



Neurodynamic correlates of response inhibition from emerging to mid adulthood



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ABSTRACT

Response inhibition, a key executive function, continues to develop in early adulthood in parallel with maturational processes of the underlying prefrontal regions known to support it. The current study examined behavioral and neurophysiological correlates of response inhibition during a visual Go/No-Go task in a large sample ($N = 120$) comprised of participants in their Early 20s (ages 19–21), Mid 20s (ages 23–27), and Early 30s (ages 28–42). The two younger groups had lower accuracy, shorter reaction times, and made more premature responses compared to Early 30s. These impulsive behavioral tendencies were reflected in a delayed N2 latency and reduced P2 and P3 amplitudes for Early 20s compared to Early 30s and were associated with personality traits such as impulsivity in an age-dependent manner. The results suggest that response inhibition may not develop fully before the approximate age of 25, as the refinement of the primarily prefrontal cognitive control network follows a protracted developmental trajectory throughout young adulthood.

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1. Introduction

The ability to voluntarily control our behavior in a flexible and context-dependent manner is an important hallmark of the maturation of executive functions. Response inhibition is an essential capacity that allows individuals to actively suppress, interrupt, or delay an action (Aron, 2011). It plays an important role in everyday tasks such as withholding inappropriate responses or delaying their execution while gathering necessary information for completion (Schel, Ridderinkhof, & Crone, 2014). Compared to other higher-order functions, response inhibition is one of the last that develops, and one of the first to deteriorate with age (Hammerer, Li, Muller, & Lindenberger, 2010).

The Go/No-Go paradigm is commonly used to investigate response inhibition. It probes the ability to selectively inhibit a prepotent motor response on No-Go trials presented among the dominant Go (response activation) trials (Aron, 2011). In addition to response inhibition, this shift in the response pattern involves attentional capture due to high salience and low frequency of the No-Go stimuli (Tian, Shanshan, & Yao, 2014; Hampshire & Sharp, 2015). Performance on this task continues to linearly improve across childhood, adolescence, and into adulthood (Hammerer et al., 2010; Johnstone, Pleffer, Barry, Clarke, & Smith, 2005). fMRI studies show recruitment of right lateralized inhibitory network in adults (Aron, 2011),

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including dorsolateral prefrontal, inferior frontal and anterior cingulate cortices, as well as the pre-supplementary motor area. Neuroanatomical studies show substantial changes in these frontal areas through adolescence and young adulthood, primarily expressed in axonal myelination and gray matter pruning (Fjell et al., 2012; Schel et al., 2014; Sowell et al., 2003), with a reduction in cortical thickness and a simultaneous increase in white matter volume (Brown et al., 2012; Westlye et al., 2010). The gradual neuroanatomical development is accompanied by functional changes promoting efficient and fast recruitment of the inhibitory networks well into young adulthood. Using MEG with co-registered MRI, Vara, Pang, Vidal, Anagnostou, & Taylor (2014) compared spatiotemporal neural processes during a Go/No-Go task between adolescents (aged 13–17 years) and adults (aged 20–35 years) and found indications of an immature inhibitory control network in adolescence. Adults showed right dominant inferior frontal activity, while adolescents showed left dominant, bilateral activity in the inferior frontal regions, but also delayed recruitment of the left inferior frontal gyrus, prolonged recruitment of the right middle temporal gyrus and additional recruitment of the superior temporal gyrus compared to adults.

It can be expected that behavioral and structural developmental changes are reflected in electrophysiological indices. In the Go/No-Go task, early event-related potentials (ERPs) that arise during first 200 ms after the stimulus onset are the negative N1 and positive P2 deflections thought to reflect early perceptual effects (Albert, Lopez-Martin, Hinojosa, & Carretie, 2013; Bokura, Yamaguchi, & Kobayashi, 2001). The N2 deflection that occurs with a latency of 200–400 ms (Hammerer et al., 2010; Randall & Smith, 2011) has been estimated to originate in the lateral orbitofrontal and anterior cingulate cortex (Bokura et al., 2001; Huster, Enriquez-Geppert, Lavallee, Falkenstein, & Herrmann, 2013), and may reflect processes involved in stimulus evaluation and conflict monitoring (Donkers & van Boxtel, 2004; Enriquez-Geppert, Konrad, Pantev, & Huster, 2010; Huster et al., 2013). The P3 deflection occurs between 300 and 500 ms and is greater during salient stimuli requiring response inhibition/execution (Randall & Smith, 2011; Smith, Jamadar, Provost, & Michie, 2013). Its generators are estimated to a wider network including lateral orbitofrontal and anterior cingulate cortices, inferior parietal lobe and pre-supplementary motor area (Albert et al., 2013; Vara et al., 2014). Studies investigating neural mechanisms underlying inhibitory control in children and adolescents showed age-related decreases in frontal N2 and increases in frontal P3 amplitude concurrent with improved behavioral performance (Jonkman, 2006; Lamm, Zelazo, & Lewis, 2006). However, developmental studies of age-related changes in ERP components of response inhibition in young adulthood are scarce.

Young adulthood is a life period that begins in early 20s, and lasts through early 40s (Carter, Brandon, & Goldman, 2010; Courtney & Polich, 2009). It is marked by life-changing challenges like completing education, finding a full time job, leaving the parental household, and reaching financial independence. Response inhibition is particularly important at this age due to a tendency of young adults to engage in inappropriate behaviors (Crone & Ridderinkhof, 2011). The prevalence of risk-taking, impulsive behaviors, like substance abuse and risky driving at high speed or while intoxicated, peaks during early 20s (Doremus-Fitzwater, Varlinskaya, & Spear, 2010). In contrast to other periods of life, the leading cause of death in adolescence and early adulthood are accidents (World Life Expectancy, 2014), and the highest rates of binge-drinking episodes (consuming five or more alcoholic drinks on the same occasion) have been found among 18–25 year olds (Carter et al., 2010; Courtney & Polich, 2009). These behaviors are linked to impulsivity traits (Doremus-Fitzwater et al., 2010), and researchers agree that a tendency to risk-taking behavior is strongly related to the immature prefrontal cortex, which governs impulsivity, judgment, planning for the future, and foresight of possible consequences (Crone & Ridderinkhof, 2011; Vara et al., 2014).

