The neurophysiology of intersensory selective attention and task switching

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Recommended Citation
The neurophysiology of intersensory selective attention and task switching

by

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A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

2015
The manuscript has been read and accepted for the
Graduate Faculty in Psychology in satisfaction of the
Dissertation requirements for the degree of Doctor of Philosophy

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THE CITY UNIVERSITY OF NEW YORK
Abstract

The neurophysiology of intersensory selective attention and task-switching

by

Jeremy William Murphy

Advisors: John J. Foxe, Ph.D. and Sophie Molholm Ph.D.

Our ability to selectively attend to certain aspects of the world and ignore others is fundamental to our day-to-day lives. The need for selective attention stems from capacity limitations inherent in our perceptual and cognitive processing architecture. Because not every elemental piece of our environment can be fully processed in parallel, the nervous system must prioritize processing. This prioritization is generally referred to as selective attention.

Meanwhile, we are faced with a world that is constantly in flux, such that we have to frequently shift our attention from one piece of the environment to another and from one task to another. This process is generally referred to as task-switching.

Neural oscillations in the alpha band (~8-14 Hz) have been shown to index the distribution of selective attention, and there is increasing evidence that oscillations in this band are in fact utilized by the nervous system to suppress distracting, task-irrelevant information. In order to elaborate on what is known of the function of alpha oscillations as well as current models of both intersensory selective attention and task switching, I investigated the dynamics of alpha amplitude modulations within the context of intersensory selective attention and task switching in neurologically typical young adults. Participants were alternately cued to attend to
either the visual or auditory aspect of a compound audio-visual stimulus while high-density electroencephalography was recorded. It is typically found that alpha power increases over parieto-occipital cortices when attention is directed away from the visual modality and to the auditory modality. I report evidence that alpha oscillations play a role in task-switching (e.g., when switching from attending the visual task versus repeating this task), specifically as biasing signals, that may operate to re-weight competition among two tasks-sets.

I further investigated the development of these same processes in school-aged children and adolescents. While exhibiting typical patterns of alpha modulations relevant to selective attention, Young school-aged children (8-12 years), compared to older participants, did not demonstrate specific task switching modulation of alpha oscillations, suggesting that this process does not fully develop until late adolescence. Finally, children and adolescents on the autism spectrum failed altogether to exhibit differentiation of alpha power between attend-visual and attend-auditory conditions—an effect present in age and IQ matched controls—suggesting that ASD individuals may have a deficit in the overall top-down deployment of alpha oscillatory biasing signals. This could result in an inability to ignore distracting information in the environment, leading to an overwhelming, disordered experience of the world, resulting in profound effects on the both social interaction and cognitive development.

Altogether, these findings add to growing evidence that alpha oscillations serve as domain general biasing signals and are integral to our flexible goal-oriented behavior. Furthermore, the flexible use of these biasing signals in selective attention and task switching develops over a protracted period, and appears to be aberrant in autism spectrum disorder.
Dedication

This dissertation is dedicated to my family. Mom, your irrational optimism has always been an essential counterweight to my irrational pessimism. Thank you. Anne and Rachel, my big sisters, you’ve been there when I needed you and I can only hope you’d say the same of me. Colleen, my partner in life, I love you; I couldn’t have done this without you. And finally, to my Dad who taught me the beauty of knowledge.
Acknowledgments

Foremost, I have to thank my advisors, Drs. Sophie Molholm and John Foxe. They have put so much more time and effort into mentoring me than I could have asked for. I am so grateful for the time and energy they so graciously put into mentoring young scientists such as me. I can only hope to pass on this dedication to mentorship in my future endeavors. I’d like to also acknowledge the tutelage and friendship of several former post-docs and graduate students from the lab: Drs. John Butler, Hans-Peter Frey, Edmund Lalor, Simon Kelly, Ian Fiebelkorn, Manuel Mercier, and Ted Altschuler.
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General Introduction

We have all been faced with a situation in which maintaining our focus on an important aspect of our environment is extremely difficult due to other distracting events. Everyday examples abound. For instance, it can be quite challenging to read a book on the subway while two individuals have an animated conversation nearby. In this case, spoken language, an auditory signal, interferes with our ability to comprehend written language, a visual signal. In this instance, the conversation is distracting and it can feel effortful to tune the interlocutors out, nevertheless, if we consider the multitude of environmental stimuli that impinge upon our senses at any given moment (e.g., a droning air conditioner, a breeze across the forearm, the shifting of shadows cast by the sway of trees outside a window, and so on), we are actually quite adept at focusing on relevant environmental sources of information and ignoring others. I will argue that this prioritization of external sources of information is an essential feat performed by the nervous system, and understanding precisely the ways in which it is performed is central to our overall understanding of the brain in health and disease.

This, of course, is only one of the many elegant features of our nervous system, and without several other features in place, it could conceivably cripple our behavior. For instance, consider a hypothetical nervous system that prioritizes information in the environment, just like the ones we are equipped with, but lacks the ability to re-prioritize external information as circumstances change. That is, as adept as we are at ignoring, for instance, the car alarm out on the street, when the fire alarm in our apartment building is triggered - a stimulus perhaps similar in intensity, spectral content, and rhythmicity to the car alarm - we are able to draw our focus
These two quite indispensable features of our nervous systems constitute the central elements of the current work. Namely, these are the neurophysiological constructs of *selective attention* and *task switching*. This work will investigate these constructs within the realm of multiple senses. That is, I will examine selective attention and task switching when the stimuli competing for cognitive resources are auditory and visual in nature. This approach is motivated for reasons both empirical and methodological. Methodologically, the brain areas processing auditory and visual stimuli are by and large regionally distant from one another allowing one to broadly attribute brain electrical activity recorded at the scalp, which is comparably poor in spatial resolution compared to other measurements of brain activity, to one or another sensory region. Empirically, less is known about the interaction of multiple senses in the areas of both selective attention and task switching. In fact, much of the work in the latter half of the twentieth century on each of these topics has focused nearly exclusively on the visual modality. Understanding how these processes operate when multiple sensory inputs are at play – something that we encounter in the natural environment from each moment to the next – is central to gaining a full picture of these brain processes.

My approach will be as follows: I first ask how these two constructs interact within the confines of a putative mechanism of top-down suppression, namely the modulation of the amplitude of alpha oscillations (to be more thoroughly introduced below) in a group of neurologically typical young adults. Next I ask how these interactions might change through childhood, adolescence, and into young adulthood. Finally, I ask how these interactions might
diverge from 'normal' in children and adolescents on the autism spectrum, a heterogeneous neuropsychiatric disorder that is frequently accompanied by alterations in both selective attention and task switching.

In the text to follow I will review the previous investigations into selective attention and task switching with particular emphasis on work that has addressed these constructs at the intersensory level. Further, I will address selective attention and task switching as they relate to brain development. Finally, I will give a general overview of autism spectrum disorder (ASD), its phenotypic manifestations, the predominating theories of the etiology of the disorder and a justification for investigating intersensory selective attention and task switching in this population.

The aim of this general introduction is to give the reader the lay of the land in these overlapping areas of research in the hopes of clarifying the impetus for, not to mention convincing the reader of the merit of, the research that follows.

1. Selective Attention

1.1. In the beginning, a cocktail party

Early work in the mid-twentieth century that paved the way for contemporary investigations of selective attention emerged from a keen interest in the so-called 'cocktail party' phenomenon (not to mention other not quite so congenial incarnations of this phenomenon, such as radio communication between radar operators and pilots during WWII)(Cherry, 1953;
Broadbent, 1957; Treisman, 1960; Driver, 2001). Specifically, the cocktail party phenomenon refers to how, in a crowded situation with many conversations occurring simultaneously (e.g., a cocktail party) we are quite good at focusing in on one conversation and ignoring others. As a result of considering this problem, early brain scientists were faced with the following fundamental questions: first, to what extent are those surrounding, ignored conversations processed by the brain, and, second, what mechanisms allow us to prioritize these competing stimulus streams with such ease, and further what properties of the stimulus streams allow for their separability by these mechanisms?

In pioneering work on selective attention, to address the questions raised above, these researchers asked participants to repeat out loud (or 'shadow') a speech stream presented over one audio channel (e.g., the left speaker in a pair of headphones), while an alternate speech stream was presented to the non-shadowed ear. Initial findings indicated that very little information could be recalled about the non-shadowed, or un-attended stream (Broadbent, 1952; Cherry, 1953; Poulton, 1953; Spieth et al., 1954; Broadbent, 1957). For instance, participants failed to notice a switch by the speaker in the unattended ear from the English language to the German language (Cherry, 1953), and participants generally failed to identify reversed speech as being such. However, these participants were able to identify certain featural changes in the unattended ear, such as a shift from a male to female speaker, or a shift from speech to a sinusoidal tone (Cherry, 1953). Work in this area led to the highly influential filter theory of selective attention proposed by Broadbent (1957). This simple yet elegant theory proposed that all stimulus inputs to the brain are processed in parallel and with equal preference up to some 'pre-attentive' point. Then, based on some property or configuration of properties (e.g., a female
voice coming from the left headphone channel) of the attended stimulus, attention acts as a filter allowing for the more complex, and possibly serial, processing of the attended stimulus and the cessation of processing of the un-attended stimulus (Broadbent, 1957; Driver, 2001).

Broadbent’s filter theory of selective attention was further refined by Treisman (1960); 1969). Treisman developed a qualified version of Broadbent’s original filter theory. This account was motivated by auditory shadowing experiments intended to refine Broadbent’s filter theory. In a classic experiment, Treisman (1960) had participants shadow one speech stream at one ear while ignoring a stream in the other, unpredictably, the attended speech stream would switch to the unattended ear while the attended ear would suddenly be presented with what was just a moment ago the unattended speech stream. Participants were instructed to shadow only the stimuli presented to the unattended ear rather than following the once relevant stream over to the other ear. While participants by and large did not shift entirely to the opposite ear to follow the attended stream, participants often repeated one or two words from the formerly relevant speech stream now presented to the unattended ear. This suggested that Broadbent’s attentional filter may not operate in an all or none fashion. The intrusions from the unattended ear occurred primarily when a prose piece switched to the unattended ear rather than when using speech streams that approximated English but were nevertheless meaningless. This suggested to Treisman that within the context of the prose piece where an upcoming word has a limited range of possible identities, the threshold of activation for statistically probable words was temporarily lowered and as such, they were able to overcome an attenuation of the unattended stream. This led to a subtle yet very important shift in the way in which selective attention was thought to
operate. Now attention dynamically attenuates certain sensory representations while possibly enhancing others rather than entirely blocking out unattended representations.

The emerging picture of selective attention is one in which a few environmental stimuli are not singled-out for exclusive processing, but rather the routing of processing resources is flexible, and dependent on many factors including context, novelty, memory, not to mention the amount of information present in a given moment as popularized by Lavie as perceptual load (Lavie & Tsal, 1994). Treisman’s conceptualization of activation thresholds and selective attenuation directly informed emerging neurophysiological investigations of top-down selective attention. Indeed subsequent human psychophysical studies as well as progress in recording from awake behaving non-human primates led to a highly influential theory of attention, which, when juxtaposed with the work of Lavie, reads as an elaboration of her original theory. This theory, popularized by Robert Desimone and John Duncan, among others, is known as the biased competition model of selective attention.

1.2. The biased competition model of selective attention

As mentioned above, building on the early behavioral work and informed by studies of single unit recordings from awake, behaving non-human primates, an enduring organizing theory of selective attention (initially confined to visual selective attention) was put forth by Desimone and Duncan (1995), dubbed the ‘biased competition model of selective attention’. The title of this conceptual model is telling. First, beginning with the ‘competition’ aspect of the model, the idea is that different sensory representations compete for limited processing resources.
Dependent on which of these representations is most pertinent to the current task at hand, the brain ‘biases’ this competition in favor of one or another representation. The source of this biasing as well as the means by which it is executed remain two fundamental questions of systems neuroscience, and are central to the present work.

Computational biases in the brain can be divided into two flavors. Salient aspects of our environment (those that are bright, loud, sudden, etc.) capture our attention reflexively, in a bottom-up manner. The nervous system is thus predisposed to be biased towards certain stimuli in the environment, whether because allocating attention to these types of stimuli was evolutionarily adaptive or because certain stimuli are relevant in the long term (e.g., our names, which pop-out so nicely at cocktail parties). While a great deal of work has been done on the brain processes that allow for bottom-up biases, the present work is geared towards another type of biasing, that of goal-driven or top-down biasing. This type of biasing refers to instances in which attention is directed towards an aspect of the environment not necessarily because of its outward salience but because it is currently relevant to the attendee.

An increasingly clearer picture of biased competition in the nervous system began to emerge alongside the development of invasive single unit recordings in non-human primate visual cortices. The organizational cascade of visual processing became clearer throughout the latter half of the twentieth century. Generally, visual sensory processing is now known to be organized hierarchically such that simple features, such as the orientations of high-contrast edges in a scene are extracted early on, followed by increasingly complex processing stages, leading ultimately towards things like object identification (Felleman & Van Essen, 1991). This organization is accompanied by increasingly large receptive fields, such that the receptive fields
of V1 neurons may span 0.5 to 0.9 degrees of visual angle, while neurons in IT may have receptive fields spanning 12 degrees of visual angle (Moran & Desimone, 1985). The dawning awareness of these organizing principles of the nervous system made the concept of capacity limitation ever more pertinent. That is, as the receptive fields of these higher order visual neurons grow to encompass ever larger patches of space, both attentionally relevant and irrelevant stimuli will be ever more likely to occupy a single neuron’s receptive field. Thus, competition could be said to increase as one travels up the processing hierarchy. Based on this structural arrangement, a compelling argument could be made that top-down biasing signals operate throughout the processing hierarchy, essentially ‘tagging’ the relevant stimuli (or the irrelevant ones for that matter).

The concept of biased competition was classically illustrated in a study by Moran and Desimone (1985). While recording single units from awake, behaving monkeys’ visual area V4, ‘effective’ stimuli that optimally drove a cell’s response when presented inside the cell’s receptive field were presented along with ‘ineffective’ stimuli, that is, stimuli that elicited little to no response when placed inside the cell’s receptive field. The monkey’s task was to indicate if a test stimulus presented at a specific spatial location matched a sample stimulus presented 500 ms earlier at the same location. The authors manipulated the stimulus content of the attended spatial location, which was mapped to the receptive field of the recorded cell. When the monkey matched an effective stimulus presented alone in the receptive field, the cell responded robustly to both the sample and test presentation of this stimulus. Likewise, when the test stimulus was an effective stimulus and accompanied by an ineffective stimulus, the cell responded equally robustly. However, when the effective stimulus was presented in the receptive field during the
testing phase, but the animal was attending to the ineffective stimulus, the response of the neuron was strongly attenuated. Importantly, these responses could only be attributable to the behavioral goal of the animal, since the stimulus configurations between these two conditions were identical – only the task changed. Thus, in this case attention seems to act by attenuating responses to the unattended stimulus (rather than enhancing responses to the attended stimulus), and only appears in operation when there are competing stimuli sharing the same receptive field. Motter (1993) reported similar findings for areas V1 and V2 in addition to V4, suggesting that competition is a strong determinant of attentional biasing throughout the visual hierarchy.

The emerging picture is one in which competition, and the resolution of such, occurs at many stages of neural processing, from sensory input to motor output (Allport, 1993). In this sense the resolution of competition might be thought of as a central organizing principle of neural computation. This leads to three general questions that will be at the crux of the present work. First, how does the brain 'know' what to devote its limited resources to? Second, in the event that the brain 'knows' how it would like to parcel out its resources, how is this accomplished? Third, and highly pertinent to the current work, does competition among stimulus representations acquired through different sensory modalities operate similarly to unimodal contexts, and are the same brain areas that give rise to biasing signals in a visual-only context also responsible for biasing stimulus representations across multiple modalities? These questions are fundamental to the successful adaptation to the demands of our environment and changes therein.
1.3. What performs the biasing and where is it? Emerging consensus on a network of top-down control

Specific neural networks have been implicated in biasing the processing of sensory representations in a goal-oriented manner. Two well established networks can generally be categorized by their fronto-parietal interactions. First, a ventral fronto-parietal network that includes the temporo-parietal junction, anterior insula and the ventral frontal cortex, is right lateralized and has been implicated in exogenous orienting (Corbetta & Shulman, 2002). Second, a dorsal fronto-parietal network includes the frontal eye fields (FEF) and intraparietal sulcus (IPS) bilaterally, which in turn exert top-down modulatory influence upon sensory-perceptual cortices and are proposed to be involved in the preparatory orienting of attentional resources (Corbetta & Shulman, 2002; Szczepanski et al., 2010). Although these two networks are unlikely to operate independently, and have been shown to interact (Umarova et al., 2009), here, again, endogenous biasing processes are central to the work at hand, and as such I focus on the dorsal fronto-parietal network.

The neuro-architectural path traveled by top-down biasing signals to lower tier visual areas has not been entirely elucidated, but tracer studies in monkeys have revealed a broad cortico-cortical network of connectivity between monkey lateral intraparietal area – a region of monkey IPS that has been strongly implicated in the control of spatial attention (Bisley & Goldberg, 2003; Buschman & Miller, 2007; Gottlieb, 2007) – and all levels of the visual hierarchy, the FEF and the superior colliculus (Blatt et al., 1990; Cavada, 2001; Grefkes & Fink, 2005). Regions within the human IPS, and to some extent within the FEF, also contain
topographically organized representations of visual space, and are relevantly active during endogenous, covert spatial attention tasks (Hopfinger et al., 2000; Silver et al., 2005; Silver & Kastner, 2009; Szczepanski et al., 2010). Analysis of the BOLD time series during a cued spatial attention paradigm suggests that IPS activity precedes activity in lower visual areas by several hundred milliseconds during the cue-target interval of an endogenous attention task, and there is an evident cascade of activation from FEF to IPS, and from FEF and IPS to lower visual areas (Bressler et al., 2008; Lauritzen et al., 2009). These findings are reliant on the admittedly sluggish hemodynamic response, during which several iterations of feed-forward and feed-back activations have most likely occurred. They nevertheless point to a tiered system of attentional deployment. In accord with this contention, stimulation of monkey FEF at a level below that which would evoke a saccade has been shown to increase the gain of V4 neuron responses to visual stimuli (Moore & Armstrong, 2003) and to improve target detection (Moore & Fallah, 2004). Thus, interactivity between FEF and IPS, with FEF generally preceding IPS activation, results in subsequent top-down modulation of visual cortices.

1.4. What’s so special about visuo-spatial attention? Intersensory selective attention

Our understanding of the manner in which the different sensory modalities interact in the nervous system has made tremendous advances in the last few decades (Foxe & Schroeder, 2005). An abundance of work has investigated when, where, and how inputs from the different senses interact in the nervous system. Evidence has mounted in support of early convergence of multisensory inputs in sensory areas traditionally considered specific to a single modality
The emerging consensus is one in which multisensory interactions occur at the level of early afferent sensory input, and continue to occur at multiple stages of processing.

A central question in multisensory interactions pertains to selective attention. While arguably the first serious empirical work investigating selective attention began in the auditory modality (e.g., Cherry, 1953; Broadbent, 1957; Treisman, 1960), perhaps due to notable advances in visual sensory processing (e.g., Hubel & Wiesel, 1968; Felleman & Van Essen, 1991), as well as work around unilateral visual neglect following lesion (Mesulam, 1981), the field of selective attention subsequently leaned heavily towards investigations in the visual modality.

Yet, ultimately, when we consider everyday life, the senses are not experienced as modular sources of information. We rather experience the world as a rich multisensory tapestry. Information acquired from different senses can at times be complementary, such as viewing an individual’s lips and face while listening to him or her speak in a noisy environment. In other circumstances these multisensory sources may interfere with one another, such as talking on a cellphone while driving. Two fundamental questions arise when one considers the operation of selective attention in a multisensory context. First, since the prevailing conceptual model of selective attention is one of biased competition, to what degree are representations from different modalities subject to overlapping capacity limitations? And second, if competition for limited processing resources does indeed take place in an intersensory context, are the biasing signals
intended to resolve this competition generated by the same fronto-parietal network of endogenous attention that has been to-date investigated largely in visuo-spatial contexts?

In addressing the first question, an excellent anecdotal illustration of competition at the multisensory level comes inadvertently from one of the very first selective attention studies ever. That is in Cherry (1953), as a participant shadowed one speech stream in the face of an overlapping speech stream, he reported that, “…The subject reported very great difficulty in accomplishing his task. He would shut his eyes to assist concentration” (p. 976). We can all sympathize with this harried research participant. When we want to listen closely to a piece of music for instance, we often close our eyes. I would argue that mechanically blocking out visual input by closing the eyes is a form of biasing – no incoming visual information will detract from the auditory signal.

What about the empirical evidence for shared processing resources and ensuing competition among the senses? Regarding capacity limitation overlap across the senses, one manner in which such limitations have been probed is by the use of so-called attentional blink paradigms (Raymond et al., 1992). These paradigms typically have participants perform a detection task that involves the rapid, serial display of several non-targets intermixed with rare targets. If a second target stimulus is presented shortly afterwards (up to about 450 ms in Raymond et al., 1992), the probability of detecting this second target drops precipitously, suggesting that, due to capacity limitations, processing of the second target is either actively gated to avoid interference with the first target or this processing simply passively fizzles due to capacity overload.
These attentional blink paradigms have been used to investigate cross-modal capacity limitations by including target stimuli from multiple modalities (De Jong, 1993; Duncan et al., 1997b; Potter et al., 1998; Jolicoeur, 1999; Dell’Acqua et al., 2001). The results of these studies have been mixed. An initial investigation suggested a complete absence of an intersensory audio-visual attentional blink even when the same tasks, preformed within each modality, produced strong attentional blink-like effects (Duncan et al., 1997b). These findings were taken to suggest that the loci of capacity limitations exist most prominently in unimodal sensory cortices. On the other hand, a number of subsequent studies were able to produce audio-visual (Arnell & Jolicoeur, 1999; Jolicoeur, 1999), audio-tactile (Dell’Acqua et al., 2001 experiments 1 and 2), and visuo-tactile (Dell’Acqua et al., 2001 experiments 3 and 4) intersensory attentional blink phenomena using similar experimental approaches. Arnell and Jolicoeur (1999) were able to show that intersensory attentional blink effects were highly dependent on presentation rates, such that the magnitude of these effects increased as the rate of stimulus presentation increased.

