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Age-related increases in within-person variability: Delta and theta oscillations indicate that the elderly are not always old

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ABSTRACT

Behavioral and electrophysiological data related to performance in an auditory Go/NoGo task were analyzed in young and older adults in the present study. Especially, differences in within-person variability in behavior and neural activity between young and older adults and changes in topography of slow event-related oscillations (EROs) were of interest. Within-person variability in behavior was assessed by reaction time (RT) variability. Event-related delta and theta oscillations were analyzed using time–frequency transformation, which can give information on the time-course of single trial event-related EEG spectral power enhancement and intertrial phase-locking (ITC). In contrast to our previous visual Go/NoGo study, no under-recruitment of task-relevant brain regions was found for the auditory theta and delta EROs. Young did not differ from older adults in RT variability or in single trial delta/theta ITC. Altered recruitment of brain activity at advanced age was indicated, first, by stronger early theta phase-locking in older compared to young adults and, second, by a Go-specific lateralization of delta/theta activity. We conclude that within-person variability may increase with age, but the degree depends on performance level and the modality investigated.

Averaged event-related potentials (ERPs) elicited by response execution and response inhibition have been found to reflect behavioral changes with advancing age, such as behavioral slowing and reduced response conflict regulation [4,8,9]. Given that aging and increases in trial-to-trial fluctuations of behavior have been shown to be linked [15,16], investigating averaged EEG-signals might not always be appropriate. Increases in trial-to-trial fluctuations of behavior are posited to be one potential consequence of age-related changes in dopamine (DA) functionality. DA receptor reductions are posited to lower signal-to-noise ratio (SNR) of neural information processing. As a consequence a variety of impairments have been hypothesized, e.g., less distinctive neuronal representations of perceptual stimuli and memory items or increased interference between different functional networks [2,14]. In turn, these impairments can cause more trial-to-trial fluctuations in reaction times (RT) or slow down performance in older adults [2]. On neuronal level, trial-to-trial fluctuations of brain responses [2,20], under-recruitment of task-relevant brain regions [2,5,18,20] and/or non-selective recruitment of other regions in advanced age reflect changes in SNR [2,9,10,20].

Whether trial-to-trial fluctuations of electrophysiological brain responses are increased within the aged brain, is not clear. The late and slow positive potential termed P3 has been studied in single trials in oddball tasks. It is found that increased variability in RTs with older age is not necessarily linked to an increase in variability of neuronal processes. Instead, instability exists in processes related to response execution and response selection [21].

Event-related oscillations (EROs) can be described with regard to the evoked activity (amplitude after averaging across trials), total activity (summation of amplitudes before averaging across trials) and the degree of phase locking (a measure of the consistency across trials; see [12] for detailed explanation of terms). Time–frequency (TF) analysis of EEG-signals provides an estimation of single trial event-related EEG spectral power and intertrial phase coherence (ITC), at each frequency and latency window [6]. ERPs and EROs are linked by the fact that the ERP waveforms are determined by the phase and amplitude of superimposed, different frequency, single trial oscillations [3,7].

Delta (~0.5–4 Hz) and theta (~4–7 Hz) activity have been reported to especially characterize and differentiate between response execution and response inhibition [13]. In our previous visual Go/NoGo study, larger ITC was found for young compared to older adults even without increased variability in RTs [20]. Go/NoGo tasks require individuals to refrain from an action (NoGo) after specified stimuli, in contrast to others, where an accelerated action (Go) is to be performed. The lower ITC was observed in the time range 200–600 ms post-stimulus in the theta-band during NoGo, only. For both Go and NoGo conditions young adults showed larger

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delta and theta power than older adults, in the same time range. Additionally, young showed a specific NoGo-related early theta power increase 0–200 ms post-stimulus, while in older adults this response was present for both conditions. Delta and theta results corresponded with larger amplitudes in the averaged Go- and NoGo-P3 ERP component. These studies imply that NoGo processes reflected by theta – but not necessarily delta – oscillations may be prone to trial-to-trial fluctuations with advancing age.

Studies assessing averaged ERPs in vision and audition indicate that there may be modality-specificity in sensory and cognitive aging [5,8,17,23]. For instance, a modality-specific inhibition process in older adults after visual, but not auditory, stimuli was reported [8]. Our visual Go/NoGo study on delta and theta oscillations supports this notion [20]. However, it is unclear whether similar age-related changes in delta and theta EROs can be observed in the auditory modality. Thus, the present study investigated auditory Go- and NoGo delta and theta responses assessed by total activity and ITC measures.

Table 1 shows the characteristics of the studied individuals. Participants gave written informed consent, were healthy according to self-report (no history of neurological or psychiatric illness, and free of medication known to influence the CNS), and had normal or corrected-to-normal vision. The local institutional ethics committee approved the procedure protocol.

As stimuli four sinusoidal tones, with duration of 1000 ms, and intensity of 80 dB, were presented binaurally through air-conducting tubes with ear inserts. Trials included a warning tone (1300 or 1800 Hz) that was followed by either a Go (1350 Hz) or NoGo (1850 Hz) stimulus (interstimulus interval: 1100 ms; intertrial interval: 1500–3400 ms). Participants were instructed to attend to the 1300 Hz warning tone (cue eliciting response preparation); if the cue was followed by the Go stimulus, a response (button press of left and right hand) was required; if this cue was followed by a NoGo stimulus, the inhibition of the anticipated response was requested. All other tone sequences were to be ignored. 50 Go, 40 NoGo and 10 distracter NoGo trials were presented in pseudo-randomized order. Positive or error auditory feedback, respectively, was given after each Go trial 1300 ms post-stimulus. Correct responses were defined as RTs ranging from 20 to 800 ms in Go trials. Hearing thresholds were individually determined and intensity of tones adjusted to achieve comparability between young and older adults. Participants were requested keep their eyes focused on a fixation cross that was presented on a monitor throughout the whole experiment.