Young adulthood is usually studied within a wide age range (from 20 to 40 years of age) making it very difficult to acquire a complete picture of response inhibition development, especially given that maturational changes are quite protracted during emerging adult years. The purpose of this study was to characterize the neural profile underlying response inhibition in young adults. Considering that successful inhibition requires rapid brain processes and that processing speed continuously changes over the adolescence and into emerging adult years, the temporal sensitivity of ERPs is critical for addressing this issue. Our aim was to investigate behavioral and neurophysiological differences in perceptual, decision making, or response inhibition processes across young adulthood, using a classical visual Go/No-Go task. We divided a large sample of young adults into three groups representing Early 20s, Mid 20s and Early 30s respectively. We hypothesized that response inhibitory control would be poorer in Early 20s, and would be reflected in lower performance accuracy, with N2 and P3 components indicating an immature inhibitory network. To the best of our knowledge, there are no other studies that have directly examined ERP correlates of response inhibition across young adulthood.

2. Material and methods

2.1. Participants

A total of 120 participants were included in the study, divided into three age groups: Early 20s, $N = 40$ (22 females), mean (\pm standard deviation), 19.9 (± 0.8) years, age range 19–21 years, Mid 20s, $N = 39$ (20 females), 24.5 (± 1.0) years, age range 23–27 years, and Early 30s, $N = 41$ (22 females), 33.2 (± 3.9) years age range 28–42 years. An additional 13 participants took part in the study but were excluded because their ERP or behavioral data exceeded three standard deviations from the mean and were therefore categorized as outliers, and 5 others were excluded due to technical difficulties. All participants were right-handed, with normal or corrected-to-normal vision. None used any medication at the time of the study and none reported any previous head-injuries or had any EEG contraindications. They were recruited on a volunteer basis via E-mails, social networking (Facebook) and advertisements at the University of Zagreb. The study conformed to the 1964 Declaration

of Helsinki, the ethical standards of the American Psychological Association (APA) and was approved by the local Ethics Committee.

2.2. Procedure

The study was conducted at the Laboratory for Psycholinguistic Research at the University of Zagreb, Croatia, and it consisted of two sessions. During the first session, participants were familiarized with the laboratory setting and the experimental procedure, and completed a battery of standardized tests and questionnaires. They were thoroughly familiarized with the task during two practice runs comprising 300 trials.

Upon their arrival to the laboratory for the second session, participants were prepared for EEG recording and were given additional 150 practice trials. They were reminded to respond as quickly and accurately as possible. The task was programmed in E-prime V2.0 (Psychology Software Tools, <http://www.pstnet.com/>). The responses were given by pressing a key on the Serial Response Box (S-R Box; Psychology Software Tools, <http://www.pstnet.com/>) with their right index finger.

2.3. Psychological testing battery

Each participant completed a battery of standardized psychological tests including the following: Cognitive Nonverbal Test (Sucevic, Momirovic, Fruk, & Augustin, 2004) which estimates non-verbal IQ; Peabody Picture Vocabulary Test III-CRO (Dunn et al., 2010) which measures receptive vocabulary and verbal ability; Letter Digit Substitution Test (van der Elst, van Boxtel, van Breukelen, & Jolles, 2006) which measures information processing speed; Barratt Impulsivity Scale (Patton, Stanford, & Barratt, 1995; Spinella, 2007) and Eysenck Personality Questionnaire (Eysenck & Eysenck, 1994) that assess impulsivity, neuroticism, psychoticism and extraversion.

2.4. Go/No-Go task

To investigate response inhibition, we used the visual Go/No-Go task (Fig. 1), during which a stream of X and Y letters was presented in an alternating order. Participants were instructed to respond with their right index finger to each stimulus alternation (X following Y = Go trials) but to withhold responses whenever the stimuli repeated (X following X or Y following Y = No-Go trials). The letters were presented for 300 ms every 1250 ± 150 ms. A total of 520 trials consisted of 75% (388) Go and 25% (132) No-Go trials, divided into three blocks which were counterbalanced across participants. No-Go trials were separated with 2–6 Go trials. The letters were presented in yellow font on a black background within the visual angle of 0.76° .

2.5. EEG recording

The EEG signal was continuously recorded using a standard 32-channel actiCAP connected to the Brain Vision system (Brain Products GmbH, Munich, Germany). During recording FCz was used as a reference. Blinks and vertical eye movements (VEOG) were recorded by means of bipolarly referred electrodes placed above and below the right eye while horizontal movements (HEOG) were recorded from electrodes placed at the outer canthus of each eye. The electrode impedance was kept below 5 kOhms.

2.6. EEG data processing

EEG data processing was carried out off-line using custom-made MATLAB (The MathWorks, Inc., Natick, MA) functions developed at the Spatio-temporal Brain Imaging Lab (Kovacevic et al., 2012) which rely partially on publicly available software packages including FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) and EEGLAB (Delorme & Makeig, 2004). Continuous EEG recordings were filtered with a band-pass filter from 0.1 Hz to 30 Hz. The data were epoched from -250 to 800 ms with respect to stimulus onset and re-referenced to the average of right and left mastoids. Noisy channels and

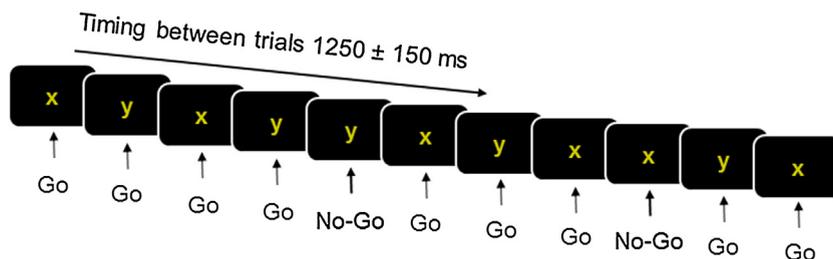


Fig. 1. The Go/No-Go task. Participants were instructed to respond with their right index finger to each stimulus alternation (e.g. X following Y = Go) but to withhold responses whenever the stimuli repeated (X following X or Y following Y = No-Go).

other discontinuities were removed by visual inspection and threshold-based rejection. Eye-blink and heart-beat artifacts were detected and removed using Independent Component Analysis (ICA) method (Delorme & Makeig, 2004). All trials were baseline-corrected with respect to a 250 ms pre-stimulus period. Only correct stimulus-locked trials were included in the analysis. Artifact-free ERP averages were obtained for $81 \pm 6\%$ trials in the Go condition and for $78 \pm 11\%$ trials in the No-Go condition.

