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Neuro-oscillatory mechanisms of intersensory selective attention and task switching in school-aged children, adolescents and young adults

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Abstract

The ability to attend to one among multiple sources of information is central to everyday functioning. Just as central is the ability to switch attention among competing inputs as the task at hand changes. Such processes develop surprisingly slowly, such that even into adolescence, we remain slower and more error prone at switching among tasks compared to young adults. The amplitude of oscillations in the alpha-band (~8–14 Hz) tracks the top-down deployment of attention, and there is growing evidence that alpha can act as a suppressive mechanism to bias attention away from distracting sensory input. Moreover, the amplitude of alpha has also been shown to be sensitive to the demands of switching tasks. To understand the neural basis of protracted development of these executive functions, we recorded high-density electrophysiology from school-aged children (8–12 years), adolescents (13–17), and young adults (18–34) as they performed a cued inter-sensory selective attention task. The youngest participants showed increased susceptibility to distracting inputs that was especially evident when switching tasks. Concordantly, they showed weaker and delayed onset of alpha modulation compared to the older groups. Thus the flexible and efficient deployment of alpha to bias competition among attentional sets remains underdeveloped in school-aged children.

Keywords

Alpha-band; Suppression; Cognition; Development; Multisensory; Cross-modal; EEG; Oscillations

Introduction

Information processing in the brain is capacity limited (Cherry, 1953; Broadbent, 1957; Treisman, 1960; Desimone & Duncan, 1995). To optimize behavior, therefore, it is necessary to selectively attend to information on the basis of behavioral objectives, whilst ignoring other potentially distracting goal-irrelevant information. Attention has been shown to be endogenously guided through top-down control mechanisms that rely on a network of frontal, parietal and subcortical regions (Mesulam, 1999; Corbetta & Shulman, 2002). At the same time, the goals of the individual are continually changing, requiring reconfiguration of task-set (and ensuing reorienting of attentional focus). Much like endogenously guided attention, task-switching requires top-down control mechanisms, involving a network of frontal, parietal, cerebellar and subcortical regions (Sohn *et al.*, 2000; Monsell, 2003; Wylie *et al.*, 2003; Shomstein & Yantis, 2004; Wylie *et al.*, 2004b).

Fundamental to both of these processes is the imperative to bias the brain's processing state toward the task at hand. Part and parcel of this is the need to filter out interfering stimuli and outdated stimulus-response mappings. Thus, one central aspect of top-down control involves ensuring that currently irrelevant stimuli and behaviors do not impinge upon the current task goals. The ability to successfully achieve this is central to everyday cognitive flexibility. An important question with implications for basic neuroscience as well as the understanding and treatment of developmental neuropsychiatric disorders involves when this cognitive flexibility emerges in typically developing children, and what brain regions and mechanisms are tied to the development of this ability.

There is evidence that relative to other brain processes, such as basic sensory and motor functioning, our ability to shift our attention and perform a new task develops over a more protracted timeframe, continuing to improve throughout childhood and adolescence (Cepeda *et al.*, 2001; Davidson *et al.*, 2006). At the same time, our ability to selectively filter out distracting information also becomes more efficient during childhood and adolescence (Enns & Girgus, 1985; Enns & Cameron, 1987; Pastò & Burack, 1997; Ridderinkhof *et al.*, 1997). Brain imaging studies also suggest that the developmental maturation of both selective attention and task reconfiguration processes is comparatively protracted relative to other brain processes, such as sensory and motor functions. For instance, there is evidence that fronto-parietal networks of attention continue to develop into early adolescence (Konrad *et al.*, 2005), and, similarly, prefrontal regions involved in task switching develop throughout childhood, with certain neural correlates of task switching showing continued development through adolescence (Crone *et al.*, 2006).

The prefrontal cortex has been widely implicated in inhibitory processes, such as inhibiting extraneous distracting stimuli in the case of selective attention or in inhibiting a pre-potent motor response (Casey *et al.*, 2000; Miller, 2000). Casey *et al.* (2000) suggested that the prolonged development of the prefrontal cortex in humans may parallel, and possibly underlie, the prolonged development of inhibitory processes in children and adolescents. This assertion is bolstered by structural neuroimaging studies showing that gray matter volume in the frontal and parietal lobes shows increases up to early adolescence (~10–12 years) followed by marked decreases in volume into young adulthood, whereas whole brain

white matter volume demonstrates a linear increase with age into early adulthood (Giedd *et al.*, 1999). Along similar lines, studies using diffusion tensor imaging (DTI) to measure long-range white matter tracts demonstrate increases in white matter integrity into early adulthood, suggesting continued age-related increases in myelination and axonal density in these tracts (Nagy *et al.*, 2004; Lebel *et al.*, 2012). These structural data suggest a period of increased long-range coupling between brain regions in adolescence. The implication is that indices of top-down cognitive control, reflecting the coordinated activity of distributed brain networks, show protracted developmental time courses partly as a result of the wiring up of these spatially disparate regions (Nagy *et al.*, 2004).

Neural oscillations have proven to be excellent indices of the allocation of top-down attention. For instance, amplitude modulations of oscillations in the alpha band (~8–14 Hz) have been extensively demonstrated to reflect the distribution of attention in paradigms manipulating visuo-spatial, both covert and overt (Worden *et al.*, 2000; Kelly *et al.*, 2009; Kelly *et al.*, 2010; Belyusar *et al.*, 2013), audio-spatial (Banerjee *et al.*, 2011), tactile-spatial (Haegens *et al.*, 2011; Haegens *et al.*, 2012), intersensory (Foxe *et al.*, 1998; Fu *et al.*, 2001; Gomez-Ramirez *et al.*, 2011; Foxe *et al.*, 2014; Mazaheri *et al.*, 2014), and visual feature-based (Snyder & Foxe, 2010) attention. There is, furthermore, increasing evidence that the deployment of alpha in a given neural population acts as a top-down suppressive mechanism of task-irrelevant activity (Kelly *et al.*, 2006; Jensen & Mazaheri, 2010; Romei *et al.*, 2010; Foxe & Snyder, 2011).

Recently, our group demonstrated differential alpha activity in healthy adults in a cued intersensory selective attention task (Foxe *et al.*, 2014). In this particular task, participants were cued to attend to either the auditory or the visual modality on a given trial, whereupon they performed a difficult detection task within the cued sensory modality. When participants were cued to switch to the visual modality, alpha amplitude decreased earlier and to a greater extent over parietal-occipital and frontal regions relative to when participants were cued to repeat the same task. We argue that neural oscillations in the alpha band play a central role in the precise titration of activity when two task-set configurations must be rapidly switched between, and competition among these tasks must be overcome for successful adaptive behavior. This work parallels work in non-human primates, such that local neural ensembles in prefrontal cortex exhibited increased alpha-band synchrony when these neurons represented a task that was to be switched away from, suggesting that competitive interactions in the prefrontal cortex among competing task-sets are mediated by alpha-band suppressive mechanisms (Buschman *et al.*, 2012).

These recent findings in human adults as well as non-human primates suggest that neural oscillations in the alpha band play a role in both selective attention and task switching, particularly one of inhibiting activity in neural populations that represent information extraneous to the locus of attention or the current task goals. Given the protracted development of the prefrontal cortex, and its putative role in inhibitory cognitive processes, an open question is that of the developmental trajectory of selective-attention-modulated oscillations in the alpha band.