Further behavioral evidence for intersensory competition comes from S1-S2 cueing paradigms, in which an initial cue (S1) indicates with some degree of certainty the identity of the upcoming imperative stimulus (S2) to which a response must be made. For instance, Turatto et al. (2002) conducted a comprehensive series of behavioral experiments in which the stimulus modalities (auditory or visual) of both the S1 and S2 stimuli were manipulated. Central to Turatto et al.’s findings was that whether a speeded detection task or a discrimination task was employed, a valid, informative S1 improved performance not only when the S1 was of the same modality as the S2 but also when it was of the alternate modality. This suggests that a cue from one sensory modality can be employed to guide endogenous attention towards another modality.
(e.g., in the case of a visual cue informing you to attend the auditory modality). Altogether, it
seems that cognitive control mechanisms are able to place the brain in a state that is biased
towards one modality over another in a goal directed manner. Interestingly, at the briefest
stimulus onset asynchrony (150 ms) between the S1 and S2, Turatto et al. (2002) found that
attention appeared to be momentarily exogenously pulled to the modality of the S1. It was only
at the longer SOAs tested (600ms and 1000ms) that participants demonstrated endogenously
guided behavioral benefits. This suggests a rough time course for the interaction of bottom-up
mechanisms that draw attention to the modality of a salient stimulus and top-down mechanisms
that utilize the implicit information of the cue in an amodal manner.

Centrally, when the brain must perform multiple tasks from different modalities either
simultaneously or in close succession to one another, there is degradation in performance
suggestive of capacity limitations. Further, informative cues from either stimulus modality can
be used to bias competing stimuli from different modalities. But where in the progression from
stimulus input to response output this competition takes place remains to be fully fleshed out.
Feed-forward intersensory convergence in early sensory cortices is now known to exist
throughout the sensory cortices (Foxe & Schroeder, 2005). Given such convergence, it may be
enticing to argue in favor of competition in early sensory cortices envisaged initially in the visual
modality by Desimone and Duncan (1995) such that afferent inputs from different
representations drive the same cell’s receptive field, and thus compete for capacity limitations.
However, early multisensory interactions in the cortex have been generally shown to be driven
by one sense (i.e., spikes are evoked), and modulated by another (i.e., the excitability state of a
Given neuronal ensemble is shifted higher or lower, perhaps by oscillatory inputs) (Lakatos et al., 2007; Schroeder & Lakatos, 2009).

Given what is known about these early multisensory interactions, it is likely that competition for processing resources across the senses is minimal in low level sensory cortices. Rather, intersensory competition is more likely to occur in higher level representations of space, particularly in the parietal lobe (discussed below); in task-set representations in the frontal and parietal cortices (discussed in section 2 of this introduction); or at the level of response selection. The level at which capacity-limited competition occurs, whether within or between sensory modalities is likely to be hugely dependent on the particular demands of a task as well as the stimuli involved.

Centrally though, the locus of competition is not *ipso facto* the prime target of top-down biasing signals. It seems more likely to be the case that one highly efficient means of biasing one cortical representation over another is to tilt the scales prior to their convergence on to a single receptive field. In the case of selecting a cortical representation in one sensory modality over another in an alternate sensory modality, biasing signals might be most effective in ‘unisensory’ regions prior to convergence on heteromodal cortical regions. Indeed, an added tenet of the biased competition model proposed by Duncan (Duncan et al., 1997a; Duncan, 2006) is that competition is integrated across several systems, such that once the representation of an object is favorably biased in one region, this bias will tend to spread to other processing stages in the hierarchy. In this manner, heteromodal salience maps of space could be subject to intersensory competition if the goal of the organism is to attend one modality over the other, while the ensuing biasing spreads via feedback to lower level ‘unisensory’ areas.
Human imaging (Haxby et al., 1994; Kawashima et al., 1995; Woodruff et al., 1996; Laurienti et al., 2002; Laurienti et al., 2003; Hairston et al., 2008; Mozolic et al., 2008; Langner et al., 2011), human electrophysiological (Hackley et al., 1990; Alho et al., 1992; Woods et al., 1992; Foxe et al., 1998; Foxe & Simpson, 2005; Foxe et al., 2005; Porcu et al., 2013), and primate electrophysiological (Mehta et al., 2000a; b) studies have provided evidence for both enhancement and suppression of activity in putative unisensory cortical regions during intersensory selective attention tasks involving pairings of audio-visual, audio-tactile, and visual-tactile stimuli.

Several imaging studies have shown that when attention is focused on one sensory modality in the presence of an irrelevant distractor in another sensory modality, activity in the task irrelevant modality decreases, suggestive of top-down suppression. This was initially shown in a positron emission tomography study by Kawashima et al. (1995) in which participants made both tactile shape and roughness discriminations. Relative to a baseline resting period, both striate and extrastriate visual cortices showed decreases in regional cerebral blood flow when participants attended the tactile modality, suggesting a state of inactivity or inhibition when the participants attended to the features of the tactile stimuli. Extending on this, Hairston et al. (2008) manipulated the difficulty of an auditory temporal order judgment task, and found that while the activation in auditory cortices was not significantly modulated by the difficulty of the auditory task, extrastriate visual cortices demonstrated increased deactivation as the auditory task was made more difficult, suggesting a top-down biasing mechanism that is engaged as the difficulty, and by extension processing resources necessary to perform the task, increases.
Attentional modulations of evoked potentials in the electroencephalograph (EEG) have been demonstrated for audio-visual (Foxe & Simpson, 2005; Karns & Knight, 2009) as well as audio-tactile (Karns & Knight, 2009) and visual-tactile (Karns & Knight, 2009) intersensory attentional pairings. These studies have demonstrated that endogenously guiding attention to one modality while ignoring another results in enhanced sensory responses in the attended modality and/or suppressed responses in the unattended modality. Complimenting these human scalp EEG recordings, non-human primate work has reported intersensory attentional modulations while recording throughout the visual hierarchy (i.e., lateral geniculate nucleus (LGN), V1, V2, V4, as well as multiple sites in the superior temporal sulcus, inferotemporal cortex (IT), and IPS) using multilaminar electrodes capable of spanning the entire extent of the cortical layers (Mehta et al., 2000a; b). Monkeys were trained to attend alternately to one modality or another while they were presented with streams of audio-visual stimuli. Mehta et al. (2000a) reported a “gradient” of attention, such that attentional modulations were largest over later visual processing stages (V4) and progressively smaller over earlier areas, with no apparent modulation found in the LGN. A similar temporal gradient of attentional modulation arose, with responses in IPS showing the earliest attentional modulations, followed by earlier visual regions. These findings along with elaborations on the cascade of attentional modulation using intersensory paradigms (Mehta et al., 2000b; Schroeder et al., 2001) again suggest the possibility of competition at higher order areas with a cascade of biased selectivity down to lower-tier unisensory regions in a feed-back manner.

While these previous studies have demonstrated attentional interactions when one sensory modality is favored over the other, in many cases these measurements may not reflect true endogenous attentional modulations as they could additionally include pre-attentive
multisensory interactions that are not due to top-down biasing *per se*. A number of highly influential unimodal endogenous attention studies in humans (e.g., Kastner *et al.*, 1999) and primates (e.g., Luck *et al.*, 1997) have shown attentionally driven shifts in activity in the absence of stimulation, during a “preparatory period” in which the participant has been cued to an aspect of the environment but no stimuli have yet been presented.

These attentional modulations in the absence of overt stimulation have been extended to intersensory selective attention designs. Using fMRI, Langner *et al.* (2011) visually cued participants to attend to a visual, tactile or auditory stimulus. Langner *et al.* (2011) found that cueing participants to one of these sensory modalities, in the absence of actual stimulation from said modality, resulted in baseline activity increases in the attended sensory regions, and corresponding deactivations in the unattended sensory regions. The authors further noted that the widespread activations/deactivations found in this intersensory experiment contrasted somewhat with unisensory paradigms in which more focal baseline modulations have been observed, suggesting that intersensory selective attention may be more systemically pervasive across a given sensory modality. Like Langner *et al.* (2011), Foxe *et al.* (2005) demonstrated that differential preparatory states are observable when a participant is visually cued to either the visual or auditory modality. In this case, broadband EEG measurements were employed to assess this preparatory activity, adding a much higher degree of temporal resolution. Intriguingly, in Foxe *et al.* (2005) the broadband activity in the preparatory interval was not suggestive of gain changes in early sensory cortices, but rather as shifts in activity in frontal and parietal cortices. This broadband EEG activity differentiated among the two cue conditions 400-600 ms after the presentation of the visual cue and prior to the onset of the audio-visual S2 stimulus at 1080 ms.
This sustained preparatory activity was greater on cue auditory trials over fronto-central regions and over parieto-occipital regions on cue visual trials. Centrally, the attentional modulations of the evoked potentials to the S2 as reported in Foxe and Simpson (2005), which used the same data as those in Foxe et al. (2005) do not show clear spatial overlap with the preparatory sustained activity reported in Foxe et al. (2005), suggesting that intersensory selective attention is manifested in a more complicated way than simple baseline shifts in early sensory cortices (although this cannot be ruled out as a piece of the overall process).

The studies reviewed here suggest that stimulus representations from different modalities compete for processing resources, and further that biasing mechanisms act to prioritize one modality over others in certain circumstances. Again, a central question is where and when the competition takes place, especially given that the original formulation of the biased competition model envisioned competition occurring at the single receptive field level of visually selective neurons. Treue and Trujillo (1999) proposed the ‘feature similarity gain model’ based on single cell recordings in primate area MT. Using coherent moving dot patterns, they found that attention influenced a given MT neuron’s tuning function in a multiplicative manner. That is, MT neurons that preferred movement in a given direction demonstrated multiplicative increases in firing across all motion trajectories rather than a sharpening of the direction selective tuning function. Important to the present discussion, attending to coherent motion outside the recorded neurons receptive field was influenced by the direction of the attended motion, such that response gain increases were evident when the attended motion outside the recorded neurons receptive field matched that of the preferred direction of the recorded neuron. This poses a problem for the initial formulation of the biased competition model. Here, properties of a
stimulus outside a cell’s receptive field influence this cell’s attentional response. Treue and Trujillo (1999) proposed that all dimensions of a behaviorally relevant stimulus are subject to attentional gain mechanisms beyond those that are strictly spatial in nature. This conceptualization could easily extend to selection among sensory modalities.

1.5. Top-down attention networks: Supramodal?

The evidence reviewed above favors competition among stimuli originating from different sensory modalities. Further, this competition is subject to top-down biasing signals. A central question then arises as to whether the same regions reviewed above are responsible for the biasing signals when resolving intersensory competition as when resolving intrasensory competition. Evidence surrounding this issue has come from imaging, electrophysiological, and neuropsychological investigations. Classically, this question was asked by Farah et al. (1989) who employed a Posner spatial cuing task using both visual and auditory exogenous cues alongside visual targets to test the overlap in the control of attention across the modalities. Crucially, participants were individuals with right parietal damage. Participant’s with damage in this area have been shown to exhibit a deficit in ‘disengaging’ attention, such that if a non-predictive visual cue is either exogenously presented in the ipsilesional hemifield or attention is endogenously guided there, responses to a subsequent target in the contralesional hemifield will be substantially slowed, as if attention is stuck in the cued region of space (Posner et al., 1982; Posner et al., 1984). Farah et al. (1989) proposed that if attentional control is at least partially supramodal then an invalid auditory cue towards ipsilesional space should result in similar
response time deficits for a visual target in contralesional space to those observed when a visual cue is used. The researchers found just this. This suggests that the parietal lobe contains representations of supramodal space that are partially responsible for disengaging attentional resources from one (supramodal) region of space and moving it to another.

Along similar lines, Shomstein and Yantis (2004) demonstrated using functional magnetic resonance imaging (fMRI) that shifts of attention to an auditory stimulus stream, and away from a visual stream resulted in increased activation in the right superior parietal lobule, left inferior parietal lobe, and the right medial frontal gyrus. Significantly, these same regions exhibited highly overlapping increased activation when participants switched attention to the visual modality and away from the auditory modality, suggesting again that these regions may generalize across modalities when it comes to attention shifting. Overlap among modalities (most prominently among the auditory and visual modalities) in the fronto-parietal network of top-down attention has been supported by additional human imaging evidence (Shomstein & Yantis, 2004; Smith et al., 2009; Langner et al., 2011) as well as in a human intracranial study (Molholm et al., 2006). The top-down control of attention may not be entirely supramodal, however. Banerjee et al. (2011) recording scalp EEG found that, while spatially cueing participants to the left or right hemifields resulted initially in overlapping topographies of oscillatory modulations in the alpha band (8-14 Hz, discussed in detail below) when participants were cued to either attend an auditory or a visual target, at later latencies in a preparatory interval just prior to the onset of the target, these topographies dissociated in a modality dependent manner, suggesting a role for both sensory-specific and supramodal mechanisms for spatial selective attention. This spatial dissociation is in line with what is known about projections to
and organization of the posterior parietal lobe (Grefkes & Fink, 2005) in which both modality specific and multimodal regions are found. Interestingly, the multimodal representations are for the large part retinotopically organized, suggesting that auditory information, which is coded initially in a definitively head centered coordinate system undergoes a transformation into largely eye centered coordinates (Stricianne et al., 1996; Cohen & Andersen, 2002; O'dhaniel et al., 2005). Similar multimodal maps have been observed in frontal cortices as well. For instance, Tark and Curtis (2009), using fMRI demonstrated that the human homologue of FEF spatially mapped the location of to-be remembered auditory stimuli. Strikingly, the FEF spatially mapped auditory stimuli presented behind the participant, where no saccade could be made, challenging the strict interpretation of this area as only coding retinotopic space. There is thus evidence for both modality specific and supramodal coding of space, and by extension, the control of attention.

1.6. Neural oscillations: Biasing mechanisms or epiphenomena?

A great deal of work has been done in outlining the regions of the brain that may give rise to biasing signals, but the nature of these biasing signals remains somewhat unclear. One proposed top-down biasing mechanism is accomplished by the modulation of the amplitude of oscillations in the alpha band (~8-14 Hz). Oscillatory activity in this frequency range, recorded as time-dependent rhythmic changes in the voltage at the scalp, was the first observation noted by Hans Berger upon the invention of the electroencephalograph (Berger, 1929). More recently, alpha band oscillations (~8-14Hz) have been implicated in the control and maintenance of attentional
allocation, particularly as an active suppressive mechanism (Foxe et al., 1998; Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Klimesch et al., 2007; Rihs et al., 2007; Foxe & Snyder, 2011). There remains some discussion as to whether alpha is an active mechanism of suppression or a passive, 'idling' state (see Palva & Palva, 2007 for a discussion of this issue), and it bares noting that the alpha band has been linked to other brain processes, most prominently working memory (Jensen et al., 2002; Sauseng et al., 2005). Furthermore, other oscillatory bands have been implicated in attention itself, such that different frequency bands may subserve different functions (Fries et al., 2001; Fries, 2005; Siegel et al., 2008). Within the alpha band, local alpha oscillations within a population have been shown to suppress downstream synaptic transmission, as this frequency is quite poor for membrane potential summation (Lopes da Silva, 1991; Fries et al., 2001; Bollimunta et al., 2011), while long-range coupling in the alpha band between distant neural populations may be vital to communication across distributed brain networks (Fries, 2005; Palva & Palva, 2007; Siegel et al., 2008; Doesburg et al., 2009).

An increasingly large body of evidence suggests the alpha band is uniquely related to attention. Sadaghiani et al. (2010) demonstrated that resting state hemodynamic fluctuations in the constituents of the dorsal attention network are correlated with fluctuations in alpha band power, and, further, the amplitude (Thut et al., 2006; Kelly et al., 2009) of these oscillations during the deployment of attention correlates with stimulus detection rates. Since attention-dependent alpha power is typically maximal over posterior cortices contralateral to ignored regions of space (Worden et al., 2000; Kelly et al., 2006; Thut et al., 2006; Rihs et al., 2007), oscillations within this band have been proposed to operate as a mechanism that gates
behaviorally irrelevant afferent sensory information. Romei et al. (2010), using repetitive transcranial magnetic stimulation (rTMS) over parietal and occipital locations, demonstrated that rTMS pulses within the alpha frequency range and not at frequencies just above or below it led to shifts in perceptual performance such that rTMS alpha induction over a given hemisphere led to decreased detection of targets in the contralateral visual field, interpreted as an induced suppression of contralateral space via the dorsal fronto-parietal network.

1.6. Intersensory oscillatory biasing signals

Just as early intersensory imaging studies reported deactivations of activity in sensory cortices when that sensory modality was unattended, intersensory electrophysiological studies have shown increases in alpha amplitude over scalp regions overlying unattended sensory cortices (Foxe et al., 1998; Fu et al., 2001; Gomez-Ramirez et al., 2011; Mazaheri et al., 2014). In a formative work, Foxe et al. (1998) employed a cued S1-S2 paradigm in which participants were visually cued by the words “BEEP” or “FLASH” to attend to the auditory or visual aspect of an audio-visual S2 presented 1085 ms after the cue word. Foxe et al. (1998) bandpass filtered the single trials around 8-14 Hz, rectified these waveforms, and averaged them. This method, termed temporal spectral evolution (TSE; Salmelin & Hari, 1994) allowed for the measurement of changes in alpha amplitude that were not necessarily phase locked to the cue stimulus but rather indexed amplitude shifts in the S1-S2 interval in ongoing oscillations. Over parieto-occipital scalp electrodes Foxe et al. (1998) found that as participants prepared to attend to the S2 stimulus, alpha power increased monotonically when attention was directed to the auditory
modality relative to the visual modality. That is, beginning at approximately 500 ms after the visual cue, the trajectories of the TSE waveforms diverged, such that alpha power was increasingly greater in the cue auditory condition relative to the cue visual condition. This divergence was found exclusively over parietal-occipital regions with a slightly rightward hemispheric lateralization. This finding suggests that alpha power modulations index the relative bias afforded to one modality over another. Two caveats make further interpretation of these results difficult.

First, the presentation of a visual stimulus like the visual word cue used in Foxe et al. (1998) results initially in a strong desynchronization of alpha power over parietal-occipital cortices that does not appear to be related strictly to endogenous attentional biasing (Vanni et al., 1997; Pfurtscheller & Lopes da Silva, 1999). It is thus difficult to ascribe the modulations of alpha on the intersensory task as the result of increased alpha amplitude during cue auditory task or as the passive return to baseline of alpha on the cue auditory condition alongside active desynchronization of alpha on cue visual trials. Importantly, Fu et al. (2001) later replicated the findings of Foxe et al. (1998), but used auditory cues to direct attention. In the case of Fu et al. (2001), parietal-occipital modulations in alpha power were again observed in the alpha band. This work indicated that, without visually-evoked alpha desynchronization from a cue stimulus, in the cue auditory condition, alpha power just prior to the onset of the S2 stimulus was statistically higher than in the pre-cue alpha power baseline period, suggesting an endogenously guided increase in alpha power. Importantly, on cue visual trials, a significant drop from baseline power was also evident, perhaps reflecting a release from tonic suppression following the cue.
The second caveat comes from the observation that in these initial audio-visual cueing studies, no clear modulation of alpha power dependent on the cued modality arose over cortices that could be said to reflect auditory processing. That is, alpha power increases over parieto-occipital regions could be said to be reflective of active suppression of the visual modality when attending the auditory modality, but there is no indication of the converse situation. The reason for this is likely methodological. Putative alpha generators in and around the primary auditory cortices would lie on the temporal plane. As such, pyramidal neurons (generally accepted to be the main neural sources of the scalp EEG record) oriented perpendicularly to the cortical surface would have to conduct through a much greater volume of cortex than their parieto-occipital counterparts. MEG is not susceptible to the resistivity of the skull and scalp as in EEG, and, given a focal tangential current source, the magnetic field is rotated 90 degrees relative to the EEG electrical potential allowing for a distribution of activity in auditory cortex directly over the temporal lobe (Huotilainen et al., 1998). With these things in mind, a MEG study using a very similar task to that of Foxe et al. (1998) demonstrated modulation of alpha activity over right temporal regions (Mazaheri et al., 2014). Interestingly, ‘auditory’ alpha modulations were localized to the right supramarginal gyrus rather than earlier auditory cortices.

Further evidence of alpha modulation in auditory cortex comes from a human electrocorticographic study in which recordings were directly from the cortical surface over the temporal lobe in patients undergoing testing prior to surgery for intractable epilepsy (Gomez-Ramirez et al., 2011). In this study of two patients, alpha amplitude was found to be higher when participants attended the visual modality in a continuous stream of audio-visual stimuli relative to attending the auditory modality. Thus, there is evidence of alpha biasing in the auditory cortex.
within the context of intersensory selective attention paradigms. A central question still remains surrounding the origin of these biasing signals.

1.7. Where do alpha oscillations come from?

As discussed above, alpha oscillations index certain cognitive processes, and there is evidence that they serve mechanistically as top-down biasing signals in the service of resolving competition. This prompts the following questions. 1) How are alpha oscillations generated? And 2) what neural sources generate them, both on a regional macroscopic scale and at the level of individual cell types? These questions have proven quite difficult to answer, but it is safe at this juncture to say that oscillations in the alpha band are not a single entity, but are manifested throughout the cortex and in subcortical structures, at times serving different functions in different regions.

