine oscillatory brain dynamics to investigate how attentional cueing can be affected in normal aging, using a modified version of the ANT (Fan et al., 2002) in young and elderly individuals. Our analysis focused on the alpha and beta frequency bands as the most sensitive frequencies to both anticipatory attention and motor-related processes (Bastiaansen and Brunia, 2001; Engel and Fries, 2010; Thut et al., 2006). In order to specifically address top-down attentional control, the duration of cue presentation and foreperiod was substantially increased as compared to the classical version of the ANT, favoring temporal orienting over alerting. This procedure also ensured adequate time resolution for the analysis of alpha and beta frequency oscillations during the foreperiod. We examined how age affects the cerebral oscillatory reactivity associated with each cue and target configuration. By contrasting the appropriate conditions, we also evaluated the influence of age on temporal orienting (temporal cue vs. no cue), spatial orienting (spatial vs. temporal cue), and conflict resolution (incongruent vs. congruent flanker pattern). In addition, for each of these attentional control components, we investigated the relationship between the oscillatory activity pattern and corresponding behavioral performance, as indexed by reaction time. Although the subtraction procedure employed may not entirely isolate complex cerebral processes such as time and space orienting, it allows for a combined interpretation with behavioral scores obtained using the same method, and facilitates the comparison with most existing reports. We report here major differences in frequency band reactivity and regional distribution in elderly compared to young individuals, suggesting that normal aging is associated with specific functional activation during temporal and spatial attention. In addition, we describe an age-independent relationship between the oscillatory activity pattern and the efficiency of spatial attention.

Material and methods

Participants

Forty-eight healthy, cognitively intact right-handed volunteers participated in the study, including 28 older adults (64.9 ± 5.3 years) and 20 younger adults (25.5 ± 4 years). The elderly participants were overall designed as “old” subjects, although they included 12 young-old (57–64) and 16 old (65–79) individuals. All individuals were screened with the Mini Mental State Examination (MMSE), the Lawton's Instrumental Activities of Daily Living (IADL), and the Hospital Anxiety and Depression (HAD) Scale (Table 1). Cognitive evaluation was performed in both groups as follows (simplified cognitive domain subdivision according to each test's main explored domain) (Deiber et al., 2011): attention (Code, Trail Making Test A), working memory (verbal: Digit Span Forward, visuo-spatial: Corsi block tapping), episodic memory (verbal: Buschke double memory 48 items, visual: Shapes), executive functions (Trail Making Test B), language (Boston naming), visual gnosis (Ghent overlapping figures). In older subjects, additional evaluation of executive functions (verbal fluency, Wisconsin card sorting) and praxies (ideomotor, reflexive, and constructional) was performed. Subjects were also evaluated with the Clinical Dementia Rating Scale, and only scale 0 cases with scores within 1.5 standard deviations of the age appropriate mean in all tests were included in the final series. All participants had normal or corrected-to-normal visual acuity, and none reported a history of major medical disorders (cancer, cardiac

Table 1
Demographic and clinical data.

Variables	Young N = 20	Elderly N = 28	P
Age (years)	25.5 ± 4.0	64.9 ± 5.3	0.001
Gender (f/m)	13/7	18/10	n.s.
Education[a]	2.7 ± 0.5	2.0 ± 0.8	0.005
MMSE	29.1 ± 0.5	29.0 ± 0.9	n.s.
IADL	8.0 ± 0.0	8.5 ± 1.0	0.05
HAD anxiety	5.1 ± 2.4	5.8 ± 2.5	n.s.
HAD depression	1.6 ± 1.9	2.5 ± 1.8	0.05

Data are presented as mean ± SD.
[a] Education levels, 1: ≤9 years, 2: 10 to 12 years, 3: >12 years. MMSE: Mini-Mental State Examination (cut off 28); IADL: Lawton's instrumental activities of daily living; HAD: Hospital Anxiety and Depression Scale (cut off is 8 for both anxiety and depression). P: probability of difference between Young and Elderly, Mann–Whitney non-parametric test (n.s., non-significant).