Here we sought to characterize the development of oscillatory indices of intersensory attention in school-aged children, adolescents and young adults. We hypothesized that top-down attention-dependent modulations in alpha band oscillations would show a developmental trajectory that parallels that of the development of the frontal and parietal cortices, as well as the white matter tracts that likely coordinate activity among these regions. Due to the mounting evidence that alpha oscillations reflect a suppressive mechanism, we further hypothesized that reduced alpha modulation in younger participants would be accompanied by a reduced ability to suppress task-irrelevant stimuli as indexed behaviorally. To this end, we investigated cued intersensory attentional deployment and task switching in three age groups: children (8–12 years), adolescents (13–17 years), and young adults (18–34 years) while recording high-density electroencephalography (EEG).

Materials and Methods

Participants

Seventy-seven individuals participated in this study, ranging in age from 8 to 34 years. All participants verbally assented to participate in the research. All adults provided informed written consent prior to the study. For children, informed written consent was obtained from a parent or guardian, and verbal or written assent was obtained from the child. The study was approved by the institutional review board at the Albert Einstein College of Medicine, and all procedures complied with the Declaration of Helsinki. Participants received a modest fee (\$12/hour) for their efforts. All participants were screened for normal or corrected-to-normal vision as well as normal hearing. As assessed by a parent history (children and adolescents) or self-report (adults) screening survey, all participants were of age appropriate educational grade, did not use any psychoactive medications or have histories of head trauma, seizures, attention deficit disorder, psychiatric, learning, or developmental disorders, or have a first-degree relative with a developmental disorder constituted exclusionary criteria. Children and adolescents were administered the Wechsler Abbreviated Scales of Intelligence, and children with a full-scale IQ below 85 were excluded.

In line with previous developmental studies of executive control (Cepeda *et al.*, 2001; Konrad *et al.*, 2005; Crone *et al.*, 2006), participants were divided into three age groups: children of 8–12 years, adolescents of 13–17 years, and young adults of 18–34 years. Four participants were not included in the study, due to excessive EOG, muscle, and/or movement artifacts. Of these four participants, one belonged to the 8–12 age group, one to the 13–17 age group, and two to the 18–34 age group. This resulted in the inclusion of 73 total participants, with 23 participants in the 8–12 age group ($M = 10.23$, $SD = 1.38$, 12 females), 30 participants in the 13–17 age group (13–17 years, $M = 14.47$, $SD = 1.38$, 13 females), and 20 participants in the 18–34 years ($M = 24.5$, $SD = 5.40$, 10 females). A Chi-Square test was run comparing the distribution of males and females among the groups. The test indicated that none of the groups differed significantly in the proportion of males to females (Chi-Square(2) = 0.45, $p = 0.80$).

Stimuli and Task

A cued intersensory attention task was employed in which each trial consisted of an instructional cue, a brief intervening blank preparatory period, followed by a task-relevant second stimulus (S2) (see FIG 1). Instructional cues were used such that participants were directed only to respond to targets within the cued sensory modality (auditory or visual) and to ignore any stimuli in the uncued sensory modality. Variations of this task have been used extensively by our group (cf. Foxe *et al.*, 2005).

Visual stimuli were presented on a gray background. The cue stimulus consisted of simple gray line-drawings depicting either a pair of headphones ($\sim 3^\circ$ square visual angle, Weber contrast = -0.14) or a computer monitor ($\sim 3^\circ$ square visual angle, Weber contrast = -0.10) presented for 200 ms. These cue stimuli instructed the participant as to which sensory modality (auditory or visual) was to be attended when the subsequent S2 arrived. The S2 stimuli took the form of either a unisensory stimulus in the cued modality or a compound bisensory auditory-visual stimulus. For both cue conditions, the likelihood of receiving a bisensory S2 was 63% and the likelihood of receiving a unisensory S2 was 37%. Participants performed a go/no-go detection task on the S2 within the cued modality, responding with a button click on a computer mouse using the index finger of the right hand. Participants were cued pseudo-randomly on a trial-by-trial basis to attend for targets in either the visual or auditory modality in the upcoming S2 event. The likelihood of a task repeat or switch (i.e. attend to the same modality as the previous trial or switch to the other modality) was manipulated such that the probability of a given trial being a repeat rather than a switch trial was 70%. Repeat trials consisted of three possible types: single repeats (35%), in which the trial corresponded to the same task as the previous trial but not the trial prior to that, double repeats (23%), in which both the trial immediately prior and two-prior corresponded to the same task, and triple repeats (12%), in which the three prior trials were task-correspondent. After situations in which three repetitions of the same task occurred, a switch to the alternate task on the following trial was certain. For the purposes of the current analysis we collapsed across the repeat trial types in order to maintain sufficient trial numbers in both the behavioral and EEG data.

The auditory S2 stimulus consisted of two sequentially presented sinusoidal tones (100 ms duration; 60 dB SPL; 10 ms rise/fall) with a 5 ms interval between presentations. On non-target trials, the two tones were of identical frequency and participants were asked to withhold responses when no difference between the tones was detected. On target trials, the two tones presented were of different frequency. One of the two tones was 2000 Hz, whereas the frequency of the other tone was psychophysically titrated based on each participant's performance using a staircase procedure administered prior to the main task (described below). In the cue auditory condition, when subjects detected a frequency difference between the pair of tones, they were to respond with a fast button push.

The visual S2 stimulus consisted of a pair of Gabor patches (100 ms duration, 4.8° diameter, 0.25 cycles/degree) centered 5.2° to the left and right of the fixation cross. On target and non-target trials, the two Gabors were of different and identical orientation, respectively. As with the auditory stimuli, the orientation difference between the Gabors was psychophysically titrated for each participant, and in the cue visual condition participants

were instructed to respond to targets with a fast button push. The likelihood of receiving a target stimulus within the cued sensory modality was set at 20%.

The stimulus onset asynchrony (SOA) between the cue and target (i.e. the Cue-S2 period) was fixed at 1300 ms similar to previous applications of this paradigm (Foxy *et al.*, 1998; Fu *et al.*, 2001; Gomez-Ramirez *et al.*, 2007; Murphy *et al.*, 2014). A black fixation cross (subtending 0.3° vertically and horizontally) was presented in the center of the monitor throughout testing. The inter-trial interval (i.e., the S2–Cue period) was randomized (2000 to 3000 ms, square distribution) during which the fixation cross remained on the screen (see FIG 1 for a schematic of the paradigm).

Procedure

Participants were seated in a double-walled, darkened, sound-attenuated, electrically-shielded booth (International Acoustics Company, Bronx, New York). Visual stimuli were presented on a LCD monitor positioned 100 cm from the participant. Auditory stimuli were presented from a single speaker centered directly behind the monitor. Stimuli were delivered using Presentation software (Neurobehavioral Systems, Albany, CA). All participants underwent a staircase procedure at the beginning of testing for each of the two tasks. This procedure, known as the Up-Down Transformed Rule (UDTR) was used to rapidly equate performance across the two tasks and across participants (Wetherill & Levitt, 1965) before the beginning of the formal experimental sessions. The UDTR procedure employs different rules that converge on specific levels of accuracy. We used a 3-up, 1-down rule, meaning that, when a participant made three consecutive correct responses, we adjusted the stimulus one step harder and for any incorrect response, we adjusted the stimulus one step easier. This rule necessarily converges on an accuracy level of 79.4%. Importantly, the UDTR procedure employed only unisensory S2s. Thus, the acquired thresholds used for the remainder of the experimental session reflected performance on the unisensory target detection task only (i.e., without a task irrelevant stimulus in the uncued modality), and as such, left open the possibility of either task facilitation or interference with the addition of the second task-irrelevant stimulus.