The median of RT and a coefficient of variation in RT (cvRT = mean absolute deviation/median) were analyzed by two-tailed *t*-tests for independent samples [16]. Accuracy was analyzed by two-factor repeated measures ANOVA: GROUP (young, elderly) × ERROR TYPE (commission errors, omission errors, too slow and too early RT).

EEG was recorded at F3, FZ, F4, C3, CZ, C4, P3, P4, T3, T4, O1 and O2 electrode sites, with linked earlobes as reference, and a sampling rate of 500 Hz (band limits: 0.5–70 Hz, 50 Hz notch filter). EOG was recorded from electrodes placed above and to the right of the right eye. EEG segments of 3600 ms (pre-stimulus: 2400 ms; post-stimulus: 1200 ms) were used for analysis. A minimum of 20 and a maximum of 31 artifact-free epochs for each condition were used for analysis (median number of trials: young 24/26; elderly 24/24 for Go/NoGo, respectively).

To calculate the total activity (sum) of all EEG activity at one frequency, each single trial was at first wavelet transformed (WT) and the absolute values averaged subsequently. Hence, the corresponding TF representation contains all activity of one frequency, no matter whether it was phase locked to the stimulus or not. Continuous WT with complex Morlet wavelets as basic functions (1–7 Hz, in 0.2 Hz steps; 1 cycle at lowest to 4 cycles at highest frequency, in 10 ms sliding windows), was calculated as follows using EEGLAB software [6]:

$$Total\_activity(f,t) = \frac{1}{n}\sum_{k=1}^{n}|F_k(f,t)|^2$$

For n trials, $Fk(f,t)$ is the spectral estimate of trial k at frequency f and time t and the TF value is the mean of $Fk(f,t)$. An epoch from 800 to 600 ms prior cue onset was used as baseline. The individual frequency, defined as the frequency showing maximum magnitude change within one out of all electrode sites and one out of both conditions investigated, was extracted and analyzed as total activity for each individual [12]. Time range and electrodes for analysis were selected according to introductory mentioned studies [8,13,17,20]: (i) early theta modulation 0–200 ms at Fz/Cz, (ii) late theta and (iii) delta modulation 200–600 ms at lateral frontal, central and parietal electrode sites. Frequency, time range and electrodes selected for analysis of the ITC corresponded to total power analysis and were calculated using EEGLAB software [6]:

$$ITC(f,t) = \frac{1}{n}\sum_{k=1}^{n}\frac{Fk(f,t)}{|Fk(f,t)|}$$

The early midline theta power/ITC measures were subjected to a three factor repeated measures ANOVA: GROUP (young/elderly) × CONDITION (Go/NoGo) × ELECTRODE (Fz/Cz). Addressing age-related changes in scalp distribution, theta and delta activity were analyzed using four-factor repeated measures ANOVA: GROUP (young/elderly) × CONDITION (Go/NoGo) × HEMISPHERE (left/right) × ANTERIOR–POSTERIOR (F3, C3, P3/ F4, C4, P4). Effect sizes were estimated by partial eta-square (η^2). Post hoc comparisons were computed using Fisher's least significant difference tests.

Behavioral data are presented in Table 1 and supplementary Fig. 1. Age-related differences were found for RTs, reflecting that young responded faster than older individuals, $t(28) = -2.92$, $p = .007$. The main electrophysiological results are shown in Fig. 1. Young did not significantly differ from older adults in the individually determined frequency (supplementary Fig. 2). For summary of significant results see Table 2. Additional descriptive results are illustrated in supplementary Figs. 2–5.

In the time window 100–200 ms after stimulus a change in theta activity can be observed with a central midline distribution (see Fig. 1c and Table 2). For Go condition lower theta power (Fig. 1c) and ITC values (Fig. 1d) were obtained than for the NoGo condition (main effect CONDITION). Young adults showed significantly lower power and ITC than older adults for Go and NoGo condition in this time window (GROUP). In contrast, 200–600 ms post-stimulus both young and older individuals were found to produce similar late theta oscillations (Fig. 1e and f) with a more posterior distribution for Go and a more anterior topography for NoGo condition (Fig. 1b; interaction effect ANTERIOR–POSTERIOR × CONDITION). Additionally, a significant interaction GROUP × HEMISPHERE × CONDITION was observed. Post hoc tests indicated that left sites ($p < .05$) showed minimally smaller late theta power increase compared to right sites in older adults for Go, but not NoGo, while in young adults no hemisphere differences were found. Irrespective of age, late theta ITC was lower for Go as compared to NoGo (CONDITION).

In the delta-band neither significant age-related differences in total delta power nor in ITC were observed (Fig. 1g and h). Power and ITC were affected irrespective of age by the CONDITION, with Go eliciting lower ITC than NoGo condition. Condition-specific distributions were similar to the late theta results, as shown in Fig. 1b, and they were reflected in a significant ANTERIOR–POSTERIOR × CONDITION interaction. Also similar to late theta a significant interaction