The timing of components of interest was determined based on the inspection of waveforms for each subject individually and in reference to the literature (Huster et al., 2013; Jonkman, 2006; Smith et al., 2013). To explore the early stages of processing, peak amplitudes and peak latencies were quantified for the N1 component from 50 to 125 ms and for the P2 component from 125 to 175 ms and were expressed as the difference between the pre-stimulus baseline voltage and largest negative peak for N1 and the largest positive peak for P2. N2 and P3 amplitudes were measured as the mean voltage for each participant and condition in a given measurement window: N2 from 175 to 325 ms and P3 from 350 to 500 ms. To investigate possible age differences in ERP onset latencies, we used a fractional (50%) peak latency measure since this has been suggested to measure onset of a component accurately and reliably across different conditions (Kiesel, Miller, Jolicoeur, & Brisson, 2008; Luck, 2014). Onset latency was defined as the time point at which the voltage reached 50% of the peak amplitude, using the same measurement windows as for mean amplitudes. For statistical analysis, amplitudes and latencies at frontal (F3 + Fz + F4) electrodes were averaged together. The data are reported for the frontal electrodes in order to reduce the number of comparisons since the components of interest have typically been reported to be most prominent at frontal electrodes (Enriquez-Geppert et al., 2010; Johnstone et al., 2007; Johnstone et al., 2005; Jonkman, 2006).

2.7. Statistical analysis

The factor of Gender was explored in an initial analysis. It was omitted from the subsequent analysis because no interactions or main effects were found.

Responses within the first 200 ms after stimulus onset were excluded from the behavioral and ERP data analysis, and were counted separately as premature responses. All variables were checked for normality (Shapiro-Wilk test), homogeneity of variances (Levene's Test of Equality of Error Variances) and sphericity (Mauchly's Test of Sphericity). Reaction times (RTs), accuracy, premature responses, nonverbal IQ, extraversion, neuroticism, and attention impulsivity variables were not normally distributed across the age groups, necessitating a non-parametric approach. Kruskal–Wallis one-way analysis of variance was applied to examine age differences on those variables and the relevant values (chi-square (X^2), degrees of freedom (df), asymptotic significance (p)) are reported. ANOVAs were performed for the variables of information processing, receptive vocabulary, psychoticism, total impulsivity, motor impulsivity, and non-planning impulsivity, with age (Early 20s, Mid 20s and Early 30s) as a between-subject factor.

In order to elucidate response strategies and provide a more detailed description of how accuracy trades off with RT between age groups, we constructed conditional accuracy functions (CAFs). CAFs are often used as a method for depicting speed-accuracy tradeoff (Heitz, 2014). We classified each subject's RTs into 50-ms bins, computed the mean percentage of correct responses in each bin for each subject, and averaged across each age group separately. CAFs constructed in this way are comparable with other studies investigating response strategies in various groups or tasks (Dambacher & Hubner, 2013; Stins, Polderman, Boomsma, & de Geus, 2008; Strack, Kaufmann, Kehrer, Brandt, & Sturmer, 2013). To check for age differences, we performed ANOVAs from 100 to 500 ms of the CAFs, where the differences were most prominent.

ERPs were analyzed with mixed design ANOVAs that additionally included stimulus condition (Go/No-Go) as a within-subject factor (SPSS for Windows). A two-tailed significance level of $p < 0.05$ was adopted. Significant main effect of age was followed by pairwise comparisons, uncorrected values are reported and compared to Bonferroni corrected alpha value for multiple comparisons $\alpha_B = 0.008$, to control for familywise error (FWE).

Pearson's correlation coefficients were calculated across the behavioral performance, ERPs, and personality variables for each group separately to determine within-group relationships. Correlations with a significance of $p < 0.01$ are reported.

3. Results

3.1. Psychological assessment

Participants were well-matched in terms of personality traits, non-verbal IQ and speed of information processing, since we did not find any age group effects on these variables (Table 1). The only age differences were found for the receptive vocabulary, showing that Early 20s had lower scores than Early 30s (Early 20s < Early 30s $p = 0.01$; Early 20s vs. Mid 20s $p = 0.71$; Mid 20s vs. Early 30s $p = 0.18$).

3.2. Behavioral performance

Age group differences were found for Go accuracy, number of premature responses and reaction times to Go trials (Table 2). Early 30s were more accurate on Go trials than both Early 20s and Mid 20s (Fig. 2). Both younger groups made significantly more premature, impulsive responses compared to Early 30s (Fig. 2). In contrast, the Early 30s showed longer RT compared to Early 20s and Mid 20s (Fig. 2). To explore these differences in response strategies, we plotted accuracy as

