Aging affects medial but not anterior frontal learning-related theta oscillations

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A B S T R A C T

Aging induces a decline in the ties that bind anatomical networks centered on the prefrontal cortex, which are critical for reinforcement learning and decision making. At the neurophysiological level, the prefrontal cortex may engage electrophysiological oscillatory synchronization to coordinate other brain systems during learning. We recorded scalp EEG from 21 older (mean age 69 years) and 20 young (mean age 22 years) healthy human adults while they learned stimulus–response mappings by trial-and-error using feedback. In young adults, theta-band (4–8 Hz) oscillatory power over medial frontal and anterior frontal cortex predicted learning after errors. Older adults demonstrated a decrease in the theta-band learning-predictive signals over medial frontal but not anterior frontal cortex. This age-related decrease in task-relevant medial frontal theta power may be related to the more general decrease in medial frontal theta power that we observed during rest. These results demonstrate a shift in cortical networks that support reinforcement learning in older adults, and shed new light on the changes in neurophysiological (oscillatory) mechanisms with neurocognitive aging.

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1. Introduction

With age, gray matter shrinks, and white matter fiber tracts thin. Age-related anatomical declines are particularly prominent in the prefrontal cortex (Bennett et al., 2010; Giorgio et al., 2010; Raz et al., 2005). These prefrontal anatomical decrements coincide with decreases in functional brain activation and in memory performance and cognitive control (Kennedy and Raz, 2009; Velanova et al., 2007; Ziegler et al., 2010), including decision making and learning (for reviews, see Brown and Ridderinkhof, 2009; Mohr et al., 2010). Although the prefrontal cortex is critical for reinforcement learning and decision making, optimal behavior requires communication with other brain areas. During learning, information transmission within and between prefrontal and other cortical systems may be subserved by electrophysiological oscillatory synchronization (Cohen et al., 2011; Engel et al., 2001; Varela et al., 2001).

Cortical theta-band oscillations (4–8 Hz) have been linked to the evaluation and use of valenced performance feedback to guide decision making (Cohen et al., 2011). In young adults, theta-band activity over midfrontal areas predicts learning from negative feedback (Van de Vijver et al., 2011), and theta-band oscillatory synchrony increases between medial frontal, lateral prefrontal, and motor cortices after errors and negative feedback (Cavanagh et al.,

2010; van de Vijver et al., 2011). We have previously suggested that these changes underlie learning from errors and guide the adjustment and communication of motor plans, possibly by shaping the effectiveness of medial frontal output (Van de Vijver et al., 2011).

Less is understood about how learning-related oscillations change with aging. Generally, frequency band-specific power topographies become more uniformly distributed with age (Babiloni et al., 2004; Dustman et al., 1985; Maurits et al., 2006). Older compared to young adults show smaller and spatially more distributed increases in frontal theta-band oscillations with increasing conflict and working memory load (Cummins and Finnigan, 2007; Missonnier et al., 2011; Schmiedt-Fehr and Basar-Eroglu, 2011). Post-error medial frontal theta-band activity decreases with age (Kolev et al., 2005, 2009). Although these results suggest that task-related oscillatory dynamics change with age, it remains unclear how these changes are related to decreased learning performance.

Thus, as an extension to our previous report on learning-related oscillatory dynamics in young adults (Van de Vijver et al., 2011), in the current study we recorded scalp electroencephalography (EEG) from both young and older adults during a reinforcement-learning task, to examine the following: (1) how healthy aging affects learning-related oscillatory theta-band activity over medial frontal cortex; (2) whether older adults demonstrate learning-related theta-band oscillations in a broader task-relevant frontal cortical network; and (3) how these changes predict learning performance. In this conceptual follow-up, we used a different feedback-learning task that should, however, tap into similar cortical learning

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networks. Moreover, we used a novel analysis approach to examine learning-related brain dynamics: We investigated how post-response and post-feedback oscillatory dynamics were related to behavior on the next occurrence of the same stimulus, rather than the immediately following trial. We hypothesized the following: that (1) post-error medial frontal theta-band activity would be smaller in older than in young adults (Kolev et al., 2005, 2009); (2) medial frontal post-error theta activity would be less predictive of learning in older adults; and (3) with age, performance- and feedback-related activity would become less centered on medial frontal scalp areas, and more distributed to a larger network of task-relevant cortical frontal and motor areas. We also recorded resting-state EEG activity to examine whether task-related age differences in oscillatory dynamics reflect tonic differences in baseline connectivity.

2. Methods

2.1. Participants

A total of 20 young (9 male; 16 right-handed) and 21 older (9 male; 19 right-handed) adults participated in this study for course credits or financial compensation, with age ranges of 18 to 35 years (mean = 21.7 years, standard deviation [SD] = 4.5 years) and 67 to 73 years (mean = 69.0 years, SD = 2.0 years), respectively. Educational level did not differ between groups (6−16 years; $t_{38} = 0.926$, $p = 0.360$). Young participants were recruited via the University of Amsterdam. Although 2 young participants also participated in our previous study (Van de Vijver et al., 2011), the learning tasks differed between the 2 studies, and no data in this article have been published in any form in other papers. Older participants were selected from a database of healthy older adults willing to participate in psychological research (www.seniorlab.nl). According to self-report, participants had no psychiatric or neurological disorders. They were informed that task performance did not have consequences for the received amount of credits or financial compensation. The study was executed in compliance with relevant laws and institutional guidelines.