During the experimental session, participants were instructed to respond as quickly and accurately as possible to targets within the cued modality and to withhold responses otherwise. Each participant completed approximately 20 blocks of 27 trials each, resulting in the collection of ~270 trials per cue condition. Of these, ~81 were switch trials and ~189 were repeat trials.

Behavioral Measurements

To obtain measures of behavioral performance, d-prime was calculated. The d-prime measure is widely used to assess the detectability of an imperative stimulus in a manner independent of a given individual's response criteria, or fluctuations thereof. d-prime is computed by taking into account the probability of correctly responding to targets when a target is present (termed a 'hit') and the probability of incorrectly initiating a response in the absence of a target (a 'false alarm') (Green & Swets, 1966). Hits were defined as correct button presses within the latency window of 200 to 2000 ms following the onset of the

second tone in the cue auditory condition, and following the onset of the Gabors in the cue visual condition.

In total, we compared 12 conditions in the behavioral analysis. First, a given trial was defined on the type of Cue presented (Cue Auditory, Cue Visual), next this trial could be characterized as a function of Trial Position (Task Repeat, Task Switch), and further the trial could be characterized by the presence or absence of a task-irrelevant stimulus in the S2 (Unisensory, Bisensory). Finally, in the case of the Bisensory S2 condition, the Response Congruity (Congruent, Incongruent) between the target and distractor added an additional experimental dimension. For example, in the case of a Cue Auditory, Repeat trial, the auditory stimulus could be presented alone or with a visual distractor. Further, in the case where a visual distractor was present, if the auditory target necessitated a "go" response, but the visual distractor indicated a "no-go" response, this was labeled an incongruent trial. An incongruent trial could likewise occur if the distractor signaled a go response but the target signaled a no-go response. It follows that congruent trials were characterized by either both the distractor and target signaling a go response or both signaling a no-go response.

The d-prime data were submitted to a $3 \times 2 \times 2 \times 3$ mixed model analysis of variance (ANOVA) with between participant factor Age Group (8–12 years, 13–17 years, 18–34 years), and within participant factors Cue (Cue Auditory, Cue Visual), Trial Position (Task Repeat, Task Switch), and S2 Type (Unisensory, Congruent, Incongruent).

EEG Acquisition and Preprocessing

Continuous EEG was recorded, with a band-pass of DC to 134 Hz, from 72 scalp electrodes (Biosemi ActiveTwo System: Amsterdam, Netherlands) at an analog-to-digital sampling rate of 512 Hz. Biosemi replaces the ground electrodes that are used in conventional EEG systems with two separate electrodes: Common Mode Sense (CMS) and Driven Right Leg (DRL) passive electrode. These two electrodes create a feedback loop, thus rendering them as references. EEG data were processed using MATLAB (The MathWorks Inc., Natick, Massachusetts). A subset of scripts from the FieldTrip toolbox (Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, the Netherlands. See <http://www.ru.nl/neuroimaging/fieldtrip>) as well as the EEGLAB toolbox (Delorme & Makeig, 2004) were applied for the analysis of the data. Specifically, independent component analysis (see below) was performed using EEGLAB, and the wavelet decomposition of the data was performed using FieldTrip, otherwise all other analyses of the EEG data were performed using in-house MATLAB scripts.

The offline analysis of the EEG data proceeded as follows. First, the recorded data were low-pass filtered at 40 Hz (Butterworth IIR, 23 dB/octave, zero-phase), high-pass filtered at 0.1 Hz (Butterworth IIR, 20 dB/octave, zero-phase), and re-referenced to the average of all electrodes. The data were next epoched from –1500 to 2500 ms around the onset of the cue stimulus. In order to retain as many trials as possible while minimizing artifactual contributions from blinks and eye movements, we employed the following artifact correction procedure. First, blinks and horizontal eye movements were detected within windows of –200 to 300 ms centered on the onset of the Cue and S2 stimuli (all S2 windows were aligned to the onset of the first stimulus in the sequence). Blinks and vertical eye movements

were identified in these windows using a rejection threshold of $\pm 100 \mu\text{V}$ in an EOG channel positioned at the nasion. Horizontal eye movements were identified using a rejection threshold of $\pm 80 \mu\text{V}$ in a bipolar channel computed from two EOG electrodes placed at the left and right outer canthi. Epochs containing data points exceeding one or both of these thresholds in either of the two time windows were excluded from further analysis. This step ensured that participants were attentively fixating during the presentation of the cue and S2.

Next, for each participant, an independent component analysis (ICA) was performed on the data, concatenated over all data epochs, using the *infomax* algorithm (Bell & Sejnowski, 1995) as implemented in the EEGLAB toolbox. Following the ICA decomposition, we used a two-step procedure to identify components reflecting oculo-motor activity. First, we computed the mutual information (MI) shared between the time-courses of EOG channels (one vertical EOG channel, and a bipolar horizontal EOG channel) and the component time-courses. Any component that exceeded a threshold of 3 standard deviations beyond the median MI was marked as artifactual. Second, the component topographies were manually inspected to ensure that the components automatically identified as EOG-related also presented close correspondence to topographies representing horizontal or vertical EOG-activity. All remaining components identified as EOG were removed, and the data were transformed back to sensor space.

Following the ICA errant electrodes were identified on a trial-by-trial basis, such that if an electrode exceeded a *z* score of 3 in 1) its variance, 2) its range, or 3) its mean, then it was considered bad. If a given trial contained more than 4 bad electrodes across the array of 72 channels, then it was discarded. Otherwise, bad electrodes were linearly interpolated using 3 to 4 nearest neighbors. Finally, over all scalp electrodes, a trial rejection threshold of $\pm 120 \mu\text{V}$ was used.

Time-Frequency Analysis

The analysis of EEG data focused on the preparatory period leading up to the S2 stimulus, and after the presentation of the Cue stimulus. This period has been extensively shown to exhibit robust modulations of alpha amplitude in tasks very similar to the current one (Foxy *et al.*, 1998; Fu *et al.*, 2001; Gomez-Ramirez *et al.*, 2007; Murphy *et al.*, 2014). Furthermore, the foci of differential alpha activity during audio-visual selective attention tasks have consistently been observed over bilateral parietal occipital regions. Thus, our main analysis focused on electrode locations over the left and right parieto-occipital scalp.

As an initial step in the visualization of oscillatory power tied to the deployment of attention to the auditory or visual modality, a wavelet time-frequency analysis was conducted on the full epoched data. This first step was used to visualize the distribution of intersensory attention effects across frequency and time in the event that one of the younger age groups exhibited a strikingly different pattern of effects, such as modulation of oscillatory activity in other frequency bands or within a different temporal window than that which has been observed in adults. This analysis utilized Morlet wavelets (3-cycles per frequency, 4–40 Hz in 1 Hz linear steps, 20 ms time steps).

The wavelet analysis suggested that the pattern of alpha power modulation across the age groups was generally in-line with the previous findings outlined above. That is, for each group a difference in the alpha power range emerged over the left and right parietal-occipital regions in the ~500 ms leading up to the S2 stimulus (FIG 2). In order to maximize the number of trials utilized in the analysis, we re-epoched the data into an 'early' (650–975 ms window after the cue) and a 'late' (975–1300 ms window after the cue). These shorter time windows allowed for the retention of many more trials, which was particularly important for Switch trials, which occurred infrequently (i.e., 30% of the time).