There is evidence that alpha oscillations are generated by thalamo-cortical interactions (Lopes da Silva & Storm van Leeuwen, 1977; Lopes da Silva et al., 1980; Steriade et al., 1993; Steriade, 1997). Yet there is also evidence that these oscillations can be generated solely within the cortex (Lopes da Silva & Storm van Leeuwen, 1977; Lopes da Silva et al., 1980; Bollimunta et al., 2008; Bollimunta et al., 2011).

Lopes da Silva et al. (1980), recording from both thalamic and cortical locations in dogs, statistically partialled out the influence of specific thalamic nuclei on the coherence in the alpha band between two visual cortical locations. This resulted in decreased coherence between the two cortical sites, suggesting that the thalamic nuclei, specifically the pulvinar and LGN, play a
role in the maintenance of alpha. The coherence of the cortical sites, however, remained high even after the elimination of the thalamic influence, suggesting that alpha is partly reliant on cortico-cortical interactions. Centrally, the effect of partialing out the pulvinar activity was much more dramatic than this effect for the LGN, further suggesting an important role in the pulvinar in thalomo-cortical alpha oscillations.

Further early evidence for an intracortical source of the alpha rhythm came again from recordings from the visual cortices of dogs. Lopes da Silva and Storm van Leeuwen (1977) found a phase reversal in the alpha band between electrodes oriented perpendicular to the cortical surface. While results varied among the three dogs tested, most showed an approximately 180 degree phase reversal of alpha when transitioning from cortical layer 1 down to cortical layer 6, with the most abrupt phase shift occurring near cortical layer 5, suggesting that this layer is the foci of alpha activity. More recent work in awake behaving non-human primates, recording neuronal activity across cortical laminae as well as coherence among different brain regions has shed some light on the generation of alpha and the effects of selective attention on alpha power across different areas (Bollimunta et al., 2008; Bollimunta et al., 2011; Buffalo et al., 2011; Saalmann et al., 2012; van Kerkoerle et al., 2014).

Bollimunta et al. (2008) recorded local field potentials and multi-unit activity in awake, behaving macaques. The monkeys performed an auditory discrimination task while neuronal activity was recorded from multi-contact laminar electrodes placed in visuo-cortical areas V2, V4 and IT. The laminar electrodes allowed the researchers to assess the relative contribution of each cortical layer to oscillations in the alpha range. In V2 and V4, alpha currents were detectable throughout infragranular, granular and supragranular layers. Granger causality
measures across these regions suggested that an infragranular source (layer 5) was driving alpha oscillations in the overlying regions, suggesting oscillations in this layer may serve as a local pacemaker for alpha throughout a cortical column. Surprisingly, this pattern did not hold in area IT, where the major driving source appeared to originate from supragranular layers. Moreover, alpha amplitude in V2 and V4 was positively correlated with performance on the auditory discrimination task in line with the idea that alpha serves as a suppressive mechanism for task-irrelevant stimuli. On the other hand, in IT this correlation reversed, such that higher alpha amplitude in IT was associated with poorer auditory performance. The findings of Bollimunta et al. (2008) are suggestive of differential roles of alpha in different regions of the visual hierarchy. These findings were further elaborated by Mo et al. (2011), who again found greater alpha power in the supragranular layers of IT to be related to better performance on a visual task. Alternately, the reverse was found to be true in V1, where decreased alpha was associated with better performance on the visual task (Bollimunta et al., 2011). The strongest sources of alpha in V1 appeared to originate from layer 4C and layer 6, and both of these layers exhibited coupled alpha activity with the LGN.

In cats, there is additional evidence that a subset of thalamo-cortical neurons fire bursts in the alpha range (Hughes et al., 2004; Hughes & Crunelli, 2005; Lörincz et al., 2008), thus a portion of the alpha rhythm could be driven by these bursting projection neurons that synapse on the granular layers of V1. The activity of this subset of LGN neurons can be modulated by activating or inactivating the metabotropic glutamate receptor, mGluR1a, which, importantly, is a postsynaptic receptor of cortico-thalamic feedback projections (Hughes et al., 2004). Specifically it was found that activation of mGluR1a receptors led to alpha rhythms in these
thalamo-cortical neurons. In recordings from slices of cat LGN, Lörincz et al. (2008) found that alpha oscillations in these cells can also be induced by the activation of muscarinic acetylcholine receptors. Thus, this subset of thalamo-cortical neurons appear to elicit alpha oscillatory burst activity in a manner that is dependent on glutamatergic projections from the cortex as well as cholinergic input from, presumably, the brainstem.

Using these two different neuromodulatory routes to the generation of thalamic alpha activity, Vijayan and Kopell (2012) developed a model of thalamo-cortical alpha oscillations. Vijayan and Kopell (2012) found that, partly due to the interaction of reticular nucleus cells, non-alpha bursting thalamo-cortical neurons fired in phase with their alpha-bursting counterparts when the muscarinic acetylcholine receptor drove this alpha activity. When this same activity was driven by the metabotropic glutamate receptors, the non-alpha-bursting thalamo-cortical neurons demonstrated no organized phase relationship with the alpha-bursting cells. According to Vijayan and Kopell (2012) these differential effects may allow alpha to play two distinct functional roles: one in which activity from distracting stimuli could be suppressed, and one in which feed-forward activity could be organized into temporal chunks.

It remains clear that a great deal of work still remains to be done regarding the functions and sources of the oscillations in the alpha band. Ultimately, more invasive work in non-human primates, recording multiunit activity and local field potentials simultaneously across different areas will be central to illuminating our understanding.

1.8. Interim Summary
Thus far I have focused on what is known about endogenous selective attention, with a particular emphasis on intersensory attention. In general, I have discussed top-down intersensory attention within the bounds of the biased competition model. I reviewed evidence that there is in fact competition for processing resources across the sensory modalities, as well as evidence that this competition can be biased in a top-down manner. A fundamental challenge to the classic biased competition model involves evidence for competition between stimuli that do not have traditional, overlapping receptive fields in unisensory cortices. This implies that competition occurs at the level of heteromodal salience maps of space, perhaps in and around the IPS. Alternately, intersensory biased competition could arise if competition and biasing arises for features beyond just spatial proximity, as suggested by Treue and Trujillo (1999).

Furthermore, I have introduced a candidate biasing mechanism: the alpha rhythm. There is evidence that alpha is deployed to regions of cortex that are task-irrelevant and serves as a suppressive mechanism. In spite of a large amount of empirical evidence that alpha indexes a biased attentional state, the cellular and interregional properties producing and manipulating this rhythm remain poorly understood. Nevertheless there is evidence that alpha relies on both intracortical as well as thalamo-cortical interactions for its instantiation, and there is the added prospect that alpha at times may be utilized by the nervous system to organize temporally coherent perceptual windows, while in other circumstances it is used to gate processing of task-irrelevant stimuli.

Implicit so far has been the idea that we can consciously move our attention from one aspect of the environment to another and from one task to another. This ability is generally termed task switching, and I will discuss it in the next section. Specifically, like selective
attention, there is evidence that task switching is subject to competitive interactions, which may be resolved through top-down fronto-parietal biasing signals.

2. Task switching

Task switching refers to our ability to successfully perform one task and then subsequently shift to an alternate task and perform that task successfully. In everyday life, we perform task switching with such ease and grace that we are rarely aware of it. Take for instance a situation in which an individual is frantically typing her dissertation. At an unexpected moment, 20 degrees of arc to the left, this individual's smart phone indicates with a trisensory cue (i.e., an auditory “ding”, a flash of an indicator light, and a vibratory buzz) that a text message has been received. This individual, being a doctoral candidate, is of (relatively) typical neurophysiological functioning, and as such she seamlessly switches her gaze and posture towards the phone and away from the computer, picks up the phone, reads the text, and rapidly types out a response on the touchscreen. Centrally, her prior task does not bleed into the current one. She does not respond to the text message with something like, “In a classic study by Treisman et al....”, but rather has rapidly shifted to the subject of the text message. She further has not only switched her line of thought, but she has rapidly switched the motor commands needed to effectively communicate these thoughts – from typing on a computer keyboard with her finger tips to typing on a small phone with her thumbs. One can spend all day thinking up the transitions and alterations to this student’s cognitive and physiological state that are needed to
perform this simple switch, and it is no surprise that this feat of the brain has become a fervent topic of investigation in the brain sciences.

Jersild (1927) was the first to employ a version of the classic paradigm used to probe task switching. Specifically, he asked participants to switch between performing addition and performing subtraction, and compared this switching activity to performing either addition or subtraction in isolation of the other mathematical operation. Experimental participants, school children and university students, were much slower when switching between two tasks compared to performing just one task, demonstrating what he called a 'shift loss,' now much more commonly called a 'switch cost'.

Investigations into task switching were largely resurrected in the 1990’s (Allport et al., 1994; Rogers & Monsell, 1995), and from this work came about the concept of the task-set. The task-set refers to the associated components needed to perform a specific task. For example, in a simple experimental task in which the participant is asked to press the “Z” button on a keyboard if a digit presented is green, and press the “?” button if the digit is red, the task-set involves orienting attention to the location of the stimuli, decoding the color of a given stimulus, thereby reaching some pre-set decision criterion as to the color of the stimulus, and initiating the appropriate motor response warranted by the decision. For the task-set to be of any use it must also be maintained as an associational chain for as long as it is needed. The initial association of the components of the task-set is very likely carried out by the prefrontal cortex (Miller, 2000; Miller & Cohen, 2001).

Within this framework, a task switch refers to the adoption of one task-set in the face of multiple other, possibly overlapping, task-sets. For instance, suppose now the participant is asked
to use the same keys to indicate if the same colored digit stimuli are even or odd rather than red or blue. A number of potential problems for the system arise here. Attention must be reallocated to the integer identity of the stimuli rather than their color, a decision must be made about this identity, and a response performed. However, in the previous task, the same motor responses were used to act on the same stimuli. How then does the nervous system prevent the old chain of associations from interfering with the performance of the new task-set?

In behavioral experiments like the one outlined above, a switch cost is highly replicable, such that participants are slower to respond on a trial after switching tasks compared to repeating the same task. This is observed if a task switch is performed after a pre-specified number of trials, an ‘alternating runs’ paradigm (e.g. a switch is performed after 3 trials of using one task-set: AAABBBAAAA) or if each trial begins with a cue informing the participant which task-set to use, and the trial order is pseudorandom. Allport et al. (1994) cued participants in advance as to whether an upcoming succession of two trials would involve two of the same task-sets or would involve a switch between two different task-sets. Strikingly, the researchers found that increasing the time between the response to the first trial and the second had no effect on the switch cost. That is, given more time (from 20 ms to 1100 ms) to prepare for a task switch, participants showed no improvement in the switch cost (see also Rogers and Monsell, 1995). This led Allport et al. (1994) to suggest that the switch cost does not strictly index the time taken for an cognitive control process to initiate a switch but rather represents interference among task-sets, such that on a switch trial the prior task-set competes with the new task-set.

In an elaboration of this idea, like the biased competition model of selective attention, it has been proposed that the performance of multiple tasks in rapid succession involves a tightly
balanced competition, and at least a portion of the switch cost can be ascribed to resolving this competition (Wylie & Allport, 2000; Wylie et al., 2004; Wylie et al., 2006; Yeung et al., 2006). This competition has been highlighted by fMRI studies that have demonstrated the continued activation in cortical regions associated with performing the switched-from task (Wylie et al., 2004; Yeung et al., 2006). Along these lines, during task switching paradigms, it is suggested that all task-sets remain active throughout, and are subject to interference from one another. Thus, one task is not ‘turned-off’ while the other is ‘turned-on’, but rather, to some degree, top-down biasing signals intervene at various levels of the task-set where competition could occur. This begs the following question: is there evidence that biasing signals are mediated by a fronto-parietal network like the one observed in selective attention?

2.1. A fronto-parietal network specific to task switching?

Several fMRI studies have demonstrated activation in frontal and parietal cortices during task switching (Sohn et al., 2000; Wylie et al., 2004; Yeung et al., 2006), suggesting that a fronto-parietal network may be central to mediating task switching. Specifically, shifts of task have been associated with increased activity in prefrontal cortex (PFC) and posterior parietal cortex (Sohn et al., 2000; Chiu & Yantis, 2009; Esterman et al., 2009). A central question surrounding these findings pertains to whether there are specific regions of the brain that are involved in many different domains of task switching (e.g., switching attention among sensory inputs, switching decisional criteria, switching stimulus-response mappings, etc.). A further question pertains to the degree of overlap between this network and that one described above that
is associated with top-down selective attention? There is mounting evidence that the medial aspect of the superior parietal lobule (SPL) is central to switching tasks across many different task types as well as task switches that could be just as easily classified as shifts of attention (Shomstein & Yantis, 2004; Chiu & Yantis, 2009; Esterman et al., 2009). This region may contain distinct neural populations that are involved in specific types of switches (Esterman et al., 2009).

2.2. Intersensory task switching

Of particular importance to the work at hand is the investigation of task switching between different sensory modalities. Investigations of switching tasks between sensory modalities are few and far between. One observation that has been made by several groups is that switching among sensory modalities that otherwise involve the same task set (i.e., localizing auditory, visual or tactile stimuli presented at identical locations) results in slower reaction times when the modality used to perform the task is unpredictably switched rather than repeated, an effect termed the Modality Shift Effect (MSE; Spence et al., 2001; Gondan et al., 2004). If the MSE is ascribable to the same processes associated with an intrasensory switch cost, then this effect could be interpreted as competitive interactions among tasks that differ only in their respective modalities.

A following question raised by the MSE is whether shifting tasks within a sensory modality involves the same brain processes as shifting tasks between sensory modalities (Hunt & Kingstone, 2004; Murray et al., 2009). In an initial manipulation of within and between modality
task-switching, Hunt and Kingston (2004) reported a subadditive interaction of between switching tasks (i.e., identifying digits as even or odd or greater than or less than 5) and switching modalities (i.e., performing either of the two digit tasks in the visual or auditory modality). That is, when either a within modality task switch was performed or a between modality task switch was performed, response times were significantly slower than a repeat of either. However, when both the digit task and the modality in which the task was performed switched, the cost of this switch was smaller than what would be found by adding the switch costs from switches within modalities only and switches between modalities only. These authors concluded that the subadditivity of the switch costs between and within the visual and auditory modalities suggests that modality switching relies on partially distinct cognitive processes, rather than entirely on a supramodal process. Murray et al. (2009) replicated these findings, and further reported an interesting pattern of correlations when investigating participants' switch costs when switching tasks (localization or identification) and switching modalities (auditory or visual), such that a given participant's switch cost was positively correlated among the two modalities, but only when switch costs were measured within a modality repeat, whereas on modality switches there was no relationship among the task switch costs of the two modalities. The authors suggested that the cost of switching depends largely on the overlap in the neural circuitry needed to perform the two tasks. When there is a high degree of overlap, greater competition among the task sets will ensue and as a result greater switch costs will be observed.

Thus, in a manner similar to the biased competition model of selective attention, the degree of top-down biasing in task switching may be dependent on the competition among the task-sets to be switched among. While there are very few investigations of intersensory task
switching, as in selective attention, task-sets containing attended stimuli from different modalities are most likely to compete in areas of heteromodal convergence, such as the parietal and frontal cortices.

2.2. Interim Summary

Top-down biasing signals that intercede to resolve competition, whether among task-sets or among competing stimuli in the visual field, may be one of the central organizing properties of the ‘higher’ cognitive processes in the nervous system (Miller, 2000). One contention of the role of frontal and parietal cortices in tasks switching is that these areas are involved in processes associated with managing competition among task-sets (Wylie et al., 2003; Wylie et al., 2004). This proposition is enticing in that it parallels the supposed role of the fronto-parietal cortex in selective attention, and it begs the question of whether alpha oscillations are also employed as top-down biasing signals when resolving competition among task-sets. Wylie et al. (2004) proposed that competition takes place at the level of the entire associated task-set, rather than only on certain components of task-sets. If this were true, one might expect biasing signals to operate throughout in a system-wide manner to bias different components of the set association over another.

3. The Development of selective attention and task switching
As neonates, human beings do not arrive fully developed. This is perhaps a laughably obvious observation. Something what may not be as immediately obvious is that our brains do not arrive fully developed, nor do they become fully developed until at least early adulthood (Giedd et al., 1996; Giedd et al., 1999). Two aspects of structural brain development that exhibit protracted developmental trajectories are the myelination of specific neuronal populations and the growth and organization of synapses.

Myelination, referring to the creation of the specialized membrane around axons that is integral for spike propagation, begins in the second trimester of pregnancy and continues into adulthood (Volpe, 2000). In vivo imaging studies suggest that regionally specific increases in white matter density and integrity occur at least into early adulthood (Klingberg et al., 1999; Paus et al., 1999; Barnea-Goraly et al., 2005) particularly in the prefrontal cortex as well as in long-range white matter tracts such as the arcuate fasciculus and corpus callosum.

Meanwhile human synaptogenesis in the cortex begins during the third trimester and continues into the first 1-3 years postnatally (Huttenlocher & Dabholkar, 1997). Somewhere between 2-6 years a process of selective synaptic elimination occurs that continues through puberty and stabilizes in early adulthood (Huttenlocher & Dabholkar, 1997; Chechik et al., 1998). Again, there is evidence that the time courses of the synaptogenic plateau and the later elimination of synapses occurs in a regionally specific manner, with the prefrontal cortex lagging behind other regions, such as the visual cortices. This has been observed in both non-human primates (Bourgeois et al., 1989; Bourgeois et al., 1994) and humans (Huttenlocher, 1990; Huttenlocher & Dabholkar, 1997).
What is the impact of these protracted developmental changes in brain structure on cognitive functioning? Given the extensive emphasis on the relatively late development of the prefrontal cortex, a reasonable question pertains to whether or not the processes associated with this brain region also show particularly long developmental trajectories. Central to prefrontal cortical functioning appears involve flexible behavior and top-down control (Miller and Cohen, 2001). These general processes are certainly at play in demanding selective attention tasks as well as switching tasks.

3.1. Development of top-down biasing

One aspect of cognitive control that appears to develop late into life involves the resistance to interference from task-irrelevant distractors as well as pre-potent motor responses (Casey et al., 2000). For instance Enns and Girgus (1985) compared younger school-aged children (6-8 years), older children (9-11) and adults in the time taken to make a discrimination of a visual stimulus in the presence of a similar stimulus (two parentheses). The researchers manipulated the distance between the two stimuli (from 0.5° to 16° apart) and found that the youngest group was significantly slower to perform the discrimination than older children and adults when the target and distractor stimuli were close together, suggesting a difficulty in managing interference from task-irrelevant stimuli.

Early imaging studies suggested that children, like adults, show recruitment of prefrontal cortices during tasks that require the maintenance of information in the presence of distractors (Casey et al., 1997; Casey, 1998), and that the volume of activation in the prefrontal cortices was
greater in children than adults (Casey et al., 1997). This study and others from the same group suggested that while at times children recruit a greater volume of the prefrontal cortex on tasks requiring resistance to interference from task-irrelevant stimuli as well as pre-potent motor responses (e.g., visual working memory tasks and go/no-go tasks), adults demonstrated more focal activity and regional specialization (Casey, 1998; Casey et al., 2000; Casey et al., 2005). Casey et al. (2000) interpreted this as reflective of the continuing organization and specialization of prefrontal regions as suggested by the prolonged period of synaptic elimination in this area.

Beyond the prefrontal cortex, what about the developmental trajectories of other regions of the top-down network of control? Enns and Brodeur (1989) utilized a variant of the Posner cueing task (cf. Posner, 1980) with children of either 6 or 8 years, and young adults of 20 years. Children were apparently as good as adults at shifting attention covertly based on cue stimuli. However, both groups of children demonstrated greater reaction time costs in reorienting to an invalidly cued target compared to adults, suggesting that even school-aged children show underdeveloped capacity to override a prior deployment of attention. This observation suggests the protracted development of frontal and parietal regions of control. In accordance with these behavioral findings, re-orienting attention after invalid cues resulted in increased BOLD activity in the right inferior frontal gyrus, the right temporo-parietal junction and the bilateral superior parietal cortices in adults, whereas a much more diffuse pattern of activity was found in children 8-12 years with increased activity in the left superior frontal gyrus as well as in the right striatum (Konrad et al., 2005). Furthermore, increases in the level of distracting task-irrelevant stimuli (task-incongruent stimuli flanking the target), resulted in greater activation of the right inferior frontal gyrus and left superior parietal cortex in adults relative to children (Konrad et al., 2005).
In contrast, children showed greater activation of the left superior frontal gyrus relative to adults with increasing distractor interference. This lateralization difference among adults and children was also observed by an independent group employing centrally presented targets flanked by distractors, although the effect was found over more ventral prefrontal regions (Bunge et al., 2002). In Konrad et al. (2005), these functional differences were paralleled by increased gray matter volume in the children relative to the adults in the frontal, parietal, and temporal lobes, suggesting again that the prolonged elimination of synapses throughout development may reflect ongoing organization of cognitive networks associated with top-down biasing and cognitive control.

I have reviewed a selection of evidence for the prolonged development of areas associated with cognitive control, particularly the prefrontal cortices, which have been shown to be central to establishing complex task-sets, maintaining task-sets in the face of interference, and reconfiguring the current task set at the network level (Miller and Cohen, 2001). The prefrontal cortex is one of the most anatomically integrative regions of the brain (Goldman-Rakic, 1987; Miller, 2000), and as such, it is ideally situated to instantiate complex task-sets and maintain these sets, particularly by biasing lower-level cortical regions in favor of the current task-set.