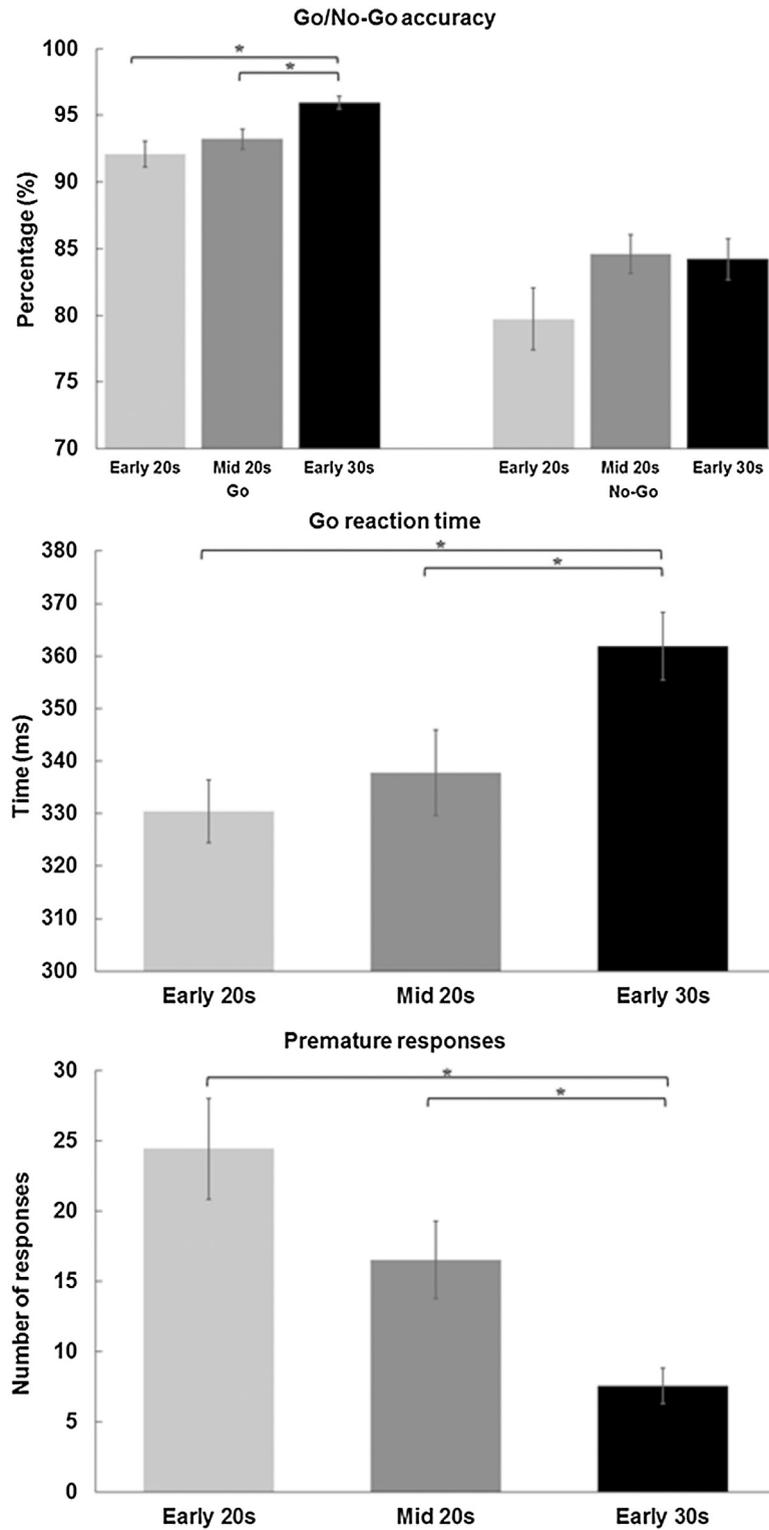


Fig. 2. Age group differences in accuracy, the number premature responses to Go trials made between 0 and 200 ms after stimulus onset, and reaction time during the Go/No-Go task (mean \pm standard error of the mean); * $p < 0.05$.

Table 1
Statistics for psychological tests.

| | F/X^2 | df | p |
|-----------------------|---------|-------|-------------|
| Nonverbal IQ | 3.16 | 2 | 0.21 |
| Info. processing | 0.30 | 2,117 | 0.74 |
| Receptive vocabulary | 4.96 | 2,117 | 0.01 |
| Extraversion | 1.65 | 2 | 0.44 |
| Psychoticism | 1.31 | 2,117 | 0.27 |
| Neuroticism | 2.77 | 2 | 0.25 |
| Impulsivity | 0.28 | 2,117 | 0.76 |
| Motor impulsivity | 0.31 | 2,117 | 0.74 |
| Attention impulsivity | 2.24 | 2 | 0.33 |
| Non-planning | 0.47 | 2,117 | 0.62 |

Note: significant differences at $p < 0.05$ are bolded. Nonverbal IQ, extraversion, neuroticism, and attention impulsivity variables were not normally distributed across the age groups, therefore here we report chi-square (X^2), degrees of freedom (df), asymptotic significance (p), as well as the results of the ANOVAs (F -values) for the rest of the variables.

Table 2
Statistics for behavioral measures.

| | X^2/F | df | p | Post-hoc |
|---------------------|---------|-------|------------------|---|
| Go accuracy | 12.16 | 2 | 0.002 | Early 20s < Early 30s $p = \mathbf{0.004}$ Mid 20s < Early 30s $p = \mathbf{0.02}$ Early 20s = Mid 20s $p = 1.0$ |
| No-Go accuracy | 1.69 | 2 | 0.43 | |
| Premature responses | 15.85 | 2 | <0.001 | Early 20s > Early 30s $p < \mathbf{0.001}$ Mid 20s > Early 30s $p = \mathbf{0.03}$ Early 20s = Mid 20s $p = 0.52$ |
| Go reaction time | 13.02 | 2 | 0.001 | Early 20s < Early 30s $p = \mathbf{0.003}$ Mid 20s < Early 30s $p = \mathbf{0.01}$ Early 20s = Mid 20s $p = 1.0$ |
| CAFs 100–149 | 5.92 | 2,117 | 0.004 | Early 20s > Early 30s $p = \mathbf{0.01}$ Mid 20s > Early 30s $p = \mathbf{0.01}$ Early 20s = Mid 20s $p = 1.0$ |
| CAFs 150–199 | 12.43 | 2,117 | <0.001 | Early 20s > Early 30s $p < \mathbf{0.001}$ Mid 20s > Early 30s $p = \mathbf{0.04}$ Early 20s = Mid 20s $p = 0.06$ |
| CAFs 200–249 | 7.04 | 2,117 | 0.001 | Early 20s > Early 30s $p = \mathbf{0.001}$ Mid 20s = Early 30s $p = 0.19$ Early 20s = Mid 20s $p = 0.20$ |
| CAFs 250–299 | 2.23 | 2,117 | 0.11 | |
| CAFs 300–349 | 0.09 | 2,117 | 0.91 | |
| CAFs 350–399 | 5.41 | 2,117 | 0.01 | Early 20s < Early 30s $p = \mathbf{0.01}$ Mid 20s < Early 30s $p = \mathbf{0.02}$ Early 20s = Mid 20s $p = 1.0$ |
| CAFs 400–449 | 5.68 | 2,117 | 0.004 | Early 20s < Early 30s $p = \mathbf{0.005}$ Mid 20s < Early 30s $p = \mathbf{0.05}$ Early 20s = Mid 20s $p = 1.0$ |
| CAFs 450–499 | 4.30 | 2,117 | 0.02 | Early 20s < Early 30s $p = \mathbf{0.01}$ Mid 20s = Early 30s $p = 0.54$ Early 20s = Mid 20s $p = 0.36$ |