2.2. Task

Participants performed a probabilistic learning task (Nieuwenhuis et al., 2002) (Fig. 1A). On each trial, participants were required to press 1 of 2 buttons within 700 milliseconds after stimulus onset. They were instructed to learn the correct stimulus−response mappings by trial-and-error using feedback. Of the 6 stimuli in each block, 2 stimuli had a feedback validity of 100%, 2 had a feedback validity of 80%, and 2 had a feedback validity of 50%. Thus, feedback validities were mixed within presentation blocks. Invalid feedback could be positive feedback after an error or negative feedback after a correct response. For the stimuli with 80% valid feedback, invalid feedback was equally distributed over the first and second half of each block. Per 2 stimuli in a block with the same feedback validity, 1 stimulus was mapped to the left and 1 to the right response button. Trials were presented in 9 blocks of 180 trials each. Per block, all stimuli were presented 30 times in random order. On average, occurrences of the same stimulus were separated by 4.84 other trials (SD = 0.03 stimuli). The same stimulus was presented on consecutive trials in 16.5% of trial pairs (SD = 0.89%). New, randomly selected stimuli were presented in each block. Stimuli were concrete pictures selected from the Snodgrass picture set (Snodgrass and Vanderwart, 1980). Positive feedback was a happy face, negative feedback a frowning face. If a participant failed to respond in time, the words "too late" were presented as feedback. Participants performed 1 block of training.
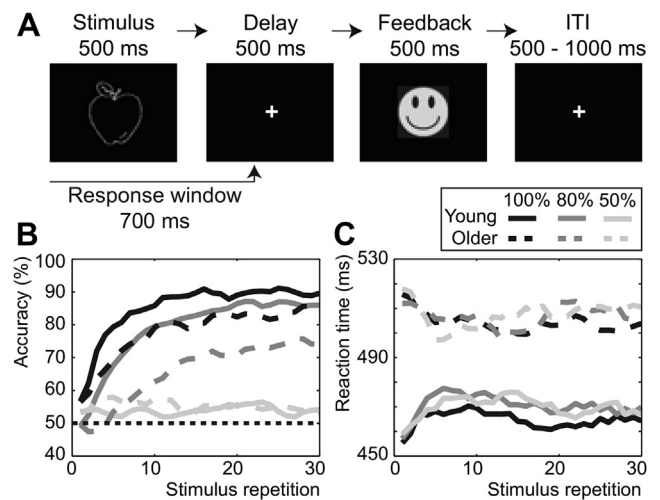

Fig. 1. Overview of the reinforcement learning task and behavioral performance. (A) Sequence of events in an example trial. During the response window, participants pressed 1 of 2 response buttons. (B) Average accuracy over stimuli and blocks represented as the percentage correct choices per stimulus repetition. (C) Average reaction times over stimuli and blocks per stimulus repetition.

2.3. Behavioral analyses

Accuracy and reaction times (RT) were compared with mixed analyses of variance (ANOVAs), with the factors Age (young, older), Feedback validity (100%, 80%, 50%), and Stimulus repetition (presentations 1−10, 11−20, 21−30). We applied Greenhouse−Geisser corrections when required (uncorrected degrees of freedom are reported).

2.4. EEG recording and preprocessing

EEG data were recorded at 512 Hz using a BioSemi ActiveTwo amplifier from 64 scalp electrodes, 2 peri-ocular electrodes, 2 reference electrodes on the earlobes, and EMG on each hand. All analyses were conducted in Matlab, using in-house written code and EEGLAB (Delorme and Makeig, 2004). The data were high-pass filtered at 0.5 Hz and re-referenced off-line to the averaged earlobe recordings. After baseline correction (−200 to 0 milliseconds pre-stimulus baseline), trials with artifacts were visually identified and removed. Blink artifacts were removed using independent component analysis in EEGLAB. EEG data were converted to the scalp Laplacian (Kayser and Tenke, 2006) to increase spatial selectivity and to minimize volume conduction. Because the Laplacian improves topographical localization of surface EEG signals, it allows the investigation of EEG coherence at smaller spatial scales (Srinivasan et al., 2007).

2.5. Trial selection for EEG analysis

For all feedback validities, trials containing invalid feedback or late responses were discarded from all analyses. Thus, only trials on which valid feedback was presented were analyzed. The remaining trials were categorized into 4 conditions according to current accuracy and to accuracy on the following presentation of the same stimulus (to assess learning): correct-correct (i.e., a current correct response and a correct response on the next trial with the same stimulus), correct−incorrect, incorrect−correct, and incorrect−incorrect. For oscillatory power analyses, all remaining trials were included. However, large trial count differences between conditions can influence intersite phase synchrony results. Per