4. Autism spectrum disorder

Autism spectrum disorder (ASD) is a neurodevelopmental disorder that is defined by deficits in social communication and interaction as well as restrictive or repetitive behaviors (APA, 2013). According to the Centers for Disease Control and Prevention, for 2010, across 11
monitoring sites in the United States, the prevalence of ASD was 14.7 per 1,000 (or one in 68) in children 8 years of age (CDC, 2014). Among 7 of these monitoring sites that had detailed IQ data, 31% of children had IQs ≤ 70, commonly a level associated with intellectual disability. Meanwhile, 23% were within the borderline range for intellectual disability (IQs in the range of 71-85), and 46% had IQs considered average or above (>85). Additionally, about one in 42 boys and one in 189 girls were identified as having ASD. This disorder is thus widespread, there is huge variability across individuals in the degree to which it impairs day-to-day functioning, and it is diagnosed far more in boys than in girls.

It is common for individuals with ASD to exhibit language deficits, exhibiting, for instance, a complete lack of speech, developmental delays in speech, echolalia (the repeating back of words or phrases), or a lack of self-generated or un-prompted speech (APA, 2013). Tightly intertwined with this are impairments in social interaction. Language is not used effectively as a tool for social interaction, and other aspects of typical social interaction are lacking in ASD children such as shared attention, eye contact, and reciprocity in behavior and communication.

In addition to showing social deficits, ASD individuals exhibit behavioral patterns that can generally be described as restricted or repetitive. At their most basic, these phenotypes might refer to motor stereotypies, such as hand flapping and finger flicking. Whereas, at a more cognitive level they may be reflected in extreme interest or focus on one object, a need for structure and predictability in the day’s routine, and, as the ASD individual becomes older, an intense interest in certain activities or areas of knowledge, such as, for example, train timetables or driving routes. Along with these core phenotypes, ASD individuals often exhibit hyper-
hypo-reactivity to sensory stimuli. Some individuals may show extreme sensitivity to sound or textures, whereas others may seek out high levels of sensory stimulation (e.g., showing an affinity for flashing lights).

As already alluded to, the manifestations of ASD are incredibly heterogeneous. Some individuals may never develop speech, while others may be hyper-articulate, albeit they may use unorthodox vocabulary, exhibit oddly inflected speech, or be highly literal minded in their communication. The wide range in IQ is also perplexing, with individuals ranging from developmentally disabled to far above average on this index of intelligence. Adherence to routines and intense restriction of interest also show variability among individuals. Importantly, this is further complicated by the fact that there does not seem to be one ASD phenotype, such that an individual with highly impaired language will show a commensurate impairment in restrictive and repetitive behaviors. The different aspects of this disorder each manifest themselves to varying, largely independent degrees from one individual to the next.

In the midst of this extreme heterogeneity, the developmental time course of the disorder does in fact show relative stability across individuals. Symptoms are typically first noticed around two years of age, but the time at which symptoms are first noted are influenced by the severity of the disorder in a given child (APA, 2013). This developmental piece of the puzzle may be central to the disorder as it seems to onset during a critical period in brain development.

ASD is heritable with siblings of individuals with ASD exhibiting a greater risk for also developing the disorder. Studies have suggested heritability as high as 70% in monozygotic twins (Abrahams & Geschwind, 2008; Geschwind, 2009). The genetic causes of ASD remain to be fully unraveled, although it is becoming increasingly apparent that in the vast majority of
cases this is a polygenic disorder. That is, a mutation in one gene is not responsible for the disorder, but ASD arises out of a complicated milieu of genetic mutations. Work that shows a great deal of promise involves investigations into copy number variations (CNVs). CNVs are forms of structural variations in the genome, such that, on specific chromosomes, regions of the genome are deleted or duplicated. In a seminal study, CNVs were found in 10% of ASD participants with no corresponding parental mutations, suggesting that these genetic anomalies in this group arose de novo (Sebat et al., 2007). Recurrent CNVs have now been identified on specific chromosomes (Abrahams and Geschwind, 2008), but a great deal of work remains to be done in order to fully understand the genetic etiology of this disorder. The fact that many overlapping genetic mutations appear to give rise to this disorder is quite intriguing. (Walsh et al., 2008) suggested that genetic heterogeneity in ASD may be central to most disorders involving the cortex, such as dementia, mental retardation, and epilepsy. Forebrain structures require more than 10,000 genes for normal brain development, and the associated plasticity of this region may result in a select few stable abnormal states onto which different genetic insults all converge (Walsh et al., 2008).

There is evidence from imaging studies that in about the first two years of life, there is a period of brain overgrowth in ASD (Courchesne et al., 2003; Hazlett et al., 2005; Courchesne et al., 2007). This overgrowth appears to be regionally specific affecting most prominently the frontal and temporal lobes (Courchesne et al., 2003; Hazlett et al., 2005; Courchesne et al., 2007; Courchesne et al., 2011) and limited evidence for overgrowth in the parietal lobe (Palmen et al., 2005). The overgrowth, found particularly in the frontal lobes, may be indicative of increased neuron number, increased synapses, or other features of the neuropil. However,
evidence that the frontal lobes show abnormal developmental trajectories is enticing given that frontal cortices are central to the higher cognitive functions that are impaired in ASD.

Alongside the altered development of brain volume in ASD are studies suggesting reductions in connectivity across brain regions. According to work using inter-regional BOLD coherence measures (Horwitz et al., 1988; Courchesne & Pierce, 2005) as well as work addressing electrophysiological coupling across sensor sites in the EEG/MEG record (Murias et al., 2007; Lazarev et al., 2010), there is the suggestion of a pattern of functional dysconnectivity in ASD individuals. This is supported by postmortem structural work (Casanova & Trippe, 2009). This has led to the so-called underconnectivity hypothesis of ASD (Belmonte et al., 2004; Just et al., 2007). The aberrant development of the frontal cortices along with evidence that, at the network level, ASD individuals may exhibit poor information transfer, suggests that a core deficit in ASD brain function may arise around top-down control and biasing.

4.1. ASD and top-down biasing

Deficits in cognitive control, or, alternately, executive function have been argued by some to be the root of many defining clinical characteristics of ASD (Ozonoff et al., 1991; Pennington & Ozonoff, 1996; Baron-Cohen, 2004; Geurts et al., 2009).

Task-set switching is a consistently reported deficit in individuals with ASD (Lopez et al., 2005; Russo et al., 2007). Several core expressions of the ASD phenotype, including perseverative, stereotyped behaviors and interests, difficulty changing perspectives in social situations, rigidity in routines, problems adapting to change and difficulties in regulation and
modulation of motor actions, are suggestive of related dysfunctions in task switching (Hill, 2004; Geurts et al., 2009). Furthermore, ASD individuals have been shown to exhibit abnormalities in switching attention between sensory modalities (Courchesne et al., 1994; Poljac et al., 2010; Reed & McCarthy, 2012).

As outlined above, central to flexible behavior is the maintenance of task goals, complex associations and motor plans in the face of competing interference. A large chunk of these processes appear to be carried out by the prefrontal cortices as well as the interaction with parietal cortices. Fundamental to the action of these cognitive control mechanisms is top-down biasing, such that the selected task-set or environmental stimulus is favorably processed while the processing of those that cause interference are suppressed. Given the abnormal architecture of the frontal lobes in ASD along with reports of structural and functional long-range underconnectivity, I would argue that one possible deficit in ASD involves dysfunction of the prefrontal cortices along with poor distribution of biasing signals throughout the cortex.

5. The present work

I began by juxtaposing selective attention and task switching. However, as my thinking progressed on these topics it began to seem as though these two psychological constructs are not as distinct as I initially thought. Rather, it seems that common to many brain processes is the competition for processing resources coupled with top-down biasing signals. Selective attention can be thought of as a subcomponent of task-switching, such that a switch of task invariably results in a shift of attention. On the other hand, depending on what you consider a switch of
task, this action can be boiled down to what Posner would describe as the disengagement, movement, and reengagement of attention. However, there are distinctions to be made, especially in more complex instances of task switching. For instance, the use of the Stroop task in task switching paradigms requires an individual to apply different rules to the same attended stimuli (e.g., report the color of the word or report the word “GREEN” written in red ink). The stimulus stays the same when the task switches, but a new rule must be adopted (but, again, attention is presumably deployed to different features of the stimulus in the two different tasks).

Furthermore, task switching paradigms often involve the remapping of stimulus-response rules. The stimulus may stay the same but how the participant acts upon it switches.

In the end, there is no clear demarcating line between the brain processes associated with selective attention and those associated with task switching. What is fairly certain is that each of these processes relies on biasing signals (Miller and Cohen, 2001; Desimone and Duncan, 1995). As reviewed above, there is a large body of evidence that alpha oscillations operate at times as biasing signals, but a great deal remains to be learned about how these signals operate on their respective cortical targets, how they are flexibly deployed, and what regions of the brain directly manipulate the properties of these rhythms such that they operate as biasing signals.

In chapters 1-3, I ask the following questions: 1) Chapter 1, what is the effect of a task switch on alpha as a biasing signal? Alpha has been observed to increase in amplitude over task-irrelevant areas. Is alpha amplitude deployed to a greater extent in the same cortical regions on a task switch versus a repeat to overcome interference from the prior task as would be predicted by the competition model of task switching (Wylie et al., 2003)? Further, are there topographical
differences in alpha amplitude between switches and repeats reflecting, for instance, the rebalancing of competing task-sets in cognitive control regions such as the prefrontal cortex?

2) Chapter 2, in a cohort of participants ranging in age from 8-34 years, I ask whether the continued development of the prefrontal cortices is reflected in age-dependent differences in the deployment of alpha during intersensory selective attention and task switching.

3) Chapter 3, finally, given the reviewed evidence for reduced cognitive control, abnormal prefrontal circuitry, and reduced interregional connectivity, I asked whether a cohort of individuals on the autism spectrum exhibited atypical alpha deployment relative to a cohort of typically developing age- and IQ-matched participants on an intersensory selective attention and task switching paradigm.

It is my hope that investigating these questions will shine some light onto alpha oscillations as top-down biasing signals, if even that light is quite miniscule, out-of-focus, or downright bewildering. It is my especial hope that what I report below with regards to typical brain development and autism spectrum disorder will aid in the diagnosis, intervention, and treatment of this devastating and mysterious disorder, again even if that aid is a fraction of one drop in the proverbial bucket of scientific knowledge.
Chapter 1

Throwing out the rules: anticipatory alpha-band oscillatory attention mechanisms during task-set reconfigurations.

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Abstract

We assessed the role of alpha-band oscillatory activity during a task-switching design that required participants to switch between an auditory and a visual task, while task-relevant audio-visual inputs were simultaneously presented. Instructional cues informed participants which task to perform on a given trial and we assessed alpha-band power in the short 1.35-second period intervening between the cue and the task-imperative stimuli, on the premise that attentional biasing mechanisms would be deployed to resolve competition between the auditory and visual inputs. Prior work had shown that alpha-band activity was differentially deployed depending on the modality of the cued task. Here, we asked whether this activity would, in turn, be differentially deployed depending on whether participants had just made a switch of task, or were being asked to simply repeat the task. It is well-established that performance speed and accuracy are poorer on switch than on repeat trials. Here, however, the use of instructional cues completely mitigated these classic switch-costs. Measures of alpha-band synchronization/desynchronization showed that there was indeed greater and earlier differential deployment of alpha-band activity on switch versus repeat trials. Contrary to our hypothesis, this differential effect was entirely due to changes in the amount of desynchronization observed during switch and repeat trials of the visual task, with more desynchronization over both posterior and frontal scalp regions during switch-visual trials. These data imply that particularly vigorous, and essentially fully effective, anticipatory biasing mechanisms resolved the competition between competing auditory and visual inputs when a rapid switch of task was required.
1. Introduction

When individuals are required to switch rapidly from execution of one task to another, goal-related task networks and attentional mechanisms are engaged to reconfigure task-specific networks, suppressing activity within circuits responsible for performance of the old task and amplifying preparatory neural processes for the anticipated novel task (Foxe & Simpson, 2005; Foxe et al., 2005). That is, competition between two potential task-set configurations must be resolved so that an effective strategy shift can be enacted. Often there is a significant performance cost in terms of both speed and accuracy upon the first instance of a new task that is taken to reflect these reconfiguration processes (Jersild, 1927; Wylie & Allport, 2000; Wylie et al., 2004b; Wylie et al., 2009). Under many such task-switching scenarios, switch costs dissipate rapidly, with near ceiling levels of performance achieved on just the second instance of the new task (De Sanctis et al., 2009). The implication is that the anticipatory neural reconfigurations necessary for optimal performance of a new task are not always achieved in one step; rather it often takes performance of at least one instance of the new task to reach optimal performance (Wylie et al., 2003a). Alternatively, if an informational cue informs participants of an upcoming task switch, and sufficient time is then allowed to elapse between the cue and the stimulus to be acted upon, individuals can accomplish an entirely effective task-set reconfiguration in that little or no switch cost is then observed (Wylie et al., 2009).

It has been long posited that a large contribution to these initial switch costs is mediated through so-called task-set inertia effects; that is, optimal performance of the new task is hindered by ongoing competition from sustained activity within the neural circuitry responsible for performing the previous, but now irrelevant, task (Allport et al., 1994; Wylie et al., 2003b;
Functional imaging studies have shown precisely this pattern of effects. In one such study, we asked participants to perform both a color task and a face identification task during a switching paradigm, while imaging activation patterns within the relevant cortical regions for analyzing these respective features. We found that activity within the circuitry responsible for color processing (e.g. V4) continued to show enhanced processing while participants performed the face task (and vice versa), despite the fact that the color task was, and would continue to be, completely irrelevant to them (Wylie et al., 2004a).

Thus, in order to perform a new task under such task-switching scenarios, it seems a reasonable supposition that there are two somewhat separable mechanisms that must be engaged in parallel. The task-set configuration (goals) of the new task must be deployed effectively, while simultaneously, some form of suppression of the former task-set must also be engaged (Foxe & Snyder, 2011). Here, we were specifically interested in how this suppression was achieved. One obvious candidate mechanism for suppressing or disengaging ongoing activity within previous task-relevant circuitry is deployment of anticipatory alpha-band oscillatory activity. Oscillations in this band (8-14 Hz) have been convincingly associated with attentional suppression across the visual (Foxe et al., 1998; Worden et al., 2000; Fu et al., 2001; Kelly et al., 2005; 2006; Rihs et al., 2007; Romei et al., 2008; Kelly et al., 2009; Snyder & Foxe, 2010), auditory (Kerlin et al., 2010; Banerjee et al., 2011; Gomez-Ramirez et al., 2011) and somatosensory (Jones et al., 2010; Haegens et al., 2011) systems. Here, we asked whether alpha-band oscillatory suppression mechanisms might not also be deployed to suppress “old” task-set configurations.

We employed a well-established intersensory selective attention task where participants were cued on a trial-by-trial basis to attend to either the visual or auditory components of an upcoming
compound audio-visual target event (Foxe et al., 1998). In turn, high-density electrical mapping was employed to assay anticipatory alpha-band activity during a fixed 1.35 second cue-to-target attentional deployment period. Comparisons were specifically made between switch trials (where the modality of the upcoming task had just changed) and repeat trials (where the cued modality was the same as in the previous trial). We reasoned that there would be considerably earlier and amplified deployments of alpha-band mechanisms in anticipation of a task-switch than in anticipation of a task-repeat trial. We also anticipated a considerably more extensive topographic distribution of this anticipatory alpha, reflecting increased engagement of a distributed task network that would likely also include executive control regions of the well-known fronto-parietal attention network (Corbetta, 1998; Foxe et al., 2003). In the case of task-repeats, our expectation was that alpha-suppression mechanisms would be deployed with a more focused topography, and with a more punctate time course, specifically titrated to the expected arrival of the imperative stimulus.

2. Methods

2.1. Participants

Sixteen (8 females) healthy volunteers participated in this experiment (mean age = 23.5 years, SD = +/-3.6, range = 18-32 years). All participants provided written informed consent and the procedures were approved by the Institutional Review Board of the Albert Einstein College of Medicine where the experiments were conducted. All procedures conformed to the tenets of
the Declaration of Helsinki. All participants reported normal or corrected-to-normal vision and normal hearing. Participants received a modest fee ($12/hour) for their efforts.

2.2. Stimuli and Task

We employed a classic S1-S2 cued attention task, where each trial consisted of a cue (S1), an intervening blank preparatory period, followed immediately by a task-relevant second stimulus (S2) (see Figure 1.1). Tasks of this type often use probabilistic cues, where participants are told to respond to all targets, even in the uncued modality or location (Posner et al., 1980). Here, instructional cues were used such that participants were directed only to respond to targets within the cued modality and to suppress/ignore all stimuli in the uncued modality. This is an important design feature since stimuli in the uncued modality served as distractors, suppression of which would be expected to benefit task performance.

The first stimulus (S1), which served as the task cue, consisted of a simple light-grey line drawing depicting either a pair of headphones or a computer monitor. In mixed task blocks, these S1 stimuli instructed the participant as to which modality (auditory or visual) was to be attended when the second stimulus (S2) arrived (Fig. 1.1). The second stimulus (S2) was a compound bisensory auditory–visual stimulus and participants performed a go/no-go discrimination task on this S2 within the cued modality. Participants were cued randomly on a trial-by-trial basis to attend to either the visual or auditory components of the upcoming bisensory S2 event.

Local switch costs, reflecting the cost related to changing tasks, were obtained by comparing switch versus repeat trials in mixed blocks (i.e. blocks where task switches were required). The
probability of a switch trial in such blocks was 50%, of a first repeat trial was 34%, and of a second repeat trial was 16%. To obtain a measure of so-called global switch costs, we also ran “pure” task blocks, where participants were instructed to perform only the visual or only the auditory task throughout a block of trials. In the visual “pure” task, the S1 was a line-drawing depicting a monitor and the S2 consisted of purely visual inputs. In the auditory “pure” task, the S1 was a line-drawing depicting headphones and the S2 consisted of purely auditory inputs. Global switch costs (also referred to as mixing costs), reflecting the cost related to performing two tasks instead of one task, were obtained by comparing repeat trials in mixed blocks versus “pure” task blocks.

The auditory part of the bisensory S2 stimulus consisted of two sequentially presented sinusoidal tones (100 ms duration, 10 ms rise/fall) with a 5 ms interval between presentations. On non-target trials, the two tones were of identical frequency (2000 Hz) and subjects were required to withhold responses when no difference between the tones was detected. On target trials, the two tones presented were of slightly different frequency. One of the two tones was 2000 Hz, whereas the frequency separation of the other tone was psychophysically titrated based on each participant’s performance (see Procedure below). When participants detected a frequency difference between the pair of tones, they were instructed to respond with a fast accurate button push.

The visual part of the bisensory S2 stimulus consisted of a pair of gabor patches (100 ms duration, 4.8° in diameter, 0.25 cycles per degree) centered 5.2° to the left and right of the fixation cross. On target and non-target trials the two patches were of different and identical orientation, respectively. As with the auditory stimuli, the orientation difference between the
gabors was psychophysically titrated for each participant (see Procedure below). The timing of the visual presentation was adjusted such that the Gabors appeared coincident with the second tone of the pair rather than the first.

The likelihood of receiving a target stimulus within the cued modality was set at 50%. The stimulus onset asynchrony (SOA) between the cue and the imperative stimulus (i.e. the S1-S2 period) was 1350 ms. A black fixation cross (subtending 0.3° vertically and horizontally) was presented in the center of the monitor throughout testing. The inter-trial interval (ITI: the S2–S1 period) was randomized ranging from 2000 to 3000 ms during which the fixation cross remained on the screen.

2.3. Procedure

Participants were seated in a double-walled, darkened, sound-attenuated, electrically-shielded booth (International Acoustics Company (IAC), Bronx, New York). Visual stimuli were presented on a LCD monitor positioned 100 cm from the participant. Auditory stimuli were binaurally presented over a pair of headphones (Sennheiser, model HD 555). Stimuli were delivered using Presentation software (Neurobehavioral Systems, Albany, CA). The sound pressure level was set to a level reported as comfortable by the participant at the beginning of testing, and held constant from then onwards. 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). UDTR employs different rules that converge on
specific levels of accuracy. We used a 3-up, 1-down rule, meaning that, for three consecutive hits we adjusted the stimulus one step harder and for any miss, we adjusted the stimulus one step easier. This rule necessarily converges on an accuracy level of 79.4%.

During the experimental session, participants were instructed to respond as quickly and accurately as possible to the detection of targets within the cued modality and to withhold responses otherwise. Participants were further instructed to refrain from eyeblinks during each trial as much as possible. Each participant completed one visual and one auditory pure-task block of 100 trials, followed by approximately 20 mixed-task blocks of 30 trials each, resulting in the collection of ~300 trials per cue condition.

2.4. EEG Acquisition and Preprocessing

Continuous EEG was recorded, with a band-pass of DC to 134 Hz, from 168 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 systems with two separate electrodes that: Common Mode Sense (CMS) and Driven Right Leg (DRL) passive electrode. These two electrodes create a feedback loop, thus rendering them as references. With the Biosemi system, every electrode or combination of electrodes can be assigned as a reference, which is done purely in software after acquisition. EEG data were processed using the FieldTrip toolbox (Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, The Netherlands). This MATLAB (The MathWorks Inc., Natick, Massachusetts) toolbox and supporting materials can be accessed at http://www.ru.nl/neuroimaging/fieldtrip. The continuous
EEG data were stored and then re-referenced to the average reference and low-pass filtered with a cut-off frequency of 40Hz. Trials with blinks and excessive eye movements were rejected based on the horizontal and vertical electro-occulogram. Over all other electrodes, a trial rejection threshold of $\pm$ 100 microvolts was used. Trials were then epoched from -200 to 1805 ms around the onset of the S1 cue-stimulus. The period of -100 to 0 ms was defined as baseline.