Note: significant effects at $p < 0.05$ are bolded.

a function of RT distribution using CAFs (Heitz, 2014) for each age group separately (Fig. 3). Early 20s and Mid 20s made significantly more accurate Go responses in the first, fastest portion of the RT distribution (0–300 ms), while Early 30s made significantly more accurate Go responses somewhat later, between 300 and 500 ms.

3.3. ERPs

3.3.1. ERP amplitudes

Age effects were observed on P2 and P3 amplitudes (Table 3 and Fig. 4). Go P2 amplitude was significantly increased (more positive) in Early 30s compared to both Early 20s and Mid 20s.

Correlations between N2 and P3 amplitudes were significant in each age group (for the Early 20s, Go N2 and Go P3 $r(38) = 0.64$, $p < 0.001$, No-Go N2 and No-Go P3 $r(38) = 0.47$, $p < 0.01$; for Mid 20s, Go N2 and Go P3 $r(37) = 0.67$, $p < 0.001$, No-Go N2 and No-Go P3 $r(37) = 0.79$, $p < 0.001$; for the Early 30s Go N2 and Go P3 $r(39) = 0.47$, $p < 0.01$, No-Go N2 and No-Go P3 $r(39) = 0.52$, $p < 0.01$). In order to control for possible confounds, N2 Go and N2 No-Go amplitudes were entered as covariates in mixed design ANOVAs when testing age effects on P3. Both Go P3 and No-Go P3 amplitudes were significantly increased in Early 30s compared to Early 20s. There were no age effects on N1 or N2 amplitude.

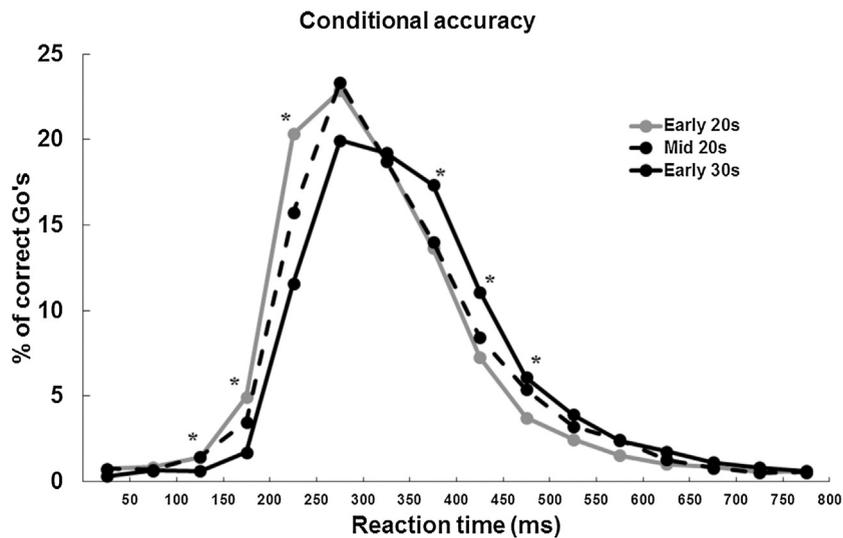


Fig. 3. Conditional accuracy functions (CAFs) plotting the percentage of correct Go responses as a function of reaction time for each age group separately; * $p < 0.05$.

Table 3

Statistics for amplitudes.

| | | <i>F</i> | <i>df</i> | <i>p</i> | <i>post-hoc</i> | | |
|----|-----------------------------|----------|-----------|------------------|--|--|--|
| | | | | | Go | No-Go | |
| N1 | age | 1.57 | 2,117 | 0.21 | | | |
| | condition | 0.77 | 1,117 | 0.38 | | | |
| | cond. × age | 0.26 | 2,117 | 0.77 | | | |
| P2 | age | 6.37 | 2,117 | 0.002 | Early 20s = Mid 20s $p = 0.99$ Early 20s < Early 30s $p = \mathbf{0.0003}^*$ Mid 20s < Early 30s $p = \mathbf{0.0003}^*$ | Early 20s = Mid 20s $p = 0.73$ Early 20s = Early 30s $p = 0.04$ Mid 20s = Early 30s $p = 0.02$ | |
| | condition | 0.12 | 1,117 | 0.73 | | | |
| | cond. × age | 1.60 | 2,117 | 0.21 | | | |
| N2 | age | 2.19 | 2,117 | 0.12 | | | |
| | condition | 18.48 | 1,117 | <0.001 | | | |
| | cond. × age | 0.05 | 2,117 | 0.95 | | | |
| P3 | age | 5.92 | 2,115 | 0.004 | Early 20s = Mid 20s $p = 0.04$ Early 20s < Early 30s $p = \mathbf{0.002}^*$ Mid 20s = Early 30s $p = 0.34$ | Early 20s = Mid 20s $p = 0.02$ Early 20s < Early 30s $p = \mathbf{0.008}^*$ Mid 20s = Early 30s $p = 0.89$ | |
| | condition | 223.50 | 1,115 | <0.001 | | | |
| | cond. × age | 0.53 | 2,115 | 0.59 | | | |
| | <i>Effects of covariate</i> | | | | | | |
| | N2 Go | 17.64 | 1,115 | <0.001 | | | |
| | N2 No-Go | 1.50 | 1,115 | 0.22 | | | |
| | cond. × N2 Go | 2.12 | 1,115 | 0.15 | | | |
| | cond. × N2 No-Go | 13.66 | 1,115 | <0.001 | | | |

Note: The comparisons significant at Bonferroni-corrected level ($p < 0.008$) are bolded and marked with *.