For both time windows, the re-epoched single-trial data were windowed rectangularly, zero-padded to a data length of one second for an interpolated frequency resolution of 1Hz, and submitted to a fast Fourier transform (FFT). Average power spectra expressed in decibels were then computed for each of the experimental conditions. As mentioned above, Repeat trials comprised 70% of the total trials relative to Switch trials. Substantial differences in trial numbers among conditions could lead to differences in the signal-to-noise ratio (SNR) and introduce artifactual differences between experimental conditions. In order to avoid this possibility, for each participant we matched the number of Repeat trials to the number of Switch trials by randomly drawing a subset of Repeat trials equal to the number of Switch trials for each participant, Cue condition, and time window. a $2 \times 2 \times 3$ mixed model ANOVA with within group factors Cue (Auditory, Visual) and Time (Early, Late), and between participant factor Age Group (8–12, 13–17, 18–34) indicated no significant differences in trial numbers among the age groups nor were there significant differences across the factors of Cue and Time (all $ps > 0.1$). Across the conditions and time windows the average number of trials for the 8–12 age group was 69.91(14.94), for the 13–17 age group it was 75.12(10.82), and for the 18–34 age group it was 81.06(28.74).

After equating for trial numbers for Switch and Repeat trials among the EEG epochs, we used all artifact free trials in the analysis of the EEG data, whether the trial included a behaviorally correct or incorrect response, to achieve adequate SNR for the analysis of the electrophysiological data. A concern might be that since both correct and incorrect trials were included, a higher proportion of incorrect trials in the youngest group might account for the reported differences in the pattern of preparatory alpha measures in this group (see Results). However, the proportion of incorrect trials (misses and false alarms) did not differ significantly between the child group ($M = 20\%$ of total trials included, $SD = 9\%$) and either of the adolescent ($M = 23\%$, $SD = 10\%$) or the adult groups ($M = 15\%$, $SD = 9\%$). In contrast, while incorrect trials were significantly greater for the adolescent group compared to adults, alpha modulation was comparable between these groups. Together, this strongly suggests that any observed statistical difference among the groups in the analysis of alpha power is not due to differences in signal-to-noise ratios resulting from different numbers of accepted trials or to differences in the proportion of behaviorally incorrect trials across the age groups.

For each of the two time windows, the average power in the 8–14 Hz range over a left and a right parietal-occipital group of electrodes (P3, P5, P7, P9, PO3, PO7, O1, and P4, P6, P8, P10, PO4, PO8, O2, respectively) was submitted to a $3 \times 2 \times 2 \times 2$ mixed model ANOVA with the between participant factor Age Group (8–12 years, 13–17 years, 18–34 years), and

within participant factors Cue (Cue Auditory, Cue Visual), Trial Position (Task Repeat, Task Switch), and Hemisphere (Right, Left).

The electrodes employed in the analysis were chosen *a-priori* based on the findings of previous research employing extremely similar experimental paradigms and methods (Foxe et al., 1998; Fu et al., 2001; Gomez-Ramirez et al., 2007; Foxe et al., 2014; Murphy et al., 2014) which have repeatedly found this type of alpha power modulation to be highly focused over parieto-occipital electrodes. In contrast to previous scalp EEG studies, MEG and intracranial studies have provided evidence of alpha biasing in the auditory cortex within the context of intersensory selective attention paradigms (Gomez-Ramirez et al., 2011; Mazaheri et al., 2014), suggesting that EEG is comparatively insensitive to neural generators of this signal in auditory cortex. Nevertheless, the data were inspected from all electrodes to ensure that important attentional biasing effects that might only be present in pediatric groups did not go unnoticed. There was no suggestion that this was the case.

Results

Behavior

The d-prime values across the conditions and groups are depicted in FIG 3A. The 8–12 and the 13–17 age groups exhibited poorer performance compared to the 18–34 group. This was indicated first by a significant main effect of the between groups factor Age Group ($F(2,70) = 3.79, p = 0.03$), and confirmed by follow-up independent samples t-tests such that the 8–12 age group ($M = 1.62, SD = 0.70$) and the 13–17 age group ($M = 1.57, SD = 0.53$) exhibited significantly lower overall d-prime as compared to the 18–34 group ($M = 2.03, SD = 0.58$) ($t(41) = -2.05, p = 0.04$, and $t(48) = -2.84, p = 0.007$, respectively). No statistical difference was evident between the 8–12 and 13–17 age groups ($p = 0.78$).

In addition to the main effect of Age Group, the ANOVA also showed a three-way interaction of $S2 \times Trial \times Age Group$ ($F(4,140) = 2.48, p = 0.04$). As is evident when the d-prime values are collapsed across the Cue conditions (FIG 3B), this interaction appears to be driven by a specific decrement in d-prime on Incongruent Switch trials in the 8–12 age group. To begin to disentangle this interaction, the data were first collapsed across Cue type, and, for each participant and S2 condition, the d-prime values on Switch trials were subtracted from Repeat trials yielding a "switch cost" measurement (Wylie & Allport, 2000; Wylie *et al.*, 2004a). Protected independent samples t-tests resulted in a significant difference in switch cost values for Incongruent S2 trials between the 8–12 ($M = 0.61, SD = 0.44$) and 13–17 ($M = 0.15, SD = 0.56$) age groups ($t(51) = 3.19, p = 0.002$) as well as between the 8–12 and 18–34 ($M = 0.19, SD = 0.61$) groups ($t(41) = 2.56, p = 0.01$). No other switch cost values across the S2 conditions differed significantly among the age groups (all $ps > 0.5$). Observation of the switch costs for both Cue Auditory (FIG 3C) and Cue Visual (FIG 3D) conditions shows a specific increase in the switch cost (i.e., Switch d-prime < Repeat d-prime) in the 8–12 age group on Incongruent trials, although this effect is numerically larger in the Cue Visual condition.

Overall, the oldest age group exhibited superior performance compared to the two younger groups. Furthermore, the 8–12 age group demonstrated particularly poor performance on

Incongruent Switch trials compared to the two other age groups (FIG 3B). This finding suggests that the youngest groups' performance was most hindered by the presence of an Incongruent distractor in the S2 when performing a task switch.

Across the groups, there was a main effect of Cue ($F(1,70) = 16.45, p < 0.001$), S2 ($F(2,140) = 36.14, p < 0.001$), and Trial ($F(1,70) = 128.51, p < 0.001$). These main effects were accompanied by a Cue $\times$ S2 $\times$ Trial interaction ($F(2,140) = 6.87, p = 0.001$). On observation of the d-prime data collapsed across the participant groups (FIG 4A), two patterns stand out from the data. First, Cue Auditory Incongruent trials resulted in a substantial decrement in performance, regardless of being a Switch or Repeat trial, and d-prime values on Unisensory Auditory and Congruent Auditory trials were also lower than their Cue Visual counterparts (FIG 4B). Second, while switch costs were observed in each Cue and S2 condition, on Unisensory trials, Cue Auditory trials exhibited a greater switch cost than Cue Visual trials, however, the opposite was true on Congruent and Incongruent trials (FIG 4C).

Given this apparent difference in the cost of switching among the Cue and S2 conditions, the switch cost (Repeat - Switch) was again computed for each of these conditions, collapsed across age group (FIG 4C). Protected paired t-tests comparing Cue Auditory to Cue Visual conditions for each of the S2 types indicated that on Unisensory trials, the switch cost was greater for the Cue Auditory condition compared to the Cue Visual condition ($t(72) = 2.56, p = 0.01$). Thus it was more difficult to switch from performing a visual task to performing an auditory task than the reverse when no distractor was present. For bisensory S2 trials, the comparison of switch costs among the Cue types in the Congruent and Incongruent trials, the switch cost was greater for the Cue Visual condition compared to the Cue Auditory condition ($t(72) = 1.71, p = 0.02$ and $t(72) = 3.05, p = 0.003$, respectively), indicating that the effect on performance when switching from an auditory task to a visual task was more detrimental than the reverse when the S2 contained a distractor.