2.5. Behavioral Measures

To obtain so-called global switching costs, we quantified the difference in reaction times (RT) and accuracy (d-prime) between mixed and “pure” task blocks. To obtain local switching costs, we analyzed differences in RT and d-prime between switch and repeat trials within the mixed blocks. The RT was measured from all correct 'go' trials (i.e., trials with a target in the cued modality). Responses were only considered valid if they occurred in the window of 200 to 1500 ms following the onset of the gabor in attend-visual conditions and the second tone stimulus in the attend-auditory conditions. The signal detection measure d-prime was used to assess response accuracy. This 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 therein. d-prime is computed by taking into account the probability of correctly responding to targets when a target is present and the probability of incorrectly initiating a response in the absence of a target (Green & Swets, 1966).

2.6. Temporal Spectral Evolution technique
To assess the time-course of oscillatory power changes in the alpha band during our cued-attention task, Temporal Spectral Evolution (TSE) waveforms were computed (Foxe et al., 1998). TSE waveforms provide a robust measure of induced oscillatory power changes (i.e., changes in amplitude of rhythmic activity in which phase varies randomly from trial to trial). The computation of the TSE waveforms in the present study took the following course: 1) Individual trials were bandpass filtered from 8 to 14 Hz (4th order digital Butterworth, zero-phase); 2) The analytic representation of the bandpass-filtered trials were acquired by applying the Hilbert transform; 3) The absolute value of the analytic representation of each trial was taken as a measure of the instantaneous amplitude in the alpha band across the trial; 4) trials in each condition were averaged.

2.7. Statistical Analysis Strategy

RT and d-prime accuracy were analyzed using a repeated measures analysis of variance (ANOVA) with Trial (switch versus repeat) and Task Modality (visual versus auditory) as within-subject factors. TSE measures were analyzed using the mean amplitude across nine electrode sites over fronto-polar (D4/D5/D6/D11/D12/D13/C28/C29/C30 in the Biosemi labeling convention) and parieto-occipital (A15/A16/A17/A21/A22/A23/A28/A29/A30) scalp regions during an early (700-900ms) and late (1100-1300ms) phase of anticipatory preparatory activity.

As a first step, our analyses detailed the time-course and topographic distribution of oscillatory power changes in the alpha band associated with task-set reconfiguration. This was
accomplished by a repeated measures ANOVA with factors Modality (visual versus auditory), Trial (switch versus repeat), Time (early versus late) and Scalp Region (fronto-polar versus parieto-occipital). If a significant Modality X Trial interaction was found, our second step was to run two protected ANOVAs, one testing task-set reconfiguration between and one within modalities in order to unpack the interaction. For the between modality ANOVA, we tested the time-course and strength of alpha power deployment contrasting switch auditory against switch visual trials and repeat auditory against repeat visual trials. The between modality ANOVA considers alpha power deployment associated with task-set reconfiguration and differences therein between "SWITCH" and "REPEAT" trials. For the within modality ANOVA, we tested time-course and strength of alpha power deployment contrasting switch auditory against repeat auditory trials as well as switch visual against repeat visual trials. The within modality ANOVA considers alpha power deployment associated with task-set reconfiguration and differences therein between "AUDITORY" and "VISUAL" modalities.

2.8. Topographical statistics:

Since we initially hypothesized that switch trials would engage distributed networks of task-set reconfiguration and top-down attention to a greater extent than repeat trials, we sought to test for topographic differences among conditions that would suggest the differential engagement of a subset of cortical generators. To test for periods of topographic modulation irrespective of changes in oscillatory amplitude, we calculated the global dissimilarity (GD) (Lehmann & Skrandies, 1980) between differential alpha-band activity (8-14 HZ) across the anticipatory
period preceding “SWITCH” trials and “REPEAT” trials. Differential activity is derived by subtracting cue-visual trials from cue-auditory trials. GD is a method to assess configuration differences between two scalp distributions, independent of their strength, as the data are normalized using the global field power. The GD is calculated as the square root of the mean of the squared differences between the potentials measured at each of the 168-scalp electrodes. For each subject and time point, the GD indexes a single value, which varies between 0 and 2 (0 = homogeneity, 2 = inversion of topography). To create an empirical probability distribution against which the GD can be tested for statistical significance, the Monte Carlo MANOVA was applied. This is a nonparametric bootstrapping procedure, wherein each subject’s data from each time point are permutated such that they can “belong” to either condition. For each time point, the dissimilarity was then calculated for each of 5000 such permutations (Manly, 1997).

2.9. Statistical Cluster Plot

To provide a more general description of the spatio-temporal properties of differential alpha-band activity as a function of task-set reconfiguration, we computed separate statistical cluster plots (SCP) for trials preceding a “SWITCH” and “REPEAT” of task. This procedure has been used effectively in post hoc analyses as a means to more fully explore complex datasets and generate pointed follow-up hypotheses (Molholm et al., 2002; Murray et al., 2002). Point-wise two-tailed t-tests between attend-visual and attend-auditory trials were calculated at each time-point for all electrodes. The results of the point-wise t-tests from 168 electrodes are displayed as an intensity plot to efficiently summarize and facilitate the identification of the onset and general
topographic distribution of differential alpha-band activity preceding a “SWITCH” and “REPEAT” of task. The x-, y-, and z-axes, respectively, represent time, electrode location, and the t-test result (indicated by a color value) at each data point. For each scalp electrode, only the first time point where the t-test exceeded the 0.05 p-value criterion for at least 11 consecutive data points (>20 ms at a 512 Hz digitization rate) is considered significant (Guthrie & Buchwald, 1991; Foxe & Simpson, 2002).

3. Results

3.1. Behavioral Data

Figure 1.2 shows reaction time (RT) and accuracy (d-prime) data for the mixed-task blocks, where participants switched between visual and auditory tasks within a block, and for the pure-task blocks, where participants performed either the visual or auditory task alone throughout a block of trials. As previously defined, local costs were obtained by comparing performance between switch and repeat trials during mixed-task blocks. Global mixing costs were obtained by comparing performance between mixed and pure task blocks.

Tests for Local Switch Costs (Reaction Times): Analysis of variance with Trial (switch versus repeat) and Modality (visual versus auditory) as independent factors revealed a Trial x Modality interaction \( F_{1,15}=8.69, p=.01 \). The interaction of Trial X Modality was driven by the fact that reaction times on Auditory Switch trials \( A_{\text{switch}}=621\text{ms} \) were marginally slower than those on repeat trials \( A_{\text{repeat}}=605\text{ms} \) – a switch cost of 16ms – whereas RTs for visual switch
trials ($V_{\text{switch}}=638\text{ms}$) were actually marginally faster than those seen on repeat trials ($V_{\text{repeat}}=657\text{ms}$) – an ostensible 19ms switch benefit. While the interaction term of the ANOVA was significant, follow-up t-tests within modality (i.e. switch versus repeat RTs) showed that neither the auditory switch cost nor the visual switch benefit reached conventional levels of statistical significance ($p>0.06$). As such, there was no evidence here of classic switch costs in terms of response speed.

**Tests for Global Mixing Costs (Reaction Times):** Two participants did not complete the pure task blocks, and were thus excluded from this analysis. An analysis of variance with factors of Block (mixed versus pure) and Modality (visual versus auditory) was conducted. While both the auditory ($A_{\text{pure}}=582\text{ms}, A_{\text{mixed}}=605\text{ms}$) and visual tasks ($V_{\text{pure}}=587\text{ms}, V_{\text{mixed}}=657\text{ms}$) suggested a marginal mixing cost - a mixing cost of 17ms and 70ms for the auditory and visual tasks, respectively - no main effects or interactions reached significance (all $p$s>0.1). As such, there was no strong evidence here of mixing costs in terms of response speed.

**Tests for Local Switch Costs (Response Accuracy):** For the $d$-prime measurement of discrimination accuracy, we observed highly similar measurements of discrimination between switch and repeat trials ($A_{\text{switch}}=2.93$ versus $A_{\text{repeat}}=2.82$ and $V_{\text{switch}}=2.81$ versus $V_{\text{repeat}}=2.85$), and an analysis of variance with factors of Trial (switch versus repeat) and Modality (visual versus auditory) unsurprisingly revealed no significant main effects or interactions. As such, there was no evidence of switch costs in terms of task accuracy.

**Tests for Global Mixing Costs (Response Accuracy):** Again, two participants did not complete the pure task blocks, and were thus excluded from this analysis. Analysis of variance with Block (mixed versus pure) and Modality (visual versus auditory) as factors revealed a main
effect of Block ($F_{1,13}=11.74$, $p=.005$), which was driven by a mixing cost in both the auditory
($A_{\text{pure}}=3.7$ versus $A_{\text{mixed}}=2.86$; $A_{\text{mixcost}}=0.84$) and visual tasks ($V_{\text{pure}}=3.5$ versus $V_{\text{mixed}}=2.84$;
$V_{\text{mixcost}}=0.76$). No other main effects or interactions reached statistical significance. In sum, there
was clear evidence for mixing costs, such that the need to switch between the auditory and visual
tasks, rather than perform each task alone in a sequence, resulted in a robust decrease in target
discrimination accuracy for both the auditory and visual tasks.

3.2. TSE analysis

Panel A of Figure 1.3 shows the topography of the differential alpha-band (8-14Hz)
oscillatory activity between all attend-auditory and all attend-visual trials (auditory minus visual)
at 1000ms (i.e. where switch and repeat trials are collapsed together). The parieto-occipital focus
of differential alpha power is highly consistent with our previous findings (Foxe et al., 1998; Fu
et al., 2001; Gomez-Ramirez et al., 2007). Panel B of Figure 1.3 depicts the alpha-band (8–14
Hz) TSE waveforms derived from the three highlighted parieto-occipital electrode sites (central
head - panel A). A sustained divergence in TSE amplitude is seen starting at ~600ms post-cue,
some 750ms before the onset of the S2 task stimulus, which occurs at 1350ms. Alpha-band
activity is greater when subjects have been cued to attend selectively to impending auditory
stimulation (i.e. to ignore or suppress concurrent visual inputs). In panel C of Figure 1.3, the TSE
waveforms for attend-auditory (red traces) and attend-visual (black traces) are further
distinguished according to trial type (i.e. switch trials (dotted traces) versus repeat trials (solid
traces)). If participants are required to reconfigure the task-set on switch trials, the divergence in
TSE waveforms is seen to start ~200ms earlier at about 400ms post-cue and reaches a maximum just before the S2 stimulus onset.

Figure 1.4 depicts the TSE waveforms for attend-auditory and attend-visual trials at six representative electrodes over fronto-polar, and parieto-occipital scalp regions, broken out for switch trials (panel A) and repeat trials (panel B). The extended electrode representation reveals that the modulation of alpha-band activity shows a considerably broader topographic distribution from the more typical focus over the parieto-occipital region, with clear divergence seen over frontal/fronto-polar scalp regions when participants are preparing for a switch of task (panel A). Early and wide-spread TSE modulation for switch compared to repeat trials is also depicted in the statistical cluster plot (SCP - far right column). For repeat trials, there is one main cluster of activation starting at ~1100 ms post-cue, which is distributed over both frontal and parieto-occipital scalp regions. For switch trials, two main clusters of differential activation are evident, an early one starting at ~600 ms and a later one starting at ~1100 ms. Both the early and late clusters show widespread scalp distributions over parieto-occipital, central, and fronto-polar scalp regions. Topographical mapping shows maximal distributions over the parieto-occipital region starting at ~700 ms and over more frontal regions starting at ~1000ms - both are enhanced on switch trials (panel C). Tests for periods of topographic differences between switch and repeat trials revealed significant differences between 900 and 1150 ms, likely indicating greater extent of differential alpha activity over more frontal scalp regions for switch trials.

Figure 1.5 depicts comparisons of the TSE waveforms between switch and repeat trials as a function of sensory modality, with the auditory modality depicted in panel A and visual modality in panel B. Almost completely overlapping TSE waveforms are observed for switch
and repeat trials in the auditory modality and the corresponding SCP map (right column) shows no evidence for any major periods of differential alpha-band activity as a function of this switch versus repeat comparison. Simply put, when it comes to anticipatory deployment of alpha-band activity in advance of performance of an auditory task, there is no evidence for differential deployment as a function of whether individuals are in the process of switching tasks versus simply repeating the same auditory task. In contrast, robust differential TSE modulations are evident for the comparison of switch and repeat trials when the brain is being prepared to perform the impending visual task. An early difference (~200-350ms) focused over frontal scalp regions is evident in the SCP, as is a more broadly distributed difference over both frontal and posterior scalp in the period between approximately 600ms and 1100ms.

Topographical mapping of differential alpha-band activity during auditory anticipation (panel C) revealed little evidence for robust differential alpha-band activity, although from approximately 700-1200 ms, a modest focus of differential activity can be seen over parieto-occipital scalp. However, as above, this differential activity did not reach conventional levels of significance. For the visual modality, on the other hand, there are two clearly defined foci of differential activity, the most prominent of which is evident over parieto-occipital scalp, with a second clear focus evident over midline fronto-polar scalp (panel D).

Formal statistical analysis of these apparent differences using repeated measures analysis of variance revealed main effects of Modality ($F_{1,15}=9.38$, $p=.008$), Time ($F_{1,15}=9.33$, $p=.008$), Scalp Region ($F_{1,15}=9.21$, $p=.008$), as well as significant interactions of Trial X Modality ($F_{1,15}=5.55$, $p=.032$). Given the significant Trial X Modality interaction, we followed up with two protected ANOVAs, testing differential alpha band activity associated with task-set
reconfiguration processes between and within modalities (see methods section for rationale). The
between modality ANOVA tests differences in anticipatory alpha power between visual and
auditory modality considering Trial (switch versus repeat), Time (early versus late), and Region
(frontal versus parietal) as factors. The within modality ANOVA tests differences in anticipatory
alpha power between switch and repeat trials considering Modality (visuals versus auditory),
Time (early versus late), and Region (frontal versus parietal) as factors. The between modality
ANOVA revealed main effects of Trial (F_{1,15}=5.55, p=.032), Time (F_{1,15}=5.26, p=.037), Region
(F_{1,15}=6.45, p=.023), and a Trial X Time X Region (F_{1,15}=8.23, p=.012) interaction. Region-
specific tests confirmed that a trend towards a Trial X Time interaction was only evident over the
parietal-occipital scalp region (F_{1,15}=3.97, p=.06). The within modality ANOVA revealed a main
effect of Trial (F_{1,15}=5.55, p=.032), and a Trial X Time X Region (F_{1,15}=8.23, p=.012)
interaction. Region-specific tests confirmed that a trend towards a Trial X Time interaction was
only evident over parietal-occipital scalp region (F_{1,15}=3.98, p=.06).

3.3. Further investigation of the behavioral indices of task-set reconfigurations

The behavioral data did not exhibit any overt indication of a classical local switch cost. Yet,
in light of the current findings regarding alpha oscillatory processes and as suggested by a
reviewer, we sought to probe deeper into the behavioral data in order to explore the relationship
of the relative behavioral success of a given task-set reconfiguration to the current findings in the
oscillatory domain. Certainly prior work has shown links between the effectiveness of alpha-
band deployment mechanisms and subsequent task success (Thut et al., 2006; Kelly et al., 2009)
To do this, we undertook a post-hoc analysis in which we sorted individual trials based on RT. On an individual participant basis, we split experimental trials based upon the median RT within a given condition (i.e., Repeat Auditory, Switch Auditory, Repeat Visual, and Switch Visual). Dividing each of these original four conditions by the median of the RT distribution yielded what we will refer to as "Fast" and "Slow" conditions for each participant and for each of the original conditions.

The reasoning behind this approach is that a Fast Switch trial reflects a more successful task-set reconfiguration than a Slow Switch trial. This comes with the necessary caveat that a raw RT value on any given trial is by no means a direct index of successful task-set reconfiguration. That is, a relatively fast response on a switch trial is not a pure index of a successful switch but necessarily indexes the multiple underlying neural events that give rise to the stochastic nature of reaction time. Thus, in an attempt to bolster the relevance of "Fast" and "Slow" trials to the successful instantiation of a new task set, we performed the following additional analysis. First, both hit trials (a correct response on a go trial) and false alarm (FA) trials (a mistaken response on a no-go trial) were included in the RT distributions of each of the experimental conditions. Next, after performing the median splits of these distributions, the proportion of hits relative to false alarms was calculated (i.e., hits/hits+FAs) yielding what we will refer to as the success rate.

Behavioral success rates were then submitted to a 2x2x2 repeated measures ANOVA with factors of Modality (visual versus auditory), Trial (switch versus repeat), and Speed (fast RTs versus slow RTs). The ANOVA revealed a main effect of Speed ($F_{1,15} = 4.72, p = 0.046$) and an interaction of Speed x Trial ($F_{1,15} = 4.55, p = 0.05$). To disentangle this interaction, the data were collapsed across Modality, and two repeated measures t-tests were conducted, one comparing the
Switch Fast condition to the Switch Slow condition, and one comparing the Repeat Fast to the Repeat Slow condition. The comparison of Switch Fast versus Switch Slow indicated a significant difference between these two conditions ($t_{15} = 2.57, p = 0.021$), reflecting the fact that the success rate was greater on Switch Fast (0.93(0.06)) versus Switch Slow (0.88(0.08)) conditions. The comparison of Repeat Fast versus Repeat Slow did not cross the significance threshold ($t_{15} = 1.48, p = 0.158$). The results of this analysis indicate that Fast Switch trials were accompanied by a greater proportion of hits to FAs compared to Slow Switch trials, suggesting that RT latency does at least partially reflect the completeness of a given task-set reconfiguration. That this relationship was specific to Switch trials and did not extend to repeat trials adds further weight to this contention.

With this established, we next sought to investigate alpha oscillatory deployment on Fast and Slow trials. From Figure 1.6 it is evident that on Auditory-Switch-Fast relative to Auditory-Switch-Slow trials a punctate increase in alpha power is evident in the last ~150ms prior to S2 onset over frontal and parietal regions. This effect is wholly absent in the SCPs comparing Auditory Repeat Fast to Auditory Repeat Slow. In the Cue Visual conditions, both Switch and Repeat comparisons exhibit greater alpha desynchronizations on Fast trials relative to Slow trials. However, on observation of the SCPs, Repeat trials show a more focal effect over parietal-occipital areas, while this effect on Switch trials is present over frontal regions as well.

4. Discussion
We set out to assess the role of anticipatory alpha-band mechanisms during preparation for the first instance of a new task relative to a repeated instance of that same task, on the premise that a key component of initial task-set reconfigurations would involve a vigorous and selective suppression of processing within circuits responsible for the “old” task. And indeed, when we compared the differential deployment of anticipatory alpha-band activity on switch versus repeat trials, by contrasting anticipatory alpha-band power between sensory modalities (i.e. preparing for an auditory versus preparing for a visual task), we found considerably greater differential activity between modalities during switch trials. Further, this differential modulation onset earlier and had a considerably more extensive topographical distribution across the scalp, with clear additional foci evident over more frontal cortical regions. On first assessment, this pattern seems entirely in line with our original thesis that greater attentional suppression mechanisms would be deployed on switch trials relative to repeat trials as the system worked to “erase” the old task-set configuration. However, inherent in this thesis is the notion that greater differential activity should be driven by increased alpha-band suppressive mechanisms during switch trials – i.e. greater synchronization over fronto-parietal control regions. This, however, is not what was found here. Instead, when we made within-modality comparisons of switch versus repeat trials, a wholly different picture emerged. The increases in differential between-modality effects were actually driven by greater desynchronizations rather than the predicted increases in synchronization. Further, these differential effects were entirely driven by changes in alpha-band power during anticipations of the visual task rather than the auditory task. When switch and repeat trials in anticipation of the auditory task were compared, there were essentially no differences found, with late increases in synchronization of alpha-band activity found to be just
as prominent during repeat trials as they were during switch trials. In contrast, desynchronizations of alpha during visual trials were found to be substantially stronger and earlier on switch trials than they were on repeat trials. These more vigorous desynchronizations also showed a more wide-spread scalp topography that included a prominent focus over fronto-central scalp in addition to the more typical parieto-occipital foci. How then do the current results accord with our original hypothesis?

4.1. Performance Measures and Alpha-Band Activity

The pattern of behavioral results is instructive here. First, when one compares task performance on mixed-task blocks to that on pure-task blocks, it is clear that the need to switch between tasks had a major impact on task accuracy. Participants were considerably less able to discriminate targets (even on repeat trials) during the blocks where switching was required as opposed to blocks where only one task was performed alone over extended periods. On the other hand, the use of instructional pre-cues to indicate which task was to be engaged during mixed blocks led to the complete alleviation of the classical switch-costs that are typically seen during mixed blocks. The implication is that whatever switching processes were deployed in advance of the switch trials must have been fully effective, in that no further improvement in performance was observed on repeat trials, neither in terms of accuracy or speed. In fact, in the case of the visual task, there was a slight slowing of performance on repeat trials that suggested that anticipatory resources were not as effectively deployed as they had been on the preceding switch trials. This latter finding is consistent with the recorded physiology in that there was clearly less
alpha-desynchronization on visual repeat trials than on visual switch trials, suggesting less effective engagement of visual cortical regions.

Why would more effortful deployment on switches lead to differential alpha-involvement during visual anticipation but not auditory anticipation? One simple answer may be that anticipatory alpha-suppression mechanisms were fully and effectively deployed during auditory switch trials and no additional enhancement of this processing strategy was possible on repeat trials. On the other hand, the strong desynchronizations seen during the visual switch trial could represent the vigorous deployment of anticipatory preparatory mechanisms in visual cortices needed to effectively prepare the new visual task, whereas the ‘relaxation’ of this desynchronization during visual repeat trials may represent the withdrawal of resources once optimal task performance levels have already been achieved on the switch trial.