Significant main effect of condition was found for N2 and P3 ERP components due to overall larger No-Go amplitudes compared to Go amplitudes (Table 3 and Fig. 5). We did not find any significant age and condition interactions (Table 3).

3.3.2. ERP latencies

Age effects were found only for N2 latency onset (Table 4 and Fig. 4), where Early 30s had earlier No-Go latency onset compared to Early 20s, while differences in Go N2 latency onset did not reach statistical significance.

Significant main effect of condition revealed overall N2 latency differences in Go and No-Go condition. We did not find any significant age and condition interactions (Table 4 and Fig. 5).

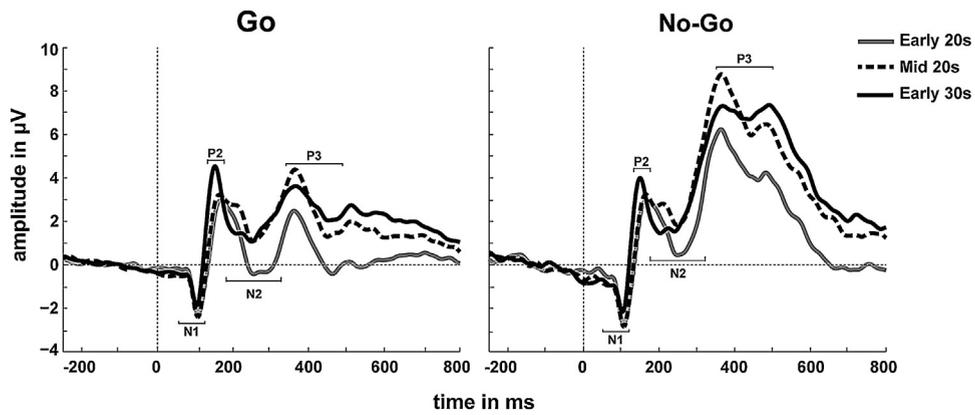


Fig. 4. Grand average ERPs for Go (left) and No-Go (right) trials showing main effects of age (positive is up).

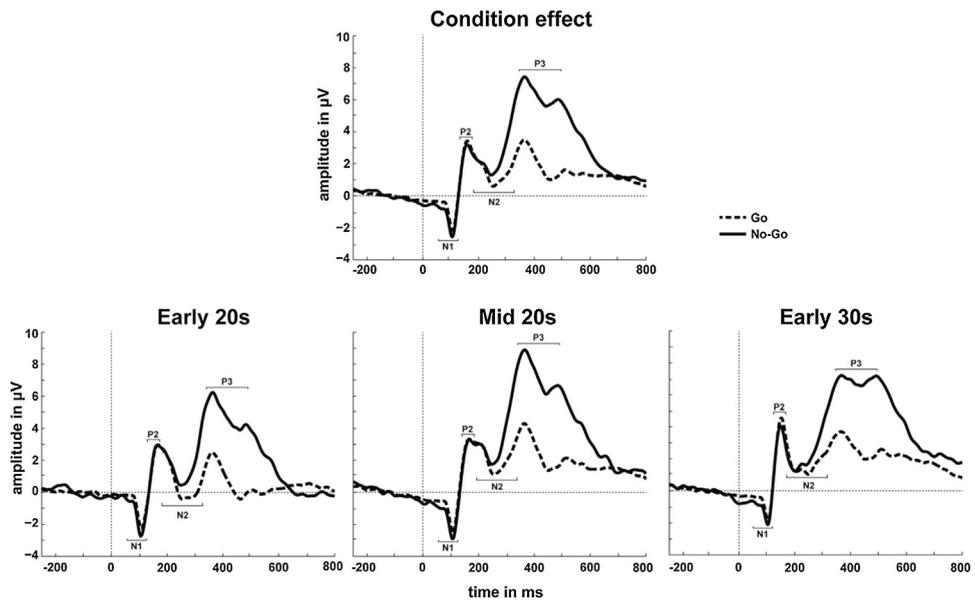


Fig. 5. Grand average ERPs showing condition effects across all participants together (upper panel) and for each age group separately (lower panel). Positive is up.

Table 4

Statistics for latencies.

| | | F | df | p | post-hoc | |
|----|-------------|------|-------|-------------|--------------------------------|-----------------------------------|
| | | | | | Go | No-Go |
| N1 | age | 2.74 | 2,117 | 0.07 | | |
| | condition | 0.24 | 1,117 | 0.63 | | |
| | cond. x age | 0.13 | 2,117 | 0.88 | | |
| P2 | age | 1.99 | 2,117 | 0.14 | | |
| | condition | 3.55 | 1,117 | 0.06 | | |
| | cond. x age | 0.71 | 2,117 | 0.50 | | |
| N2 | age | 3.84 | 2,117 | 0.02 | Early 20s = Mid 20s $p=0.63$ | Early 20s = Mid 20s $p=0.26$ |
| | condition | 8.01 | 1,117 | 0.01 | Early 20s = Early 30s $p=0.08$ | Early 20s > Early 30s $p=0.003^*$ |
| | cond. x age | 0.20 | 2,117 | 0.82 | Mid 20s = Early 30s $p=0.20$ | Mid 20s = Early 30s $p=0.06$ |
| P3 | age | 0.14 | 2,117 | 0.99 | | |
| | condition | 0.30 | 1,117 | 0.59 | | |
| | cond. x age | 3.14 | 2,117 | 0.06 | | |

Note: comparisons reaching Bonferroni corrected p -value < 0.008 are bolded and marked with *.

3.4. Correlations between personality, behavioral measures and ERPs

In Early 20s, higher total impulsivity scores were associated with lower (less positive) No-Go P3 amplitudes ($r(38) = -0.42$, $p < 0.01$), while higher psychoticism was associated and earlier Go P2 peak latency ($r(38) = -0.41$, $p < 0.01$).