Overall, participant's sensitivity was diminished on Cue Auditory trials relative to visual trials, particularly when the S2 contained an incongruent distractor. This suggests that for all age groups visual distractors were particularly disruptive to task performance compared to auditory distractors, an effect reminiscent of the so-called Colavita effect (Colavita, 1974; Koppen *et al.*, 2009) in which visual stimuli in many circumstances appear to dominate over and even extinguish the perception of simultaneously presented auditory stimuli. Interestingly, the Colavita-like effect was accompanied by a complex pattern of task switching effects, which we will return to below.

Electrophysiology

Early latency (650–975 ms post cue)

Overall Alpha power: Across the groups, overall alpha power (i.e., alpha power irrespective of other experimental factors) differed significantly ($F(2,70) = 17.60, p < 0.001$) such that both the 8–12 ($M = 5.18, SD = 2.52$) and the 13–17 ($M = 3.43, SD = 2.57$) age group exhibited higher alpha power than the adult group ($M = 0.28, SD = 3.15$) ($t(41) = 5.66, p < 0.001$, and, $t(48) = 3.87, p < 0.001$, respectively). Further, alpha power was significantly greater in the 8–12 group compared to the 13–17 group ($t(51) = 2.48, p = 0.02$).

Furthermore, a main effect of Hemisphere ($F(1,70) = 40.82, p < 0.001$) indicated that across the groups and experimental conditions alpha power over the parieto-occipital region of interest was greater for the right hemisphere ($M = 3.54, SD = 3.32$) compared to the left hemisphere ($M = 2.69, SD = 3.36$)

Task-modulated alpha power: The ANOVA in the early latency period revealed a main effect of Cue ($F(1,70) = 18.12, p < 0.001$) and a main effect of Trial ($F(2,70) = 14.05, p < 0.001$). These main effects were accompanied by an interaction of Cue $\times$ Trial $\times$ Age ($F(2,70) = 4.40, p = 0.02$). As an initial step in addressing this interaction, separate 2×2 repeated measures ANOVAs were run for each of the three age groups with factors Cue (Auditory, Visual) and Trial (Switch, Repeat), collapsing across the factor Hemisphere.

First, The ANOVA on the 8–12 Age Group showed only a main effect of Trial ($F(1,22) = 5.30, p = 0.03$) indicating that alpha power on Repeat trials ($M = 5.25, SD = 2.59$) was increased relative to Switch trials ($M = 5.11, SD = 2.46$). No other main effects or interactions reached significance.

Next, The ANOVA on the 13–17 Age Group indicated a main effect of Cue ($F(1,29) = 16.82, p < 0.001$) and an interaction of Cue $\times$ Trial ($F(1,29) = 7.41, p = 0.01$). Two approaches were taken to untangle the interaction of Cue $\times$ Trial. First, the difference between Cue Auditory and Cue Visual was computed for the Switch and Repeat conditions separately, and a paired t-test was computed for the Switch versus Repeat difference measures. This test indicated that Cue related alpha modulation (i.e., Cue Auditory alpha power minus Cue Visual alpha power) was significantly greater on Switch trials relative to Repeat trials ($t(29) = 2.72, p = 0.01$). Second, in order to determine whether one of the Cue conditions alone was driving this difference in Cue-related alpha modulation, two paired t-tests were run comparing Switch trials to Repeat trials within each of the Cue conditions (i.e., Cue Visual Switch vs. Cue Visual Repeat, and Cue Auditory Switch vs. Cue Auditory Repeat). These comparisons indicated that, while Cue Auditory Switch trials were not significantly different than Cue Auditory Repeat trials ($t(28) = 1.14, p = 0.26$), Cue Visual Switch trials ($M = 3.21, SD = 2.76$) were accompanied by significantly reduced alpha power compared to Cue Visual Repeat trials ($M = 3.44, SD = 2.64$) ($t(28) = -2.73, p = 0.01$).

Finally, the ANOVA on the 18–34 Age Group showed a main effect of Cue ($F(1,19) = 5.06, p = 0.03$) a main effect of Trial ($F(1,19) = 7.58, p = 0.01$) and a Cue $\times$ Trial interaction ($F(1,19) = 8.43, p = 0.009$). The same approach as that taken in the 13–17 Age Group was again used to disentangle the Cue $\times$ Trial interaction. This indicated that Switch trials were again accompanied by greater Cue-related alpha power modulation compared to Repeat trials ($t(19) = 2.90, p = 0.009$). Comparing within Cue conditions further indicated that while Repeat and Switch alpha power did not differ significantly on Cue Auditory trials ($t(19) = 0.49, p = 0.63$), on Visual trials this difference was significant, such that Switch trials ($M = -0.04, SD = 3.09$) were again accompanied by significantly reduced alpha power compared to Repeat trials ($M = 0.38, SD = 3.29$) ($t(19) = -3.67, p = 0.002$).

Next we sought to test the differences among the three age groups on these conditions. Given the significant differences in alpha-band activity between switch and repeat trials in

the two older age groups, driven by modulations within the Cue Visual conditions, the difference between Switch and Repeat Cue Visual trials was computed for each of the three age groups and independent samples t-tests were computed among the three age groups. There was no significant difference between the 8–12 age group and the 13–17 age group ($t(51) = 1.25, p = 0.14$), nor was there a difference between the 13–17 age group and the 18–34 age group ($t(48) = 1.45, p = 0.15$). However, the difference between the 8–12 age group and the 18–34 age group reached statistical significance ($t(41) = 2.62, p = 0.01$), indicating a larger difference between the Switch Visual and Repeat Visual conditions in the 18–34 ($M = -0.41, SD = 0.50$) age group compared to the 8–12 age group ($M = -0.08, SD = 0.32$).

Late Latency (975–1300 ms post cue)—This time-window represents the late anticipatory period immediately preceding the onset of the imperative S2 stimuli.

Overall Alpha power: As in the early latency window, overall alpha power was significantly different among the age groups ($F(2,70) = 15.81, p < 0.001$) such that both the 8–12 and the 13–17 age group exhibited higher alpha power than the adult group ($t(41) = 5.40, p < 0.001$, and $t(48) = 3.63, p = 0.001$, respectively). Further, alpha power was significantly greater in the 8–12 group compared to the 13–17 group ($t(51) = 2.25, p = 0.02$). A main effect of Hemisphere ($F(1,70) = 35.69, p < 0.001$) again indicated that alpha power over the right hemisphere ($M = 3.70, SD = 3.69$) was greater than that over the left hemisphere ($M = 2.83, SD = 3.78$).

Task-modulated alpha power: The ANOVA in the late latency period revealed a main effect of Cue ($F(1,70) = 45.11, p < 0.001$), and a main effect of Trial ($F(1,70) = 9.43, p = 0.003$). These main effects were accompanied by an interaction of Cue $\times$ Age Group ($F(2,70) = 3.12, p = 0.05$). To unpack this interaction, the difference in alpha power between Cue Auditory and Cue visual conditions was computed (i.e., Cue Auditory *minus* Cue Visual) for each of the age groups separately, and independent pairwise t-tests were then computed among the three groups. These tests indicated that while the difference in overall alpha power modulation approached significance when comparing the 8–12 ($M = 0.39, SD = 0.58$) age group with the 13–17 ($M = 0.70, SD = 0.60$) age group ($t(51) = -1.91, p = 0.06$), and this difference was significant between the 13–17 and 18–34 ($M = 0.32, SD = 0.59$) age groups ($t(48) = 2.24, p = 0.03$), it was not significant when comparing the 8–12 to the 18–34 age group ($t(41) = 0.42, p = 0.67$).