A more nuanced view emerged, however, when we conducted post-hoc analyses of these behavioral patterns. Based on the suggestion of a reviewer of this manuscript, we sought to establish whether more effective switches of task were associated with more vigorous deployments of alpha-band mechanisms. Prior work, for example, has shown that the strength of modulation of anticipatory alpha-band processes is related to subsequent success rates in difficult visual discrimination tasks (Thut et al., 2006; Kelly et al., 2009). It is not entirely straightforward, however, to derive a behavioral measure of “more successful” switches with the current design, since the perceptual discriminability of the stimuli to be acted upon was not manipulated. One possibility though, was that faster switches might represent more effective switches, and so we divided the reaction time distribution of each participant into a FAST and a SLOW half. In support of the notion that faster switches were more effective switches (i.e. trials
where the switch cost was most ameliorated), we found that commission error rates were also significantly lower for fast switches than slow switches. That is, participants were much less likely to respond in error when they responded more quickly. In turn, when we examined the alpha-band processes associated with the fast vs. slow switches, we found that alpha synchronization was amplified in the late anticipatory phase in the attend-auditory condition, and that alpha desynchronization was more vigorous in the attend-visual condition. Since this pattern of results was uncovered during post-hoc analyses, it will bear replication in future work, but these data do point to the link between more effective alpha-band deployments and more effective task-set reconfigurations during switch trials.

4.2. Is Alpha-band Activity Exclusively a Visual Mechanism?

Another possibility is that alpha-band activity represents a mechanism exclusive to the visual system, and as such, all alpha-modulations should be interpreted insofar as they represent changes in visual receptiveness. A number of recent studies, however, suggest otherwise. First, that alpha-band processes over parieto-occipital scalp are also engaged during audio-spatial selective attention tasks has been shown in a pair of recent studies. Kerlin and colleagues showed distinct lateralization of alpha-band activity over posterior (presumably visual) regions when participants were required to deploy attention to competing spoken sentences presented either to the left or right side of space (Kerlin et al., 2010). Compellingly, the strength of this alpha-band lateralization was related to the amplification of speech-related activity within the attended stream, suggesting that alpha suppressive mechanisms were indeed involved in biasing audio-
spatial attention. Similarly, our group examined anticipatory alpha-band activity during a purely audio-spatial task, also showing clear lateralization of oscillatory activity over parieto-occipital scalp, suggesting that even when no visual events were to be anticipated, visuo-spatial oscillatory processes were engaged (Banerjee et al., 2011). In that study, we also compared anticipatory alpha-band processes between the audio-spatial and a closely matched visuo-spatial paradigm. When attentional deployments to left and right space were collapsed so that the involvement of more general anticipatory alpha-band control processes could be examined, it was clear that there was a strong focus over right parietal scalp sites for both the auditory and visual tasks. Compellingly, the topography of this activity was completely distinct between sensory modalities, such that a strong focus over medial inferior-parietal scalp was observed during visuo-spatial deployments, whereas a more lateral right parietal focus was observed for audio-spatial deployments. As such, the data pointed to the involvement of distinct anticipatory alpha-band processes in both auditory and visual spatial attention deployments, and that these were generated in sensory-specific control fields within the right parietal attention network. In agreement with these results, sensory-specific selective attentional fields within the inferior parietal sulcus (IPS) complex have also been recently shown using functional neuroimaging where auditory spatial control regions were found to be more lateral than visual control regions (Kong et al., 2012). Lastly, in a study employing direct intracranial subdural recordings from the lateral surface of the temporal lobe in humans performing an intersensory selective attention task, our research group found clear evidence for locally-generated auditory-cortical alpha-band activity, and for its involvement in selectively biasing auditory cortical processing (Gomez-Ramirez et al., 2011). In that study, participants were asked to sustain their attention to either the
auditory or visual modality while a constant stream of competing bisensory inputs was presented. They performed a difficult perceptual task within the attended sensory stream and we asked what the role of oscillatory activity in modulating auditory cortex would be. We found that activity in the delta band (1-2 Hz) entrained to the regular presentation rates of the task stimuli, but that the phase of delta reversed depending upon which sensory modality was to be attended on a given block of trials. We also found that modulation of alpha-band power was coupled to the phase of the ongoing delta entrainment, and that this led to increases in alpha-band power over auditory cortex that were coincident with the presentation of to-be-ignored auditory stimuli when attention was specifically deployed to the difficult visual task. As such, there was clear evidence for a role for alpha-band activity in modulating the responsiveness of auditory cortex, and the pattern of results was entirely consistent with the notion that this activity served in a suppressive role. The implication of this series of studies is that alpha-band activity is very much involved in the deployment of attentional resources within auditory cortex.

Consequently, a more likely explanation for the lack of obvious alpha-modulation from auditory cortical regions in many of the studies that have used non-invasive scalp recorded EEG methods, including the current one of course, may pertain to simple issues of cortical geometry. The projection of auditory cortex to fronto-central scalp necessitates propagation of activity across a considerable distance. It seems a distinct possibility that auditory cortical generators of the relatively high-frequency oscillatory activity of the alpha-band, largely buried as they are along the supratemporal plane, may not allow for effective signal propagation to the fronto-central scalp surface.
A recent behavioral study by our group may also inform the present results in that it too points to the engagement of particularly vigorous task inhibition processes on switch trials (Weaver et al., submitted). In that study, participants were free to choose which of two visual tasks to adopt on a given trial, indicating their choice with a button push. They then received a cue that typically matched their choice, but on the occasions when the cue unexpectedly contradicted their initial choice, clear costs ensued. The key observation was that costs were especially severe on trials when participants had just chosen to switch tasks but then had to unexpectedly repeat the previous task. The implication is that suppression of the old task must have been markedly stronger in response to one’s choice to switch, such that the necessity to go back and engage (i.e. repeat) the old task proved particularly cumbersome. The present results accord well with this pattern in that the most vigorous preparatory neural processes are clearly evident on the switch trial, manifest as enhanced desynchronization of alpha activity for switch-visual trials. This pattern of effects is quite consistent with the tenets of a biased competition model. When two tasks must be juggled, it is a reasonable proposition that both are held in neural states of relative readiness, and both neuroimaging (Wylie et al., 2004a; 2006) and ERP data (Foxe et al., 2005a) clearly support this contention. Stated otherwise, it seems highly improbable that each task representation would be instantiated *de novo* whenever a switch of task is called for. The obvious next question then is what the nature of the balance between the two task representations might be and how might these differ on switch versus repeat trials? The most economical set point would likely be a situation where the balance between competing task representations is quite finely tuned, such that the currently disengaged task, while temporarily ‘dormant’, can be readily reinstated. It seems reasonable to suppose that the fine balance between
representations would be more easily titrated during repeat trials, whereas switch trials might be characterized by more dramatic swings in this balance to ensure that the new task is properly instantiated.

In fact, it is worth considering what the nature of the cue stimulus and the temporal trajectory of cue-decoding would be in a paradigm such as the one used herein. The cue stimuli clearly serve a dual purpose. The first purpose is to act as a warning stimulus, marking the beginning of a temporally stereotyped trial, and this information is provided by the cue very early during the processing hierarchy. That is, the semantic information content of the cue (i.e. which task is to be engaged), which is encoded in the pictorial representation, will not be available until relatively later in processing (likely after 150 ms) (Thorpe et al., 1996). In contrast, simple detection of the occurrence of the cue is registered some 80-100 ms earlier. This raises an interesting dichotomy and one that bears on the instantiation of preparatory processes. It is entirely likely that initial registration of the cue as a temporally predictive warning stimulus would initiate parallel preparation of both task-set configurations before the system has any access to the semantic content of the cues, and that it is only later, as this content is decoded, that the system begins to bias preparatory processes towards the cued task. Again, the notion that the now irrelevant task preparatory processes would somehow be aborted completely is not consonant with the nature of ongoing neural processing dynamics. Rather, the probability is that preparation for the irrelevant task begins to decay, or is actively suppressed, as preparation for the relevant task begins to be actively enhanced.

4.3. Previous explorations of the role of oscillations during switches of task
Results from a recent audio-visual task-switching study are in very close agreement with those reported herein (Rapela et al., 2012). In mixed blocks, a stream of interspersed auditory and visual stimuli were presented and occasional cues (the words “look” and “hear”) instructed participants to switch to the task within the cued modality. Strong desynchronization of alpha-band activity was measured when the cue counseled a switch to the visual task, a desynchronization that subsequently attenuated substantially once sustained attention had been established for the visual stream (i.e. for repeat trials). When attention was switched to the auditory modality, a clear synchronization of high alpha-band activity emerged, and as here, this synchronization did not significantly attenuate over time as attention was sustained on the auditory inputs. Unfortunately, the authors did not report performance measures on the tasks, so the modulations of oscillatory activity cannot be interpreted accordingly. Nonetheless, there is striking similarity between the physiological effects they report and those of the current study.

The modulation of alpha-band activity over parieto-occipital scalp as a function of task switches versus repeats has also been addressed in studies where both tasks were performed on visual stimuli (i.e. within-modality). In one such study, for example, participants were free to choose which of a pair of tasks to perform on a set of geometric shapes (either a location or a color task) (Poljac & Yeung, 2012). Performance measures made it clear that the location task proved easier in that participants were both faster and more accurate on this task. What these authors found was that alpha-desynchronizations were equivalent preceding switches to both tasks, whereas there was a distinct increase in synchronization preceding repeats of the easier location task, an effect not seen for repeats of the more challenging color task. Similar to the
differences seen here for switch versus repeat visual trials, these data suggest that equally vigorous desynchronizations were employed to switch to each visual task, regardless of difficulty, but that once a switch had been made and the participants were ‘locked onto’ the task at hand, resources could be withdrawn from the easier location task. More vigorous alpha-desynchronizations over parieto-occipital scalp preceding switch versus repeat trials in purely within-modality visual task-switching designs have now been reported by a number of groups (Sauseng et al., 2006).

This issue of differential oscillatory suppression as a function of task difficulty was also recently addressed in a study in non-human primates (Buschman et al., 2012). Recording from prefrontal cortex, monkeys were required to switch between performing a color discrimination task and a line orientation discrimination task. Saccadic reaction times were significantly slowed by a switch away from the orientation task to the color task, but not vice versa. This pattern led Buschman and colleagues to consider the orientation task as 'dominant' over the color task. Performing the 'non-dominant' color task was accompanied by an increase in alpha coherence in neuronal populations showing selectivity for the orientation task, whereas performance of the dominant orientation task did not result in increased alpha coherence in neurons selective for the color task. In line with the notion of alpha-band activity as a suppression mechanism, these authors contended that performing the non-dominant task required active suppression of the dominant ensembles through an oscillatory gating mechanism, implying that this gating mechanism may be asymmetrically deployed dependent on the predisposition of the brain towards one competing task versus another.
A key distinction between these studies of within-modality switches and our between-modality study is that the two tasks are typically afforded by the same stimuli in the former, whereas in the current design, the participants switch between both the task and the stimuli affording those tasks. When one switches between auditory and visual inputs, the suppression of the potentially distracting sensory inputs can putatively be achieved by a relatively indiscriminate suppression of a large swath of cortex, likely involving early sensory regions. On the other hand, when both tasks are afforded by the same object (e.g. the printed words in a Stroop task), then the suppression mechanisms would need to target much more specific, feature-level representations. In a recent study, we assessed this issue by asking individuals to switch between a color and a motion task, where both features were afforded by the same random dot field arrays (Snyder & Foxe, 2010). Consistent with a feature-based suppression account, we found that alpha power increased within dorsal visual regions when motion was to be suppressed (i.e., when color was the relevant feature), whereas alpha power increased in ventral visual regions when color was irrelevant. One could certainly argue that in the current experiment, the auditory and visual inputs to be acted upon had no natural relationship to each other. Thus, although they are presented simultaneously and compete for resources, they may be perceived as separable objects, and the level of competition between them would likely then be less than if the tasks were afforded by features of the same object. It may be of considerable interest in future work, to employ audio-visual stimuli where there is a clear semantic relationship between the constituent inputs (e.g. animals and their related vocalizations) (Molholm et al., 2004; Molholm et al., 2007; Fiebelkorn et al., 2010).
4.4. Conclusions

We observed clear behavioral mixing costs in a cued audio-visual task, but no apparent switching costs, suggesting that preparatory processes during the cue-target period allowed for the entirely successful resolution of competition among the two task-sets. We argue that, within our design, the competing tasks are held in close states of readiness, and then "tipped" in favor of one or the other of the tasks by neural biasing mechanisms. Our findings support the contention that one of these mechanisms very likely involves the distribution of alpha oscillations among relevant cortical regions. Further work is required to fully tease apart the contribution of alpha synchronizations and desynchronizations to task-set reconfigurations.
Acknowledgements

This work was primarily supported by a grant from the U.S. National Science Foundation (NSF) to Dr. Foxe (BCS1228595). The authors would like to thank Mr. Jason Adler and Ms. Sarah Walkley for help with initial data collection. Additional support for the work of Dr. Foxe derives from a grant from the U.S. National Institute of Mental Health (NIMH RO1 MH085322).

Participants in this study were recruited and evaluated at The Human Clinical Phenotyping Core, a facility of the Rose F. Kennedy Intellectual and Developmental Disabilities Research Center (IDDRC) which is funded through a center grant from the Eunice Kennedy Shriver National Institute of Child Health & Human Development (NICHD P30 HD071593).
References


Figure legends

**Figure 1.1: Stimulus configuration.** The cue stimulus (S1) onsets at 0 ms, followed 1350 ms later by the compound bisensory S2, which consists of a pair of bilateral visual gabor patches and a pair of sequentially presented bilateral tone pips. Participants perform a difficult orientation task by comparing the orientations of the left and right Gabor patches when the visual task is cued (Cue = Image of computer monitor). Participants perform a difficult frequency discrimination task by comparing the pitch of the first and second tone pips when the auditory task is cued (Cue = Image of headphones). Fixation is maintained throughout each trial.

**Figure 1.2: Performance Data.** Reaction time (RT) data (top panel) and accuracy levels expressed as *d-primes* (bottom panel) are plotted for both mixed and pure task blocks for the auditory (red) and visual (black) tasks. For mixed task blocks, data are plotted for both switch and repeat trials. For the pure task blocks, there are by definition only repeat trials.

**Figure 1.3: Anticipatory Alpha-Band Suppression effect.** Alpha-band oscillatory activity is selectively modulated by deployment of anticipatory attention to different sensory modalities. **Panel A.** Topographic maps show the differential alpha effect over parieto-occipital scalp between attend-visual and attend-auditory trials (plotted for the 1000ms time point). **Panel B.** Corresponding alpha-band (8–14 Hz) TSE waveforms derived from the three highlighted electrode sites (central head - panel A). A sustained divergence in TSE amplitude is seen starting at ~600 ms post-cue, some 750 ms before the onset of the S2 task stimulus, which occurs at 1350
ms. Alpha-band activity is significantly greater when subjects have been cued to attend selectively to impending auditory stimulation. **Panel C.** Alpha-band TSE waveforms are ‘broken out’ as a function of whether participants were anticipating a switch trial (dotted traces) or a repeat trial (solid traces).

**Figure 1.4: Between Modality Anticipatory Alpha-Band Suppression effect. Panel A.** Alpha-band TSE waveforms during the anticipatory period preceding impending switch trials are displayed for a trio of representative fronto-polar electrode sites and a similar trio of parieto-occipital sites. Of note is the divergence in alpha-power between attend-auditory (red dotted traces) and attend-visual (black dotted traces) over the frontal scalp sites. The statistical cluster plot to the right shows substantial periods of both early and late alpha differentiation that encompasses both posterior scalp and frontal scalp. **Panel B.** In contrast, alpha-band TSE waveforms plotted for the same sites during anticipation of repeat trials shows no such early modulation over frontal sites. Significant alpha-band effects are only observed robustly during the late anticipatory period (1100-1300ms). **Panel C & D.** Flattened scalp projections of differential alpha-band activity (8-14 Hz) across the anticipatory period preceding “SWITCH” trials and “REPEAT” trials. It is evident that alpha-band activity is of higher differential amplitude, begins earlier in the anticipatory period and encompasses a more extensive scalp distribution for “SWITCH” trials than for “REPEAT” trials.

**Figure 1.5: Within Modality Anticipatory Alpha-Band Suppression effect. Panel A.** Alpha-band TSE waveforms during the anticipatory period preceding impending switch and repeat
trials within the auditory modality. No or minimal TSE modulations are seen and the related SCP map (right column) shows no robust periods of differential alpha-band activity as a function of this switch versus repeat comparison. **Panel B.** Alpha-band TSE preceding impending switch and repeat trials for the visual modality and the corresponding SCP reveal robust modulations between approximately 600ms and 1100ms. **Panel C & D.** Scalp maps of differential alpha-band activity for the auditory and visual modality. The most prominent focus of differential activity over parieto-occipital scalp is evident for the visual modality.

**Figure 1.6: RT-median-split Anticipatory Alpha-Band Suppression effect. Panel A& B.**

Auditory alpha-band TSE waveforms and related SCP maps comparing fast and slow RT-trials for switch trials (panel A) and for repeat trials (panel B). A robust cluster of differential alpha-band activity immediately preceding the presentation of a switch trial is associated with RT. **Panel C & D.** Visual alpha-band TSE waveforms and related SCP maps comparing fast and slow RT-trials for switch trials (panel C) and for repeat trials (panel D). Robust TSE modulations immediately preceding the presentation of the target stimulus in both switch and repeat trials are associated with RT.
Figure 1.1.

<table>
<thead>
<tr>
<th>Auditory Events</th>
<th>Visual Events</th>
<th>Tone 1</th>
<th>Tone 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cue</td>
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<td>100</td>
</tr>
<tr>
<td><strong>Time (ms)</strong></td>
<td>200</td>
<td>1350</td>
<td></td>
</tr>
</tbody>
</table>

or

![](image_url)
Figure 1.2.
Figure 1.3.

A. Topography

B. TSE by attended modality

C. TSE by attended modality and task-set (re)configuration
Figure 1.4.

A. Switch Trials

Switch auditory  
Switch visual  

Switch auditory versus Switch visual

B. Repeat Trials

Repeat auditory  
Repeat visual  

Repeat auditory versus Repeat visual

C. Switch Trial Topography: switch auditory minus switch visual

D. Repeat Trial Topography: repeat auditory minus repeat visual
Figure 1.5.

A. Auditory modality

Switch auditory  

Repeat auditory

B. Visual modality

Switch visual  

Repeat visual

C. Auditory modality Topography: switch auditory minus repeat auditory

D. Visual modality Topography: switch visual minus repeat visual

- 0.8

microVolt

- 0.8

milliseconds
Figure 1.6.

A. Auditory Switch Trials

B. Auditory Repeat Trials

C. Visual Switch Trials

D. Visual Repeat Trials
Chapter 2

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

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Submitted for publication at Developmental Science, John Wiley and Sons.
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. What's more, amplitude in this band modulates systematically when individuals switch between 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, likely due to still maturing top-down fronto-parietal networks of cognitive control.
1. 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.

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).

2. Methods

2.1. 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 questionnaire (children and adolescents) or self-report (adults), all participants were of age appropriate educational grade, did not use any psychoactive medications or have histories of developmental, psychiatric, learning or attention difficulties.

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) = 0.41, p > 0.8).

2.2. 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 2.1). 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 (~3° square visual angle, Weber contrast = -0.14) or a computer monitor (~3° 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 (Foxe 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 2.1 for a schematic of the paradigm).

2.3. 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.
2.4. 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 gabor 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 x 2 x 2 x 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).

2.5. 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). 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.

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. Next, 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. For each participant, an independent component analysis (ICA) was performed on the data, concatenated over all data blocks, 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 occulo-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 procedure, data were epoched from -1500 to 2500 ms around the onset of the cue stimulus. 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 ±120 μV was used.

2.6. 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 (Foxe 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 steps, 20 ms time steps). The data were then baselined from -875 to -375 such that the mean of this window was subtracted from the entire time series, and divided by its standard deviation, yielding deviations from the baseline period in units of standard deviation (Roach & Mathalon, 2008).

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 2.2). 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.

After equating for trial numbers for Switch and Repeat trials, a 2 x 2 x 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 $p$s>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 13-17 age group it was 81.06(28.74).
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 x 2 x 2 x 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).

3. Results

3.1. Behavior

The d-prime values across the conditions and groups are depicted in FIG 2.3A. 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 < 0.05, and t(48) = -2.84, p = 0.007, respectively). No statistical difference was evident between the 8-12 and 13-17 age groups (p>0.7).

In addition to the main effect of Age Group, the ANOVA also showed a three-way interaction of S2 x Trial x Age Group (F(4,140) = 2.48, p < 0.05). As is evident when the d-prime values are collapsed across the Cue conditions (FIG 2.3B), 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 ($t(41) = 2.56$, $p < 0.02$). No other switch cost values across the S2 conditions differed significantly among the age groups (all $p$s $> 0.5$). Observation of the switch costs for both Cue Auditory (FIG 2.3C) and Cue Visual (FIG 2.3D) 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 2.3B). 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 x S2 x Trial interaction ($F(2,140) = 6.87$, $p = 0.001$). On observation of the d-prime data collapsed across the participant groups (FIG 2.4A), 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 2.4B). 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 2.4C).

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 2.4C). 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 ($t(72) = 2.56, p < 0.02$). 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 ($t(72) = 1.71, p < 0.03$ 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.