In Mid 20s, both lower Go accuracy ($r(37) = -0.45$, $p < 0.01$) and higher number of premature responses ($r(37) = 0.41$, $p < 0.01$) were associated with higher (more positive) Go P2 amplitude. Higher psychoticism was associated with lower Go accuracy ($r(37) = -0.43$, $p < 0.01$) and No-Go accuracy ($r(37) = -0.41$, $p < 0.01$); higher neuroticism was associated with higher (more positive) No-Go P2 ($r(37) = 0.47$, $p < 0.01$) and Go P3 amplitude ($r(37) = 0.50$, $p < 0.001$), and higher attention impulsivity was associated with higher Go P2 amplitude ($r(37) = 0.44$, $p < 0.01$) and No-Go P2 amplitude ($r(37) = 0.50$, $p < 0.01$).

There were no significant correlations between ERPs and behavioral measures for Early 30s.

4. Discussion

The current study investigated behavioral and neurophysiological correlates of response inhibition during a visual Go/No-Go task in a large sample ranging from 19 to 42 years of age, comprised of three age groups: Early 20s, Mid 20s and Early 30s. When compared to Early 30s, the two younger groups showed lower accuracy on Go trials and shorter reaction times. Both Early 20s and Mid 20s made more premature, impulsive responses compared to Early 30s. On the neurophysiological level, we found increased P2 amplitudes in Early 30s compared to both Early and Mid 20s, whereas the P3 was increased in Early 30s compared to Early 20s. Also, the N2 latency onset was delayed in Early 20s compared to Early 30s on No-Go trials. Our results provide an important insight into the changes of behavioral and brain-based indices of response inhibition in a cross-sectional study during the transition into adulthood.

Response inhibition relies on the capacity to intercept a dominant, already prepared response. Successful performance on response inhibition tasks such as the Go/No-Go paradigm involves preparation for an upcoming response while keeping the task goals in mind as they are updated in a continuous manner, i.e., to respond as quickly as possible to the Go stimuli and to withhold responding the response to the No-Go stimuli (Aron, 2011). In behavioral measures, proactive inhibition is commonly reflected in the speed-accuracy tradeoff, whereby the accuracy is increased on trials with slower RTs (Heitz, 2014). Indeed, in our study, participants in the oldest group (Early 30s) had longer reaction times and higher accuracy in comparison to both younger groups whose responses were faster but less accurate. The differences in response strategies were further illustrated in the CAFs (Fig. 3), showing that the majority of responses from the two younger groups were in the lower part of the RT distribution. In addition, Early 20s and Mid 20s made more premature responses that were executed before the stimulus evaluation was complete, indicating premature, impulsive tendencies at this age. Taken together, this suggests that younger individuals engage in a different response strategy than more mature individuals. In many developmental studies maturity is not reached by the highest age of the participants included in the study such as adolescence (Segalowitz, Santesso, & Jetha, 2010), leaving a gap in our understanding of typical development during transitioning into adulthood. Age-dependent changes in behavioral correlates of response inhibition are more drastic before young adulthood, e.g. in school age children (Johnstone et al., 2005, 2007), but the present findings suggest that response strategies which would assure stable performance resembling adult levels may not be reached until the approximate age of 25. Impulsivity is often described as a tendency to act prematurely without foresight. These types of impulsive behavioral tendencies in adults have been associated with different harmful behaviors, such as substance misuse (Carter et al., 2010; Courtney & Polich, 2009), road traffic accidents (Bicaksiz and Ozkan, 2016), gambling (Hodgins & Holub, 2015) and overeating (Schag, Schonleber, Teufel, Zipfel, & Giel, 2013). Impulsive responding also characterizes behavior under acute intoxication and is associated with hyperactivity and antisocial tendencies (Marinkovic, Halgren, Klopp, & Maltzman, 2000). Inability to refrain from counterproductive behavior is maladaptive and it may negatively affect personal goals such as career or social relationships in early adulthood (Doremus-Fitzwater et al., 2010).

Previous studies have interpreted both N2 and P3 components as indices of motor inhibition, focusing mainly on the response control function that is engaged on No-Go trials (Huster et al., 2013). However, response demands are also conflated with attentional demands in such paradigms. Recent studies show that these two components reflect functionally dissociated performance-monitoring ERPs (Huster et al., 2013; Pires, Leitao, Guerrini, & Simoes, 2014). When a task requires ongoing monitoring of events, the N2 component may be elicited on trials requiring additional attentional control and potential need for behavioral response adjustments (Enriquez-Geppert et al., 2010; Smith, Smith, Provost, & Heathcote, 2010). The frontal P3 is related to attentional demands and novelty processing (Halgren, Marinkovic, & Chauvel, 1998; Marinkovic, Halgren, & Maltzman, 2001; Polich, 2007) but increased frontal P3 amplitude is also associated with increased response inhibition (Wessel & Aron, 2015).

It has been shown that the N2 amplitude and latency decrease with increasing age, starting at age 6–7 and reaching maturity in late adolescence (Jonkman, 2006), which suggests a more efficient engagement of cognitive control with age. In a study using an auditory Go/No-Go task, frontal N2 latencies decreased with age (age range 7–12 years) for No-Go stimuli (Johnstone et al., 2007). This may indicate increased optimization of the frontal performance-monitoring process with age on tasks with inhibitory demands. Studies of typical development of the visual P3 have shown that the P3 amplitude increases through childhood and adolescence and reaches maturity in young adulthood (Segalowitz et al., 2010). Jonkman (2006) examined N2 and P3 during a CPT-AX task comparing children (6–10 years) and young adults (19–23 years), and reported that the N2 latency decreased linearly with age, whereas the P3 amplitude increased with age, and in association with