The relationship of alpha power modulation to behavior: A specific difference in preparatory alpha power modulation was found in the current study among the three age groups. Namely, in the early latency window, the 13–17 and 18–34 age groups demonstrated a significant difference between the Cue Visual Switch and Cue Visual Repeat conditions that was not present in the 8–12 age group, and a direct comparison among the age groups showed that the 18–34 age groups showed significantly greater modulation of alpha power between Cue Visual Switch trials and Cue Visual Repeat trials compared to the 8–12 age group. These differences among the age groups in alpha power modulation were accompanied by group differences in behavioral performance. That is, the 8–12 age group showed a greater switch cost compared to the two older age groups on trials that contained a

response incongruent distractor in the to-be-ignored sensory modality. Furthermore, this increased switch cost was numerically greater on Cue Visual trials (FIG 3D) compared to Cue Auditory trials (FIG 3C). These two parallel findings motivated a correlational analysis between the alpha power modulations that differed among the age groups (i.e., Visual Switching modulations) and the switch cost incurred during Visual Incongruent trials for which a similar age difference was found.

In order to assess this relationship, the difference in alpha power in the early latency window between Cue Visual Repeat and Cue Visual Switch conditions was computed for each participant (i.e., Visual Repeat *minus* Visual Switch) at the left and right sensor groups used in the primary analyses. Next, the switch cost on Cue Visual Incongruent trials was computed from the d-prime measures (Visual Incongruent Repeat *minus* Visual Incongruent Switch). These data were collapsed across age groups to assess the relationship of alpha modulation to behavior generally. As is apparent from the scatter plots in FIG 6, this analysis showed a significant negative correlation across the participants over the left parietal-occipital sensor group ($r = -0.29$, $p = 0.01$) but not over the right sensor group ($r = -0.08$, $p = 0.51$). In an additional exploratory analysis, the correlation between the switch-cost behavioral metric and alpha power modulation was computed at all sensor sites. As illustrated in FIG 6, significant clusters of negative correlations were found over left parietal and right fronto-temporal regions. Thus, those individuals who showed decreased alpha power in these regions on Cue Visual Switches relative to Cue Visual Repeats also demonstrated less of a decrement in performance on Switch relative to Repeat Cue Visual trials.

Discussion

Previous behavioral work has established that the executive functions of distractor filtering, task switching and response inhibition develop throughout early childhood, adolescence, and in certain cases even into young adulthood (Enns & Girgus, 1985; Enns & Cameron, 1987; Pastò & Burack, 1997; Cepeda *et al.*, 2001; Davidson *et al.*, 2006). Similarly, imaging research has demonstrated the protracted development of the prefrontal cortex – a region strongly implicated in a wide range of executive control processes (Goldman-Rakic, 1995). Activity in this region, as well as activity in the posterior parietal cortex, has been linked to the development of the aforementioned executive functions (Casey *et al.*, 1997; Casey *et al.*, 2000; Durston *et al.*, 2002). Additionally, long-range white matter tracts connecting these brain areas develop late into adolescence and early adulthood (Ashtari *et al.*, 2007; Lebel *et al.*, 2008; Asato *et al.*, 2010; Lebel & Beaulieu, 2011). Clearly these developmental changes in fronto-parietal circuitry are related to protracted maturation of executive functions (e.g., Casey *et al.*, 1997; Casey *et al.*, 2000; Durston *et al.*, 2002; Nagy *et al.*, 2004).

How these developmental changes impact the specific brain mechanisms involved in executive control processes remain largely unknown. The present study set out to gain insight into the development of dynamic neural processes related to selective attention, task switching, and distractor inhibition. Parallel work in healthy adults has linked oscillatory activity in the alpha band (8–14 Hz) to the suppression of distracting information in a top-down manner (see Foxe & Snyder, 2011 for review), and this activity is sensitive to task

switching contexts (Foxy *et al.*, 2014). The increasing evidence that the deployment of alpha oscillations acts to suppress task-irrelevant brain activity (Foxy & Snyder, 2011) suggests that oscillations in this frequency band are a prime candidate for one such mechanism. We therefore hypothesized that alpha power modulations during a cued intersensory selective attention task - previously described for healthy adults - would become more efficient over the course of development, and would be related to developmental changes in performance.

With regard to performance, we found clear evidence for increasing proficiency across development using this cued intersensory attention task. To be specific, children 8 to 12 years of age were far more hindered compared to adolescents and adults when switching tasks, and particularly so when this task contained an incongruent distractor. This falls in line with the previous behavioral work on task-switching and inhibitory control in children in this age range (Enns & Girgus, 1985; Enns & Cameron, 1987; Pastò & Burack, 1997; Cepeda *et al.*, 2001; Davidson *et al.*, 2006). Interestingly, while the youngest age group was indeed behaviorally poorer relative to the two older groups at switching when the S2 stimulus contained an incongruent distractor, an accompanying reduction in the switch cost in this age group was not evident when the S2 contained a *congruent* distractor. That is, one might predict that if the youngest age group was indeed failing to initiate a task switch on a proportion of trials, this group would show a relatively small switch cost on congruent trials in so far as the distracting stimulus signaled a response congruent with the target stimulus. As is evident in FIGs 3C and 3D, switch costs are highly similar among the age groups for both cue types except when the S2 contained an incongruent distractor, at which point the youngest group demonstrated the aforementioned increased switch cost. One possibility is that there is a specific deficit in this young group in resolving interference from the previous task. In a related set of findings, Hyafil *et al.* (2009) employed a visual task switching paradigm in which healthy adult participants were required to indicate the direction indicated by either a centrally presented isosceles triangle or a word superimposed on top of it. These investigators first found that while there was a general switch cost when switching among the triangle and word stimuli, there was a particularly exacerbated switch cost when an incongruent switch trial occurred after an incongruent trial performed on the other set of stimuli. Accompanied with this, Hyafil *et al.* (2009) reported that activity in the anterior cingulate cortex, as indexed by fMRI, modulated according to task switches versus repeats regardless of the congruency among the stimuli. Meanwhile, activity in the dorsolateral prefrontal cortex (dlPFC) demonstrated switch-related activity that was modulated by congruity, in so far as this region showed the greatest modulation on incongruent switch trials that followed an incongruent trial on the alternate task. These findings were interpreted by the authors as indicative of separable task-switching mechanisms, with the dlPFC playing a specific role in regulating and overcoming interference among competing task sets. These findings speak nicely to the present data in that they suggest that the youngest age group exhibits similar patterns of switching generally when compared to the two older groups, but when interference arises on a switch of task, this group is selectively impaired relative to the older groups. Our current findings suggest that attentional biasing by alpha power may play a role in resolving this interference. Moreover, when taking into account the findings of Hyafil *et al.* (2009), although highly speculative at this point, this suggests that the

functioning of mechanisms in the dlPFC or connectivity among this region with parietal and sensory regions may be key foci in the developmental differences reported here.