3.2. Electrophysiology

3.2.1. 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 x Trial x Age ($F(2,70) = 4.40, p < 0.02$). As an initial step in addressing this interaction, separate 2 x 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, $p < 0.04$) indicating that alpha power on Repeat trials ($M = 5.25$, SD = 2.59) was increased relative to Switch trials ($M = 5.11$, SD = 2.2.46). 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 x Trial (F(1,29) = 7.41, $p < 0.02$). Two approaches were taken to untangle the interaction of Cue x 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 ($t(29) = 2.72$, $p < 0.02$). 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 ($t(28) = 1.01$, $p > 0.3$), 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) ($t(28) = -2.73$, $p < 0.02$).
Finally, the ANOVA on the 18-34 Age Group showed a main effect of Cue (F(1,19) = 5.06, \( p < 0.04 \)) a main effect of Trial (F(1,19) = 7.58, \( p < 0.02 \)) and a Cue x 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 x 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, \( p > 0.6 \)), 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).

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, \( p > 0.2 \)), 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, \( p < 0.02 \)), 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).
3.2.2. 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 ($t(51) = 2.25, p < 0.03$). 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 x 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 ($t(41) = 0.42, p > 0.6$).
3.3. 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 2.3D) compared to Cue Auditory trials (FIG 2.3C). 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 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 2.6, this analysis showed a significant negative correlation across the
participants over the left parietal-occipital sensor group ($r = -0.29, p < 0.02$) but not over the
right sensor group ($r = -0.08, p > 0.5$). In an additional analysis, the correlation between the
switch-cost behavioral metric and alpha power modulation was computed at all sensor sites. As
illustrated in FIG 2.6, 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.

4. 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 (Foxe et al., 2014). The increasing evidence that the deployment of alpha oscillations acts to suppress task-irrelevant brain activity (Foxe & 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
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 2.5), 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 likely 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.

4.1. 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 2.4B), 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 2.4C). 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).

Applying 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.
4.2. 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.

4.3. 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.
Acknowledgements

The authors extend their sincerest appreciation to Sarah Ruberman, Joanna Peters, and Frantzy Acluche for help with data collection. This work was supported by the U.S. National Institute of Mental Health (MH085322 to S.M. and J.J.F.) and the U.S. National Science Foundation (BCS1228595 to J.J.F and S.M.). Participants in this study were recruited and evaluated at The Human Clinical Phenotyping Core, a facility of the Rose F. Kennedy Intellectual and Developmental Disabilities Research Center (IDDRC) which is funded through a center grant from the Eunice Kennedy Shriver National Institute of Child Health & Human Development (NICHD P30 HD071593).
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Figure legends

**Figure 2.1. 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 Gabor, presented at 1355 ms.

**Figure 2.2. 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 standard deviation relative to the pre-cue baseline.

**Figure 2.3. 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 2.4.** 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 2.5.** 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 2.6.** 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.
Figure 2.1.
Figure 2.2.
Figure 2.3.
Figure 2.4.
Figure 2.5.
Figure 2.6.
Chapter 3

Susceptibility to distraction in autism spectrum disorder: Probing the integrity of oscillatory alpha-band suppression mechanisms.

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Abstract

When attention is directed to one information stream over another, the brain can be configured in advance to selectively process the relevant stream and suppress potentially distracting inputs. One key mechanism of suppression is through the deployment of anticipatory alpha-band (~10Hz) oscillatory activity, with greater alpha-band power observed in cortical regions that will ultimately process the distracting stream. Atypical attention has been implicated in autism spectrum disorder (ASD), including greater interference by distracting task-irrelevant inputs. Here we tested the integrity of these alpha-band mechanisms in ASD using an intersensory attention task. EEG was recorded while participants were cued on a trial-by-trial basis to selectively deploy attention to the visual or auditory modality in anticipation of a target within the cued modality. Whereas typically developing children showed the predicted alpha-band modulation, with increased alpha-band power over parieto-occipital scalp when attention was deployed to the auditory compared to the visual modality, this differential pattern was entirely absent at the group level in the ASD cohort. Further, only the ASD group showed impaired performance due to the presence of task-irrelevant sensory information. These data suggest that impaired modulation of alpha-band activity plays a role in increased distraction from extraneous sensory inputs in ASD.
1. Introduction

In a crowded noisy restaurant, one might employ selective attention to focus on the menu while ignoring the discussions at neighboring tables. In this situation, both visual (the text printed on the menu) and auditory (the surrounding conversations) inputs compete for limited neural resources. Selective attention serves to bias competition between multiple inputs toward the input that immediately serves the behavioral goals of the organism (e.g., choosing an entree at the restaurant) (Desimone and Duncan 1995), both by enhancing processing of relevant sensory inputs and by suppressing processing of those that are irrelevant. Canonical features of Autism Spectrum Disorders (ASD), particularly those falling within the diagnostic category of rigid and repetitive behaviors, have been hypothesized to result in part from atypical selective attention (Ciesielski, Courchesne et al. 1990; Townsend and Courchesne 1994; Ciesielski, Knight et al. 1995; Teder-Salejarvi, Pierce et al. 2005; Remington, Swettenham et al. 2012). Previous investigations have suggested 'overselective' attention in ASD (Lovaas, Schreibman et al. 1971), referring to a tendency to attend intensely to one stimulus while completely disregarding other sources of information, as well as impairments in the orienting and subsequent reorienting of attention (Wainwright-Sharp and Bryson 1993; Burack 1994; Courchesne, Townsend et al. 1994; Iarocci and Burack 2004; but see Iarocci and Burack 2004). More recently, however, there is mounting evidence that individuals with an ASD also have a specific deficit in filtering out, or inhibiting, distracting task-irrelevant information (Christ, Holt et al. 2007; Christ, Kester et al. 2011; Adams and Jarrold 2012). For example, in variations on the flanker visual filtering task (Eriksen and Eriksen 1974), in which participants must detect a
visual target that is surrounded by varying degrees of distracting information, individuals with an ASD are more impaired by the presence of distractors than are TD individuals (Christ, Holt et al. 2007; Christ, Kester et al. 2011; Adams and Jarrold 2012). Further support comes from an fMRI study on selective attention by Ohta, Yamada et al. (2012) in which there was reduced suppression of distractor information in visual cortex in ASD compared to TD adults. Unfortunately, with ceiling performance for both groups, there was no behavioral correlate to this reduced suppression of neural activity and thus it is not clear if this reflected impaired visual suppressive mechanisms in ASD, or alternatively that such suppression was simply not necessary to perform the task. Yet additional evidence for suboptimal biasing of the brain's neural resources in ASD comes from electrophysiological investigations of selective attention, which have reported poorer discrimination performance and more false alarms to non-target stimuli, and reduced selective neural processing of information that is to be attended versus ignored in ASD (Ciesielski, Courchesne et al. 1990; Ciesielski, Knight et al. 1995; Teder-Salejarvi, Pierce et al. 2005).

Non-invasive high-density recordings of the brain's electrical activity have demonstrated that spectral power in the alpha rhythm (~8-14 Hz) modulates in accord with the distribution of attention. This has been shown under spatial (Worden, Foxe et al. 2000; Kelly, Lalor et al. 2006; Rihs, Michel et al. 2007; Banerjee, Snyder et al. 2011), feature-based (Snyder and Foxe 2010), and intersensory (Foxe, Simpson et al. 1998; Fu, Foxe et al. 2001; Gomez-Ramirez, Kelly et al. 2011) manipulations of attention. Alpha is typically greater over task-irrelevant cortical areas, and it is thought that alpha activity acts to filter out irrelevant sensory input (Foxe, Simpson et al. 1998; Fries 2001; Kelly, Lalor et al. 2006; Thut, Nietzel et al. 2006; Rihs, Michel et al. 2007;
Capotosto, Babiloni et al. 2009; Romei, Gross et al. 2010; Bollimunta, Mo et al. 2011; Foxe and Snyder 2011; Buschman, Denovellis et al. 2012). Since individuals with an ASD show abnormalities in the suppression of task-irrelevant information, here we sought to evaluate, for the first time to the best of our knowledge, the integrity of these alpha suppression mechanisms.

We recorded high-density EEG while children and adolescents with an ASD and age and IQ matched typically developing controls performed a cued intersensory selective attention task. In this paradigm, on each trial participants receive a cue followed by a unisensory or bisensory stimulus. The cue informs them whether to perform a visual or an auditory target detection task, thus biasing their attention toward one sensory modality and away from the other. Previous work from our laboratory has shown this to induce robust suppression of information in the task irrelevant sensory modality, as indexed by increases in alpha power in the interval between the cue and the imperative stimulus over parieto-occipital regions when an individual is attending the auditory modality and must ignore distracting information in the visual modality (Foxe, Simpson et al. 1998; Fu, Foxe et al. 2001; Gomez-Ramirez, Kelly et al. 2011). This has been interpreted as a 'full-field' suppression of visual inputs, which are wholly irrelevant when the participant has been cued to attend only to the auditory stimuli. Here we assessed the degree to which both ASD and TD children deploy alpha strategically, and related this to behavioral indices of distractibility by task-irrelevant sensory information.

2. Methods

2.1. Participants
We chose to restrict the participant age-range to between 9 and 16 years, a range within which participants were expected to be able to follow task instructions. Twenty ASD children and adolescents (4 female) and 20 age and nonverbal IQ matched TD children and adolescents (4 female) participated in the experiment (see Table 1A for participant descriptives). An additional 7 participants (4 ASD) were excluded from the study due to an inability to successfully perform the task. Five (3 ASD) had chance-level behavior during a preliminary psychophysical titration session, and an additional 2 (one ASD) passed this stage of the study, but performed below chance during the experimental session (see Table 1B for excluded participant descriptives).

For the ASD group, diagnoses of ASD were made using both the Autism Diagnostic Interview-Revised (ADI; Lord, Rutter et al. 1994) and the Autism Diagnostic Observation Schedule (ADOS; Lord, Rutter et al. 1999) and confirmed by judgment of an experienced clinician. All participants passed the algorithmic thresholds for diagnosis of ASD on both the ADI and ADOS. Of the 20 children in the ASD group, 9 had a diagnosis of autistic disorder and 11 of Asperger’s disorder. Parents were asked to refrain from giving their children (n=4) stimulant medication in the 24 hour period prior to the testing session. Five children were taking other psychoactive medications (aripiprazole, sertraline, gabapentin, atomoxetine) at the time of participation.

Exclusionary criteria for both groups included a nonverbal IQ below 80, and a history of head trauma, epilepsy, or premature birth. Nonverbal IQ was measured with the Wechsler Abbreviated Scale of Intelligence (Weschler 1999), the Wechsler Abbreviated Scale of Intelligence-Second Edition (Weschler 2011), or the Wechsler Intelligence Scale for Children-
Fourth Edition (WISC-IV; Weschler 2003). All participants were screened for normal or corrected-to-normal vision as well as normal hearing. Exclusion criteria for the TD group included use of psychoactive medications or a history of developmental, psychiatric, learning, or attention difficulties as assessed by a parent history questionnaire. TD children were also excluded if they had a biological first-degree relative with a known developmental disorder.

Participants were matched in a pair-wise fashion, such that no TD-ASD pairing exceeded a threshold of ± 1 SD with respect to performance IQ (PIQ) or ~1 year of age. An analysis of variance (ANOVA) indicated that there were no significant differences between participant groups in age (F(1,38) = 0.003, $p = 0.95$), PIQ (F(1,38) = 0.007, $p = 0.93$), or full-scale IQ (FSIQ) (F(1,38) = 2.40, $p = 0.13$). A between groups effect, however, did reach significance on the measure of verbal IQ (VIQ) (F(1,38) = 7.46, $p = 0.009$), reflecting that the ASD group tended to have lower (though within normal range) VIQ scores than their TD counterparts.

Before participation, a parent or legal guardian of each child provided written informed consent, and written or verbal assent was obtained from each child. All procedures were approved by the Institutional Review Board of the Albert Einstein College of Medicine, where the experiments were conducted, and conformed to the tenets for the responsible conduct of human research as laid out in the Declaration of Helsinki. Participants received a modest fee ($12/hour) for their efforts.

2.2. Stimuli and Task
A cued intersensory attention task was employed in which each trial consisted of an instructional cue, an intervening blank preparatory period, followed by a task-relevant second stimulus (S2) (see FIG 3.1). 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.

Visual stimuli were presented on a gray background. The cue stimulus consisted of a simple gray line-drawing depicting either a pair of headphones (~3° square visual angle, Weber contrast = -0.14) or a computer monitor (~3° square visual angle, Weber contrast = -0.10). These cue stimuli instructed the participant as to which sensory modality (auditory or visual) was to be attended when the 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 pseudorandomly on a trial-by-trial basis to attend to either the visual or auditory components of the upcoming S2 event. The likelihood of a task switch or repeat (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%.

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 (see Procedure below). When subjects
detected a frequency difference between the pair of tones, they were instructed to respond with a
fast, accurate button push.

The visual S2 stimulus consisted of a pair of Gabor patches (100 ms duration, 4.8° in
diameter, 0.25 cycles per 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 (see Procedure below), and participants were
instructed to respond to targets with a 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 or 1350 ms\(^1\) similar to previous applications of this paradigm from our
laboratory. 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 3.1 for a schematic of the stimulation paradigm).

2.3. 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 on 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 and 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.
2.4. Behavioral Measurements

To obtain measures of behavioral performance $d$-prime and reaction time (RT) measures were calculated. Only correct RTs (i.e., hits) 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, were included.

The $d'$ 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. $d'$ 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 and Swets 1966). For the estimation of $d'$, hits were calculated using the same 95% threshold time window as in the case of the RTs. Correct responses to targets outside this window were labeled as misses. Inspection of the behavioral data ($d'$) on a block-by-block basis, indicated that several participants had temporarily waned in task performance, or even ceased to perform the task, for certain blocks. In order to restrict our analyses to periods in which participants were clearly performing the task, we discarded any blocks in which the average $d'$ value in either the cue-visual or cue-auditory conditions fell to zero or below. $d'$ values of zero indicate that the probability of a false-alarm is equal to the probability of a hit, and thus detection can be said to be at chance. This threshold is quite liberal but it ensured that participants were performing the task above chance for all analyzed blocks.

Prior to the exclusion of blocks based on these criteria, the TD group completed a mean 21.15 ($SD = 2.98$) blocks, and the ASD group completed a mean 21.15 ($SD = 3.25$) blocks. Of
these blocks, 9.42% (SD = 12.68) were rejected in the TD group and 14.16% (SD = 17.80) were rejected in the ASD group. An Independent samples t-test indicated that rates of block rejection were not statistically different between diagnostic groups (p > 0.3). Across diagnostic groups the rate of block rejection bore no statistically reliable relationship to the age of the participant (r = 0.07, p > 0.6). Block rejection showed a negative trend as a function of PIQ, but did not reach statistical significance (r = -0.26, p = 0.09), and breaking this analysis out among the two diagnostic groups did not reveal a significant relationship for either group (TD: r = -0.18, p > 0.4; ASD: r = -0.32, p > 0.2). Furthermore, across the two groups, the relationship between block rejection and VIQ was not significantly different (r = -0.21, p > 0.2), nor was this relationship significant within either of the two groups (TD: r = -0.03, p > 0.8; ASD: r = -0.27, p > 0.3).

2.5. 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). 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 and Makeig 2004) were applied for the analysis of the data.
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 0.5 Hz (Butterworth IIR, 20 db/octave, zero-phase), and re-referenced to FPz, a central fronto-polar site. Next, 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. For each participant, an independent component analysis (ICA) was performed on the data, concatenated over all data blocks, using the *infomax* algorithm (Bell and Sejnowski 1995) as implemented in the EEGLAB toolbox. Following the ICA decomposition, we used a two-step procedure to identify components reflecting oculomotor 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 procedure, data were epoched from -1000 to 2500 ms around the onset of the cue stimulus. 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 3 bad electrodes across the array of 72 channels, then it was discarded. Otherwise, bad electrodes were interpolated using 3 to 4 nearest neighbors. Finally, over all scalp electrodes, a trial rejection threshold of ±120 μV was used.
2.6. Frequency Analysis

To measure changes in oscillatory power in the preparatory period, the data were analyzed using a short-term Fourier transform (STFT) approach (as implemented in the EEGLAB function newtimef), with fixed data segments of 250 ms multiplied by a hanning window, and 5 ms steps. Only bisensory S2 stimuli, which accounted for 67% of the total trials, were submitted to this analysis. This resulted in physically identical stimuli (within participant) across the two cued attention conditions. Since the STFT technique employed a fixed window size of 250 ms for all frequencies examined, a given time point in the STFT time-course reflects the spectral decomposition of the original data over this entire window. Although the hanning window employed in the analysis emphasizes data in the center of the window relative to the edges, care must still be taken when interpreting the output of the STFT. To avoid spectral input from the post-stimulus period, we used a causal STFT technique. Specifically, rather than centering the window around a data point of interest for the STFT, the window incorporated data from -250-0 ms for a given time point in the decomposition. Although this temporally smears the data forward in time to an extent, it nevertheless insures that a given data point in the STFT only reflects activity up to that point, and not after it. The power spectra were then baselined by subtracting the mean power spectra from -750 to 0 ms prior to cue onset, and dividing by the standard deviation in this period. This method produces baseline-adjusted $z$ score values (Roach and Mathalon 2008), thus normalizing across possible inter-subject variability in raw power. All alpha power indices are in these baseline-adjusted $z$-scores unless otherwise noted.
3. Results

3.1. Behavioral data

A UDTR procedure was performed to equate performance among participants on the unisensory S2 conditions as described above. The mean frequency difference between the 2000 Hz standard and the deviant tone, as estimated by the UDTR, was 98.00 Hz ($SD = 65.54$) for the ASD participants, and 77.75 Hz ($SD = 69.25$) for the TD participants. Likewise, for the visual target, the mean polar angle of the deviant gabor relative to the horizontally oriented standard was $14.00^\circ$ ($SD = 10.66$) for the ASD participants, and $13.40^\circ$ ($SD = 10.02$) for the TD participants. The threshold estimates between the diagnostic groups were not statistically different for the auditory ($t(38) = .93$, $p > 0.3$) or the visual ($t(38) = 0.18$, $p > 0.8$) tasks.

3.1.1. Detection (d-prime) analysis

D-prime data for each condition is presented in Table 2A. Within the cue-visual task, the TD exhibited a slight increase in detection on bisensory relative to unisensory S2 conditions ($V_{bi} = 2.14(.83)$ versus $V_{uni} = 2.06(.85)$), whereas the ASD group exhibited a decrease on bisensory relative to unisensory trials ($V_{bi} = 1.89(1.00)$ versus $V_{uni} = 2.10(.93)$). Within the cue-auditory task, both groups showed a decrease in detection on bisensory trials relative to unisensory trials.
This difference was numerically greater in the ASD group (ASD: $A_{bi} = 1.45(.95)$ versus $A_{uni} = 1.90(.70)$, TD: $A_{bi} = 1.62(.83)$ versus $A_{uni} = 1.86(.68)$).

The d-prime data were statistically analyzed using a mixed model ANOVA with diagnosis group (ASD, TD) as the between-groups factor, and Cue (cue to visual, cue to auditory), S2 (unisensory S2, bisensory S2), and Trial (switch trial, repeat trial) as within-groups factors. A main effect of Cue ($F(1,38) = 5.953, p = 0.019$) reflected that detection was better for the cue visual ($M = 2.05, SD = 0.85$) compared to the cue auditory trials ($M = 1.71, SD = 0.74$). A main effect of S2 ($F(1,38) = 13.26, p = 0.001$) further supported that target detection was better on unisensory (mean = 1.98, SD = 0.65) than bisensory trials ($M = 1.77, SD = 0.75$). Interpretation of these main effects is modulated by several interactions.

Interference effects: A Cue x S2 interaction ($F(1,38) = 8.48, p = 0.006$) was followed-up with paired t-tests comparing unisensory to bisensory S2 conditions within each cue condition (collapsed across Diagnostic Group). This revealed a significant effect of S2 in the cue auditory condition ($t(39) = 4.49, p < 0.001$), but not in the cue visual condition ($t(39) = 0.87, p > 0.4$). On cue auditory trials, detection was better on unisensory ($M = 1.88, SD = 0.68$) compared to bisensory trials ($M = 1.54, SD = 0.88$), whereas on cue visual trials this relationship did not hold up statistically.

A Diagnostic Group x S2 interaction ($F(1,38) = 5.05, p = 0.030$) was followed up with separate paired t-tests comparing unisensory to bisensory S2 conditions (collapsed across Cue conditions) within each of the diagnostic groups. There was no significant effect of S2 for the TD group ($t(19) = 1.15, p > 0.30$). Within the ASD group, there was a significant effect of S2 ($t(19) = 3.690, p = 0.002$) that was driven by a decrease in d-prime on bisensory trials ($M = 1.67$, $SD = 0.75$).
SD = 0.86) relative to unisensory trials (M = 2.00, SD = 0.72). These results indicate that task irrelevant sensory information in the bisensory trials interfered with performance in the ASD but not the TD group (FIG 3.2A).

**Switch effects:** A Cue x Trial interaction (F(1,38) = 8.90, p = 0.005) as well as a Cue x S2 x Trial interaction (F(1,38) = 6.07, p = 0.018) also reached significance. In order to disentangle these, follow-up two-way ANOVAs with factors S2 and Trial were performed, for each cue type. The ANOVA on the cue-auditory data revealed only a main effect of S2 (F(1,38) = 20.17, p<0.001), that was driven by better overall detection in the unisensory trials (M = 1.88, SD = 0.68) compared to the bisensory trials (M = 1.54, SD = 0.88). The ANOVA on the cue-visual data showed a main effect of S2 (F(1,38) = 9.85, p = 0.003) as well as an interaction of S2 x Trial (F(1,38) = 9.50, p = 0.004). Follow-up paired t-tests revealed a significant reduction in target detection for unisensory switch trials compared to the unisensory repeat trials (t(39) = 3.23, p = 0.003), whereas the comparison of cue-visual bisensory repeat trials to their switch counterparts did not reach statistical significance (t(39) = .57, p > 0.6).