improved task performance. Similar effects have been found in auditory tasks with age-related reduction in N2 latency and increase in P3 amplitude in frontal regions (Johnstone et al., 2005; Segalowitz et al., 2010). Our results are aligned with this evidence but extend age effects as the N2 latency is decreased and the P3 amplitude is greater in Early 30s compared to Early 20s. It is possible that N2 may serve as an index of the duration of the response selection process (Gajewski, Stoerig, & Falkenstein, 2008). Previous evidence associates a later frontal N2 component with more time necessary to evaluate ongoing task events during development (Jonkman, 2006; Lamm et al., 2006). Lower P3 amplitudes during development are often interpreted as a sign of immature response inhibition (Jonkman, 2006; Stige, Fjell, Smith, Lindgren, & Walhovd, 2007). A reduction in P3 amplitude has been correlated with poorer self-regulation in highly functioning college students with ADHD (Woltering, Liu, Rokeach, & Tannock, 2013), and the authors proposed that individuals with ADHD direct fewer resources toward response inhibition processes. Our findings are consistent with previous studies showing opposite patterns of No-Go N2 and P3 amplitude development. The N2 is largest in young children (ages 6–7) and it decreases with age, while the P3 amplitude starts to develop at around age 9 and continues to increase into young adulthood (ages 19–23; Jonkman, 2006). However, most studies involve younger participants (usually 18–23 year olds) while our study indicates that the P3 amplitude increase is observed well into mid 20s. Lamm et al. (2006) suggested that developmental changes in amplitudes may reflect changes in the regions of cortex giving rise to ERP components. Numerous studies indicate the involvement of the frontal regions, namely inferior frontal and anterior cingulate cortices during response inhibition (Aron, 2011; van Noordt & Segalowitz, 2012). These brain areas show a protracted maturation slope which continues until late adolescence or early adulthood (Fjell et al., 2012; Sowell et al., 2003; Westlye et al., 2010). Recruitment of inferior frontal and medial prefrontal cortices increases with age, suggesting that these areas continue to mature through adolescence and young adulthood and support more effective response inhibition control (Rubia, Smith, Taylor, & Brammer, 2007; Rubia et al., 2006; Vara et al., 2014). Frontal cortical networks undergo refinement in adolescence and early adulthood through synaptic pruning and myelination (Fjell et al., 2012; Schel et al., 2014; Sowell et al., 2003). These changes could have a direct effect on the efficiency of related cognitive functions, e.g., response inhibition, by enhancing functional communication between different brain regions (Luna & Sweeney, 2004; Velanova, Wheeler, & Luna, 2008).

Even though we did not find age differences in personality traits, significant associations between personality and ERPs were expressed differently among age groups. In the Early 20s group, higher total impulsivity was associated with lower No-Go P3 amplitudes. Studies with clinical samples such as ADHD have reported that reduced No-Go P3 is associated with performance deficits (Dimoska, Johnstone, Barry, & Clarke, 2003; Liotti, Pliszka, Perez, Kothmann, & Woldorff, 2005). In non-clinical samples, participants with high trait impulsivity similarly show poorer behavioral performance and reduced No-Go P3 compared to those with low impulsivity (Messerotti Benvenuti, Sarlo, Buodo, Mento, & Palomba, 2015; Ruchow et al., 2008; Russo, De Pascalis, Varriale, & Barratt, 2008), suggesting that impulsivity may be associated with impaired inhibitory control even in healthy individuals. Attention impulsivity is one of the second order impulsivity dimensions. It encompasses difficulties in maintaining sustained attention on monotonous tasks which may be due to a less efficient ability to inhibit task-irrelevant information or ignore additional information intake (Russo et al., 2008). It has been suggested that the P2 amplitude is related to evaluation of task relevant stimuli and performance optimization (Gajewski et al., 2008; Potts, 2004). Indeed, in our Mid 20s group, the Go and No-Go P2 amplitudes were associated with higher attention impulsivity and neuroticism. Individuals with higher neuroticism scores are more prone to attending to task-irrelevant stimuli which has been interpreted as having a hypervigilant attentional processing system (Eysenck, Derakshan, Santos, & Calvo, 2007; Fjell et al., 2012). Also, uncertainties about upcoming events or their performance may create considerable discomfort for more neurotic individuals (Gray & McNaughton, 2000). Higher neuroticism scores have been related to increased P2 and P3 amplitudes (Premkumar et al., 2015), and a larger feedback-related negativity (FRN) in response to uncertain feedback compared to positive or negative feedback (Hirsh & Inzlicht, 2008). Whereas personality traits were associated with both performance and ERPs in the two younger age groups in our study, no significant correlations were found for the Early 30s group. In general, studies of age differences in personality traits across young adulthood are scarce. In our study, age groups differed on behavioral performance and on ERP indices, suggesting that personality may modulate those measures differently and in an age-dependent manner during young adulthood.

We did not find age effects on N1 component, showing relatively similar early sensory ERPs in Early 20s, Mid 20s and Early 30s. This is not surprising since the level of perceptual load in our task was quite low as the stimuli consisted of two letters (X, Y). Early sensory components with latencies of <200 ms are estimated to be generated in the posterior cortex and the ventral visual stream for both Go and No-Go conditions (Bokura et al., 2001), reflecting the early stages of visual processing.

It has already been proposed that some frontal ERP components, e.g. Error Related Negativity (ERN) or Contingent Negative Variation (CNV), mature late, at least well into adolescence (16–18 years) (Bender, Weisbrod, Bornfleth, Resch, & Oelkers-Ax, 2005; Segalowitz et al., 2010). The present results extend previous studies indicating that the visual N2 and P3 components show slow maturation which is associated with poorer performance up to the age of 25. It is possible that the Early 20s are a transitional state of inhibitory network refinement, possibly due to the slow maturation of frontal cortical networks, which are not developed fully and may not be to be recruited effectively even at this age (Brown et al., 2012; Crone & Ridderinkhof, 2011).

In conclusion, we have found clear differences in behavioral performance coupled with neurophysiological underpinnings of response inhibition between Early 20s and Early 30s, confirming our hypothesis. Self-reported personality traits were associated with behavioral performance and ERPs in an age-dependent manner across young adulthood. This suggests that

the refinement of the motor inhibition network is still ongoing in the early 20s and is reflected in impulsive behavioral response tendencies. These findings are relevant to future clinical and nonclinical developmental studies and underscore the importance of including narrow age-range cohorts when investigating development of response inhibition in young adulthood.

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Conflict of interest

The authors declare no conflict of interest.

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