Electrophysiological measures of corresponding brain activity revealed robust alpha modulation over posterior regions in the 325 ms leading up to the onset of the S2 for all three age groups, such that alpha power was greater on Cue Auditory trials compared to Cue Visual trials. This is a well replicated finding (Foxe *et al.*, 1998; Fu *et al.*, 2001; Gomez-Ramirez *et al.*, 2007; Mazaheri *et al.*, 2014) and it has been interpreted as an active, top-down suppression of visual sensory processing when this modality is irrelevant on Cue Auditory trials. However, notable differences in task-relevant alpha power modulation were also found among the age groups. In the earlier latency window (650–975 ms post-cue), the youngest group did not demonstrate this difference among the cueing conditions (FIG 5), while in the two older groups this difference was already in evidence. When comparing Switch trials to Repeat trials at this latency, it became apparent that the early portion of the alpha modulation in the two older age groups was driven primarily by Switch trials. Thus, in the two older groups, alpha differentiated among the Cue modalities earlier on Switch trials. When this was probed further, it became apparent that this was driven by a *decrease* in alpha power on Cue Visual Switch trials rather than by an *increase* in alpha power on Cue Auditory Switch trials. This pattern of alpha power modulation replicates recently reported findings from our group (Foxe *et al.*, 2014).

Among the age groups the present pattern of oscillatory power modulation dovetails nicely with the behavioral findings. The youngest age-group performed the poorest overall, and the adults outperformed both of the younger age groups. The youngest age group, furthermore, showed a behavioral specific switch cost that was greater than the two older groups. This occurred on task-switch trials that were accompanied by a task irrelevant distractor (i.e., a tone or Gabor that was task-*relevant* on the previous trial). To be specific, this behavioral difference among the age groups was specific to switch costs incurred when only the target and distractor stimuli signaled incongruent responses (i.e., go/no-go or no-go/go). Thus, the youngest group showed poorer ability to selectively attend to one stimulus modality and ignore the other under more demanding situations (i.e., on task switches). If we accept the prevailing conceptualization that oscillations in the alpha band reflect the relative excitability of a cortical region, such that high alpha power reflects low excitability and vice versa, then the weak modulation of alpha in children on switch trials suggests an inability to get this process online as rapidly as the older groups. This in turn could contribute to the observed increased susceptibility to distraction by task-irrelevant stimuli. In line with this interpretation, there was a significant negative correlation between alpha power for Cue Visual Repeat versus Cue Visual Switch trials and behavioral switch cost for Cue Visual Incongruent trials. That is, those with lower behavioral switch costs also showed a greater reduction in alpha power on Switch relative to Repeat trials, suggesting that the strategic deployment of alpha is key to overcoming interference from distractors.

If alpha power is indeed indicative of cortical excitability as we and others have suggested (Jensen & Mazaheri, 2010; Foxe & Snyder, 2011), such that low alpha power reflects a state of active receptivity to afferent input and high alpha power a state of active suppression, then alpha power desynchronization over posterior-parietal cortices on cue-visual switch trials

perhaps reflects a top-down preparatory mechanism that is utilized to re-tip the scales among the two competing tasks. Interpreted as such, the desynchronization of alpha power over visual sensory areas reflects a reweighting of biased competition among two tasks performed in different sensory modalities. One possible result of immature fronto-parietal circuitry is the inflexible and or ineffectual deployment of alpha oscillations involved in the suppression of task-irrelevant activity. Our data show that in the youngest group, children showed a small but significant strategic deployment of alpha that was particularly weak on task-switches, after which the adolescent group demonstrates a very robust deployment of alpha power similar to that of adults, but this deployment was actually greater than in the adults. This hints at the possibility that alpha power modulation herein indexes a developmental trajectory whereby its instantiation is quite effortful in the youngest group and is readily but inefficiently deployed in adolescents relative to adults. Thus there is a pattern of increasing cognitive efficiency and flexibility pertaining to inhibiting irrelevant information (or alternately enhancing relevant information) throughout childhood.

Intersensory task-switching, asymmetrical switch costs and alpha modulation

In the behavioral data an interesting pattern of effects emerged that was present across the groups. When participants switched from the cue auditory condition to a cue visual trial that contained a distractor, the switch cost was reliably higher than when switching to the cue auditory condition and performing the task in the presence of visual distractors. Moreover, these greater switch costs in the cue visual conditions were observed when overall performance was greater on the cue visual condition. This pattern of switching effects is highly reminiscent of previous behavioral work investigating so-called asymmetrical switch costs.

Asymmetrical switch costs refer to situations in which, when switching between two tasks, switching to one task is more costly (i.e., greater reduction in response speed, more errors) than switching to the other task. Asymmetrical switch costs have been most thoroughly investigated using Stroop tasks (Stroop, 1935) in which a participant is asked to alternately name the color of a colored word or name the word itself (e.g., Allport & Wylie, 2000; Wylie & Allport, 2000; Yeung & Monsell, 2003). What is typically found on Stroop tasks is that while naming the printed word is relatively easy for participants even when the color of the printed word is incongruent (e.g., 'BLUE' printed in yellow ink), when participants are asked to name the color of the word, the word, if incongruent with the printed color, interferes greatly with performance.

Interestingly, when using Stroop stimuli within the context of task-switching tasks, switching to the word naming task is more costly than switching to the color naming task (Allport & Wylie, 2000; Wylie & Allport, 2000; Yeung & Monsell, 2003). Allport and Wylie (2000) interpreted this as the result of Task Set Inertia (TSI) referring to a carryover of priming from the previous trial. In this case, the 'easy' task could be considered the dominant task (i.e., the word naming task), and must be strongly suppressed (or the hard task strongly enhanced) to perform the hard, non-dominant task. Subsequently, switching back to the easy task after this task set has been strongly inhibited results in a situation in which this

suppression persists into the next switch trial and interferes with performance on the dominant but momentarily suppressed task.

Thus, there is strong evidence that the carryover of suppressed neural circuitry into a switch trial is a large component of the pattern observed in asymmetrical switch costs. In the present study, across participant age groups, the visual stimuli interfered to a greater extent than the auditory stimuli when these stimuli were task irrelevant and incongruent with the auditory stimuli (FIG 4B), yet when switch costs were evaluated, the visual task resulted in higher switch costs when this task was accompanied by a task incongruent auditory stimulus (FIG 4C). This pattern of effects is reminiscent of previously observed asymmetrical switch costs found within the visual modality (Allport & Wylie, 2000; Wylie & Allport, 2000; Yeung & Monsell, 2003). In this manner, the pattern of switch-related alpha modulations observed here and in Foxe *et al.* (2014) can be interpreted as follows. First, on auditory trials, alpha power is deployed over visual cortices equally on repeat and switch trials as the performance of this 'non-dominant' task, identified as such due to the strong degree of interference from the visual distractors, requires the strong instantiation of suppression in visual cortices to overcome this pre-existing bias. This suppression is carried through into switch visual trials resulting in the observed asymmetrical behavioral switch cost. Top-down preparatory biasing mechanisms act to increase cortical excitability in visual cortices on visual switch trials to overcome (with varying degrees of success) this suppression, reflected as decreased alpha power over occipital regions. On subsequent visual repeat trials this increased top-down biasing is no longer necessary since the base state of task asymmetry has been re-established. This relaxation of top-down control is in-line with theories that posit a system that tends toward the minimum biasing necessary to perform a task (e.g., Goschke, 2000).

Relating this to the differences observed here among the age groups suggests that while the youngest age group is able to apply the necessary suppression of the visual cortices via the deployment of alpha oscillations, the subsequent 're-tipping' of the scales back towards the visual modality occurs less efficiently. This is particularly apparent in FIG 5C. In the late time period, all three groups demonstrate highly similar alpha power modulation among switches and repeats. Furthermore, the alpha power difference in this later time period is dominated by the cued modality, and this difference is significant for each of the age groups. In contrast, in the time period preceding this, alpha power modulation differentiates among switches and repeats in the extent of the cue-related alpha power differences, but only for the two older age groups. This raises the possibility that the processes of modality biasing and task-set reconfiguration as reflected in alpha power modulation are somewhat decoupled from one another, with task-set reconfiguration preceding a more general modality biasing.

It is important to consider that in the present design, a visual cue was used to direct participants' attention to either the auditory or visual modality. A concern might be that integral to the cue auditory condition is an intersensory switch of attention (from the visual cue to the auditory S2 stimulus), a condition that is not present for cue visual trials. Reassuringly, results regarding alpha power modulation are highly comparable between studies employing either visual (Foxe et al., 1998) or auditory (Fu et al., 2001) cues on tasks otherwise nearly identical to the current one. Furthermore, behavioral evidence indicates that

at cue-target intervals similar to those used here an informative cue in one modality (e.g., the auditory modality) improves performance on a task in an alternate modality (e.g., the visual modality) (Turatto et al., 2002). Thus cognitive control mechanisms appear capable of placing the brain in a biased state towards any given modality regardless of the modality in which a cue is delivered.

Another concern might be that since both correct and incorrect trials were included in the analysis of the EEG data, a higher proportion of incorrect trials in the youngest group might account for different pattern of alpha in that group. However, proportion of errors did not differ significantly between the child group and either of the adolescent or the adult groups.

Implications for developmental neuropsychiatric disorders

Recently our group reported a lack of alpha power modulation in a group of children and adolescents on the autism spectrum (Murphy *et al.*, 2014). The paradigm in Murphy *et al.* (2014) was identical to the one employed here, and while a typically developing control group matched on age and performance IQ showed robust differences in alpha power between the Cue Auditory and Cue Visual conditions, the participants with a diagnosis of autism showed no statistical difference in alpha power across the two Cue conditions. A central question that follows is whether the lack of robust alpha modulation in the autism spectrum participants might be due to a delay in the developmental trajectory of these processes in autism. The age range of the participants in Murphy *et al.* (2014) was 9 to 16 years. The current findings suggest largely intact alpha power modulation is present within the context of intersensory selective attention in the youngest age group tested (8–12 years). This fact, taken in light of the relatively homogenous absence of alpha power modulation in the context of the intersensory selective attention task in an ASD cohort of a wide age range, suggests that the effects in the ASD group may not simply be reflective of a skewed developmental trajectory, but rather a phenomenon that might be stable over the lifespan in the etiology of this disorder.

Conclusion

The present study tracked the relationship of alpha power modulation to the deployment of intersensory selective attention and task switching from childhood through early adulthood. A well replicated finding is that alpha power is greater over parietal-occipital cortices on Cue Auditory trials compared to Cue Visual trials. Because alpha power has been strongly implicated as a top-down suppressive mechanism, the interpretation of this is that increased alpha power over visual sensory cortices when performing an auditory task reflects the suppression of distracting visual inputs. Here we found that this pattern is present throughout childhood, adolescence and adulthood, with the youngest group of 8–12 year olds showing robust alpha modulation in the 325 ms leading up to the onset of the target stimulus. In line with previous research, the 8–12 year olds were worse than the two older groups when switching tasks, specifically when the switched-to task was accompanied by an incongruent distractor in the irrelevant sensory modality. In an earlier latency window (650–925 ms post cue), however, the two older groups showed a larger difference in alpha power between Cue Visual and Cue Auditory trials on Switch trials compared to Repeat trials. No such difference was present in the data of the youngest group. On closer inspection this

switch related alpha power modulation was found to be driven solely by the Cue Visual condition. These findings point towards the protracted development of top-down oscillatory neural mechanisms that facilitate the reweighting of task-set configurations. These underdeveloped mechanisms could be a result of not-yet fully developed long-range connectivity between prefrontal, parietal, and sensory cortical areas.

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Research Highlights

- Selective attention to either the visual or auditory modality was examined in a group of participants ranging in age from 8 to 34 years of age while high-density electroencephalography (EEG) was recorded.
- Modulation of the amplitude of oscillations in the alpha band (~10Hz), a proposed mechanism for suppressing distracting sensory information was found to be present even in the youngest participants.
- Younger participants behaviorally showed greater distractibility when switching to a new task compared to repeating it.
- Specific patterns of alpha amplitude modulations followed this behavioral deficit in the younger participants, suggesting that functional cortical oscillations employed in task switching and distractor suppression develop into adolescence.

Figure 1. The task

From trial to trial, Participants were visually cued to attend to either an auditory stimulus (by the illustration of the headphones) or a visual stimulus (by the illustration of the computer monitor) in a pseudorandom fashion. Cue stimuli (200 ms duration) were 100% valid, meaning a target stimulus (S2) always contained stimuli in the cued modality. The S2 stimuli be presented alone or accompanied by a stimulus from the un-cued modality. The auditory stimulus consisted in two 100 ms tones presented in rapid succession, the first at 1300 ms after the onset of the cue stimulus followed by the second after a 5 ms gap at 1405 ms. The visual S2 consisted of two bilaterally presented Gabors, presented at 1355 ms.

Figure 2. Preliminary wavelet analysis

Preliminary wavelet analysis broken out by age groups. Time-frequency plots reflect the subtraction of all Cue Visual conditions from all Cue Auditory condition. Waveforms depict the time course in the frequency range of 8–14 Hz for the Cue Auditory condition (blue) and Cue Visual condition (red). All units are in decibels. Note the different y-axes on the waveform plots across the three age groups.

Figure 3. D-prime data

(A) D-prime data for all conditions and participant groups. Error bars reflect standard error of the mean (SEM). (B) D-prime data collapsed across the Cue Auditory and Cue Visual conditions. (C) Switch costs (Repeat *minus* Switch) for the Cue Auditory conditions. (D) Switch costs for the Cue Visual conditions. Here the 8–12 age group shows a marked difference from the other two groups on incongruent trials. Error bars reflect standard error of the mean.

Figure 4. D-prime data collapsed across the age groups

(A) All conditions collapsed across the three age groups. (B) D-prime collapsed across both the three age groups and Switch and Repeat trials. (C) Switch costs, computed as Repeat *minus* Switch (greater switch costs are more positive), collapsed across the three age groups. Error bars reflect standard error of the mean.

Figure 5. Alpha power modulation and effects of task switching

(A) Topographic representations of Cue modality alpha power modulation (Cue Auditory *minus* Cue Visual) in decibels for the three age groups, the two time windows, and Switch and Repeat trials. (B) Topographic representations of task-switching related alpha power modulation (Switch *minus* Repeat) for each of the three age groups, the two time windows, and the two Cue conditions. (C) Error bars depicting alpha power modulation for the three age groups, the two time windows, and Switch and Repeat trials. Power modulation values were computed from the average over the left and right parieto-occipital sensor groups. Error bars reflect the standard error of the mean.

Figure 6. Relationship of alpha power to behavior

Scatter plots depicting the relationship of alpha power modulation (Cue Visual Repeat *minus* Cue Visual Switch) to the switch cost on Cue Visual Incongruent trials over all age groups. Left and right scatterplot panels reflect the left and right parietal-occipital sensor groups, respectively. Far right: the same relationship computed for each EEG sensor. Red “x”s indicate a significant correlation at the $p < 0.05$ level. Color in the topographic map codes for the r value of the each correlation.