Thus, within the cue-visual task, a cost of switching was observed in the unisensory (switch: M = 1.88, SD = 0.99, repeat: M = 2.27, SD = 0.93) but not the bisensory S2 trials (switch: M = 2.00, SD = 0.94, repeat: M = 2.02, SD = 0.90). Notably, the lack of an interaction between Trial and Diagnostic Group in the main ANOVA indicates that this switch cost did not differ statistically between ASD and TD groups.

### 3.1.2. Reaction-time analysis
RT data for each condition is presented in Table 2B. A 2 x 2 x 2 x 2 mixed model ANOVA was conducted on the RT data with the within group factors of Modality (auditory, visual), Trial (repeat, switch), and S2 (unisensory, bisensory), and the between group factor Diagnosis (ASD, TD).

Across the diagnostic groups, participants were faster to respond to visual targets ($M = 848.95$ ms, $SD = 184.41$) compared to auditory targets ($M = 904.30$ ms, $SD = 193.63$) as indicated by a main effect of Modality ($F(1,38) = 5.33, p = 0.027$). Participants were also marginally faster to respond to unisensory targets ($M = 862.46$ ms, $SD = 177.34$) compared to bisensory targets ($M = 890.80$ ms, $SD = 180.65$) ($F(1,38) = 4.06, p = 0.051$).

**Interference effects:** The main effects of Modality and S2 were mediated by a three-way interaction of Modality x S2 x Diagnosis ($F(1,38) = 6.77, p = 0.013$). In order to further investigate this interaction, we performed paired t-tests within each diagnostic group and modality comparing unisensory and bisensory targets. Of these, only the comparison of visual unisensory to visual bisensory targets within the ASD group reached significance ($t(19) = -2.91, p = 0.009$)(FIG 3.2B). This indicates that the three-way interaction of Modality x S2 x Diagnosis was driven by a modality specific (visual) difference between RTs to unisensory and bisensory targets within the ASD group, such that, in this group, unisensory visual targets ($M = 834.31$, $SD = 227.25$) were responded to faster than bisensory visual targets ($M = 912.06$, $SD = 225.81$)(FIG 3.2B).

### 3.2. Electrophysiological data
Observation of the spectral activity in the alpha band (8-14 Hz) in FIGs 3.3 and 3.4 reveals clear task-dependent alpha power modulation in the expected direction in the TD group starting at about 1000 ms after the presentation of the cue stimulus. In contrast, in the ASD group there is very little indication of task-based modulation. Statistical analyses were focused on the last 200 ms prior to the onset of the S2 stimulus since previous work has shown that the strongest task-dependent modulations in the alpha-band occur in this timeframe (Foxe, Simpson et al. 1998; Worden, Foxe et al. 2000; Rihs, Michel et al. 2007; Gomez-Ramirez, Kelly et al. 2009). Within this latency window, electrodes over parieto-occipital scalp, where intersensory selective-attention alpha modulations are typically observed (Foxe, Simpson et al. 1998; Fu, Foxe et al. 2001; Gomez-Ramirez, Higgins et al. 2007), were selected (P1, P3, P5, P7, PO7, PO3 and O1 on the left, and P2, P4, P6, P8, P10, PO8, PO4, and O2 on the right). These data were subjected to a 2 x 2 x 2 mixed model ANOVA with factors Cue, Hemisphere, and Diagnostic Group.

A main effect of Cue (F(1,38) = 10.08, p = 0.003), and a Cue x Diagnostic Group interaction (F(1,38) = 4.67, p = 0.037) reflected that TD participants exhibited greater task-dependent alpha power modulations (cue auditory: Mean = 1.42, SD = 3.48; cue visual: M = -0.81, SD = 1.51) than the ASD participants (cue auditory: M = 0.40, SD = 1.89; cue visual: M = -0.02, SD = 1.19). Additionally, a main effect of hemisphere (F(1,38) = 4.27, p = 0.046) indicated that alpha power in this time window was greater over the right hemisphere (M = 0.41, SD = 1.79) than over the left (M = 0.08, SD = 1.83) across conditions and diagnostic groups.

Follow-up paired t-tests within each diagnostic group comparing cue-auditory alpha to cue-visual alpha (collapsed across right and left hemisphere) were run to unpack the Cue x Diagnostic Group interaction. The t-test on the TD group revealed a significant difference
between cue conditions ($t(19) = 3.32, p = 0.004$) due to greater alpha power in the cue-auditory condition. The analysis of the ASD group showed no significant difference between cue conditions ($t(19) = 0.85, p > 0.4$). FIG 3.5A depicts the topographic distribution of alpha in the two cueing conditions as well as their difference. It is evident that the task-related alpha modulation is largest over the posterior scalp in the TD participants. To explore whether the apparent differences in alpha modulation between the ASD and TD groups were the result of the regions on the scalp that were selected for analysis, paired t-tests were performed within each diagnostic group comparing alpha power in the two cueing conditions over all scalp electrodes. As before the average alpha power in the 200 ms leading up to the onset of the S2 stimuli was used for the analysis. The False Discover Rate (FDR) was used to correct for multiple comparisons (Benjamini and Yekutieli 2001). In the TD group, a pattern of significant difference between cueing conditions distributed over posterior scalp regions was again evident (FIG 3.5B bottom). Comparisons in the ASD group yielded no significant electrodes (FIG 3.5B top). Of note, in the ASD group, even prior to FDR correction no comparisons reached significance.

3.3. Exploring the relationship between task-based modulation of alpha power and task performance

An exploratory correlation analysis was performed to test the relationship between modulations in alpha power and behavior. If increases in alpha power over parieto-occipital cortices reflect active suppression of visual throughput when performing a demanding auditory task, then greater alpha power increases during the auditory task relative to the visual task should
be positively related to performance on the auditory task. Generally, previous work has used one of two approaches in relating alpha indices and behavior, either by (1) comparing these metrics within participants by sorting individual trials (Thut, Nietzel et al. 2006; Kelly, Gomez-Ramirez et al. 2009), or (2) by comparing these metrics across individuals (Dockree, Kelly et al. 2007; Hanslmayr, Aslan et al. 2007; Yamagishi, Callan et al. 2008). Within participant approaches are arguably more sensitive to alpha-behavior relationships, as they exploit the fact that the attentional system - and the nervous system as a whole - is not time-invariant, and as such these measures can exhibit high variance throughout an experimental session. On the other hand, to the degree that this mechanism is successfully deployed in all neurologically typical individuals, one might predict a weak between participant relationship for alpha and behavior. Nevertheless, here we were more interested in inter-individual relationships between alpha and behavior, under the assertion that the reduced task-dependent alpha modulation in the ASD group reflects the atypical functioning of a mechanistic process with behavioral consequences. We were further motivated to take a between participant approach due to the relatively low trial numbers within conditions for each participant (i.e., binning alpha power into quintiles as a function of performance, as is sometimes done, would produce extremely noisy estimates).

For each participant the data point within the original 200 ms window of analysis for which the subtraction of cue visual alpha from cue auditory alpha yielded the highest value was used. We reasoned that this alpha modulation index between conditions ought to more faithfully index strategic deployment of alpha, compared to absolute alpha power on one or the other cueing conditions. We further focused on alpha activity over the right hemisphere where it tends to be largest (Foxe, Simpson et al. 1998; Gomez-Ramirez, Higgins et al. 2007; and the present data),
using the same right hemisphere electrodes as in our original analysis. For the performance metric, we took the d-prime value for the cue-auditory condition, averaged for uni- and bi-sensory targets.

For the ASD group the correlation was significant at $r = 0.56, p = 0.01$, whereas for the TD group it was not ($r = -0.25, p = 0.29$)(FIG 3.6A). For completeness we performed the same analyses for the corresponding left hemisphere electrodes, which revealed no significant relationships between the two measures (ASD: $r = 0.32, p = 0.17$; TD: $r = -0.21, p = 0.38$). When the above analyses were performed using only d-prime values from bisensory cue auditory trials the same pattern of relationships were obtained.

As suggested by a reviewer, we additionally explored the correlation between VIQ and task-related alpha power modulation, as well as the relationship between VIQ and behavioral performance. The two participant groups, while matched for age, sex, and PIQ, nevertheless had different mean VIQ scores (ASD: $M = 107.50, SD = 13.26$; TD: $M = 119.15, SD = 13.70$).

The alpha modulation index demonstrated a significant positive relationship to VIQ among the ASD participants, over the right hemisphere ($r = 0.45, p = 0.05$). This relationship was not statistically significant over the left hemisphere for the ASD participants ($r = 0.03, p > 0.8$), nor was it for either hemisphere in the TD participants (Left: $r = -0.2, p > 0.4$; Right: $r = -0.1 p > 0.5$). Performance on the visual task was positively correlated with VIQ in the TD participants ($r = 0.5, p = 0.02$), but not the ASD participants ($r = 0.4, p > 0.09$). VIQ was not significantly related to d-prime on the auditory task in TD participants ($r = -0.01, p > 0.8$) or in ASD participants, although this exhibited a trend toward significance ($r = 0.4, p = 0.08$).
4. Discussion

Recent evidence points to impaired inhibition of irrelevant sensory information in autism. Here we tested a key mechanism by which the processing of irrelevant sensory information is thought to be suppressed, task-dependent modulation of oscillatory power in the alpha band. Whereas the TD group showed alpha modulation as would be predicted based on highly replicated findings in adults, in the ASD group there was no evidence at the group level for task-based modulation of preparatory alpha power. The behavioral data were well aligned with these neurophysiological findings. That is, task irrelevant sensory information interfered with performance in the ASD but not the TD group. Specifically, the ASD group showed significant reductions in target detection for the bisensory versus unisensory S2 stimuli, and was slower to respond to visual targets that were accompanied by irrelevant auditory information. In contrast, TD group performance was not significantly affected by the extraneous sensory information. These behavioral data suggest a higher degree of interference in ASD participants within contexts involving distracting information in task-irrelevant modalities. Together these findings point toward reduced suppression of task-irrelevant distracting information in ASD, and altered functioning of neural oscillatory mechanisms employed in top-down selective attention.

4.1. Previous findings on the integrity of alpha oscillatory activity in ASD

Previous investigations examining alpha band activity in individuals with an ASD have employed either resting-state paradigms, in which the participant sits inactive while EEG is
recorded (Chan and Leung 2006; Murias, Webb et al. 2007; Coben, Clarke et al. 2008; Mathewson, Jetha et al. 2012) or recorded during passive visual stimulation (Isler, Martien et al. 2010; Milne 2011). Findings regarding alpha power over posterior parieto-occipital areas in ASD individuals relative to controls are highly ambiguous, and often contradictory. Alpha power at rest has been reported to be greater (Chan and Leung 2006), reduced (Murias, Webb et al. 2007), and no different (Coben, Clarke et al. 2008). Mathewson, Jetha et al. (2012) proposed that a degree of variability in the findings may be due to whether the participants were at rest with their eyes open or closed. This is of particular interest as it has been known since the early EEG recordings by Berger (Berger 1929) that alpha power is greater over posterior scalp when the eyes are closed and that it reduces substantially when the eyes are opened. Mathewson, Jetha et al. (2012) reported that alpha power was similar between groups during an eyes-closed resting condition, but ASD individuals exhibited greater alpha power in an eyes-open resting condition. This was interpreted as greater alpha modulation as a function of cue condition in the TD group relative to the ASD group, similar to what we observe in the current findings. Investigation of alpha oscillatory activity during visual stimulation has suggested reduced desynchronization during periods of stimulation in ASD children compared to TD controls (Isler, Martien et al. 2010), although without a pre-stimulus measurement of alpha power it remains unclear whether this was a reflection of differential modulation of alpha power with visual stimulation or an overall increase in alpha power in the ASD group. Further, it has also been reported that inter-trial phase locking in ASD adolescents is reduced relative to controls (Milne 2011). Thus, there is some evidence in the literature of decreased alpha modulation and increased variability of phase in the alpha band with visual stimulation.
4.2. Correlations between task-dependent deployment of alpha and performance in ASD

In our data, exploratory analysis revealed that greater task-related modulation of alpha power predicted better performance on the auditory selective attention task in the ASD group. It is important to note however that the ASD group exhibited a unique pattern of task-modulated alpha power in which half of the participants had either no alpha modulation or showed alpha modulation in the opposite of the predicted direction (greater alpha on cue-visual than cue-auditory trials; FIG 3.6B). Significantly, it is the participants who had this opposite pattern of modulation who performed worst on the auditory task. These alpha 'misfires' likely help power the relationship found in the ASD group. The specific relationship between performance on the auditory task and right hemisphere alpha in the ASD participants suggests that when these mechanisms are effectively deployed, they engage right-hemisphere biased posterior top-down attentional control mechanisms. A right hemisphere bias for posterior attentional processes is a highly replicated finding in the literature (Mesulam, 1981; Corbetta et al., 1993; Szczepanski et al., 2010), and alpha modulation on selective attention tasks has been shown to parallel this right hemisphere bias (Fu et al., 2001; Gomez-Ramirez et al., 2007; Banerjee et al., 2011). In contrast, the TD group did not reveal a significant relationship between alpha modulation and performance. This may be considered surprising in the face of a number of reports showing alpha power modulation to be predictive of performance on visual spatial selective-attention tasks (Thut, Nietzel et al. 2006; Yamagishi, Callan et al. 2008; Kelly, Gomez-Ramirez et al. 2009), a detection task (Hanslmayr, Aslan et al. 2007), and a sustained attention task (Dockree, Kelly et
al. 2007). As noted earlier, we were constrained in our approach to investigating the relationship between alpha modulation and behavior. A likely explanation for the failure to observe a significant relationship in the TD group is that without the negative alpha values that were present in the ASD group we were simply underpowered to observe such a relationship (see results section).

When we probed the relationship between verbal IQ (VIQ) and our dependent measures we found that in the ASD group task-based alpha modulation correlated with VIQ, whereas this was not the case in the TD group. As for the behavioral data, only the TD group demonstrated a significant relationship between VIQ and performance, and only for the visual task, but there were trends toward significant correlation between behavior-VIQ in the ASD group as well. Together these findings hint at a role for language in the effective deployment of cued attention. Indeed, the disruption of inner speech has been shown to affect performance on a cued attention task where the cue required a degree of decoding, such as in the present study (i.e., retrieving the association between a symbolic cue and the appropriate task)(Miyake et al., 2004), and inner speech has been hypothesized to be reduced in ASD participants (Williams and Jarrold, 2010; Lidstone et al., 2009; Wallace et al., 2009; Whitehouse et al., 2006). Alternately, the nature of the observed correlation between VIQ and alpha modulations in ASD could be mediational in nature insofar as ASD individuals with high verbal ability could use inner speech to compensate for dysfunction elsewhere in the cortical networks of executive function and selective attention. While these propositions are appealing in that they tie together the language dysfunction and attentional abnormalities observed in ASD individuals, these interpretations are nevertheless highly speculative, and a relationship between VIQ and cued attention is only modestly
supported by our current post hoc analyses. Further work is clearly needed to adequately explore the complex relationship of language to neurophysiological and behavioral indices of selective attention, and the interplay of cue decoding, in both TD and ASD individuals.

4.3. Alpha oscillations, top-down attention, and the neural dysconnectivity hypothesis of ASD

A distributed network of top-down attention is theorized to direct alpha-band attentional mechanisms in sensory cortices (Klimesch, Sauseng et al. 2007; Foxe and Snyder 2011). This is necessarily subserved by long-range white matter tracts that allow for communication between dorso-lateral prefrontal cortex, the frontal eye fields, parietal cortex, and sensory specific areas. The current data as it pertains to ASD individuals could thus reflect inefficient communication between spatially separated regions of the dorsal network of top-down attention.

There is compelling multimodal evidence for disordered neural connectivity in ASD (Courchesne and Pierce 2005; Uhlhaas and Singer 2006; Murias, Webb et al. 2007; Casanova and Trippe 2009; Lazarev, Pontes et al. 2010; Just, Keller et al. 2012). Some of the more consistent evidence comes from diffusion tensor imaging (DTI) studies, which have reported reduced integrity of several white matter tracts in this group (see Müller, Shih et al. 2011 for review). Importantly, differences in white matter integrity do not appear to reflect a global reduction in ASD individuals but rather evidence is emerging in support of a pattern of sparing of certain tracts (and even increased integrity in some tracts relative to controls, for instance see Thomas, Humphreys et al. 2011) and reduced integrity of others.
Among the investigated tracts, the superior longitudinal fasciculus (SLF) has been associated with reduced indices of integrity (Sahyoun, Belliveau et al. 2010; Shukla, Keehn et al. 2011). The SLF is the primary candidate tract for top-down attentional signals originating in the frontal cortices and traveling to the posterior parietal cortex. Damage to the SLF produces visual neglect (Doricchi and Tomaiuolo 2003) and direct electrical stimulation of this tract in the right hemisphere results in a profound rightward bias on a line bisection task (Thiebaut de Schotten, Urbanski et al. 2005). Our findings indicate reduced modulation of preparatory alpha power during top-down selective attention. Given the compelling case for long range dysconnectivity in ASD, this dysfunction may well indicate reduced long-range communication between cortical regions that play an interactive role in top-down selective attention.

A recent functional imaging study from Ohta, Yamada et al. (2012) lends support to both dysconnectivity among brain regions in ASD as well as reduced suppression of irrelevant sensory information. In a visual spatial-selective attention fMRI design, as previously mentioned, these authors found that suppression of distracting information in visual cortex was reduced in adult ASD participants, and that while functional connectivity between the intraparietal sulcus (IPS) and visual cortices increased with the demands of the task (and thus presumably the need to suppress the unattended stimuli) in the TD participants, it did not in the ASD participants. Reduced top-down suppression of task-irrelevant information via connectivity between the parietal lobe and visual cortices may thus be central to deficiencies of selective attention in ASD.

4.4. Evidence for typical task switching in ASD
In addition to investigating alpha suppressive mechanisms in ASD, our design was also sensitive to whether intersensory switching was compromised in ASD, as would be suggested by clinical observations as well as by some experimental findings (Courchesne, Townsend et al. 1994; Reed and McCarthy 2012). Contrary to what one might predict based upon the literature, there was not an increase in the cost of switching tasks in ASD under the current conditions. Both diagnostic groups exhibited similar, albeit delimited, switch costs (i.e., performance decrements following task switches compared to repetitions of the same task). Specifically, d-prime values were poorer for trials in which participants switched to the visual task after previously performing the auditory task as compared to repeating the visual task. This switch cost was only present for the unisensory target stimuli (i.e., a visual stimulus alone with no auditory distractors). Thus within the visual modality there was an advantage to repeating the task on unisensory trials, but this advantage was lost on bisensory trials. It is thus possible that the presence of distracting stimuli in the unattended modality offset the behavioral benefit conferred by a repetition of the task. To summarize, a rather specific switch cost was observed in our measure of detection, and this did not differ between the ASD and TD groups.

These findings add to a body of research regarding task switching in ASD (see Geurts, Corbett et al. 2009 for review). The rigid and repetitive behaviors often observed in ASD individuals have led to the reasonable proposition that cognitive mechanisms associated with task switching are impaired in this group. As yet, there is no consensus on the severity (or presence) of task switching deficits in ASD. One study that was similar to the present did identify such deficits (Courchesne, Townsend et al. 1994). In this study participants switched between a visual and an auditory task, both of which required the detection of a rare oddball
stimulus. ASD participants demonstrated poorer accuracy relative to controls when a target occurred between 400 and 2500 ms after a task switch, but their performance was very similar to the TD group at latencies beyond this, suggesting a switching deficit in the ASD group only at short preparatory intervals. Importantly, the detection of a target in the attended modality served as the cue to switch attention to the alternate modality. In the present study, on every trial, a visual cue explicitly cued one of the two attention conditions, and this onset 1250 ms prior to the arrival of the to-be-attended stimuli. This might be considered a more overt and effective cue than the one used by Courchesne, Townsend et al. (1994).

The current findings indicate that ASD individuals are able to switch between simple auditory and visual tasks in a manner much like that of their neurotypical counterparts. This combined with null findings from several other studies gives grounds for caution surrounding assertions of a global deficit in task switching in ASD individuals (Pascualvaca, Fantie et al. 1998; Poljac, Simon et al. 2010; Stoet and Lopez 2011; de Vries and Geurts 2012).

4.5. Conclusions

While we are presented with many instances in which the integration of information from multiple sensory modalities confers greater insight into our environment (e.g., face-to-face conversation in a noisy conference hall)(Ross, Saint-Amour et al. 2007; Ross, Molholm et al. 2011), there are other instances in which sensory information from one modality can interfere with performance of a task requiring sensory input from another modality. Here we find evidence that mechanisms of selective attention are not as effectively instantiated in ASD as they
are in TD. Namely, the typical modulation of preparatory alpha band activity, which is associated with the suppression of the processing of task-irrelevant sensory information, was not observed in the ASD group. Further, behavioral data revealed that task-irrelevant sensory inputs interfered with performance in the ASD but not the TD group, indicating that "irrelevant" information is not typically dampened in ASD. This finding provides a potential explanation for the delimiting of the environment that is commonly observed in ASD.
Acknowledgements

We thank Frantzy Acluche and Sarah Ruberman for their tremendous help with data collection. Foremost, we are exceedingly appreciative of the time and effort of the individuals who participated in this study and their families. Primary funding for this work was provided by a grant from the U.S. National Institute of Mental Health (MH085322 to S.M. and J.J.F). The Human Clinical Phenotyping Core, where the children enrolled in this study were clinically evaluated, is a facility of the Rose F. Kennedy Intellectual and Developmental Disabilities Research Center (IDDRC) which is funded through a center grant from the Eunice Kennedy Shriver National Institute of Child Health & Human Development (NICHD P30 HD071593).
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Dockree, P. M., S. P. Kelly, et al. (2007). Optimal sustained attention is linked to the spectral content of background EEG activity: greater ongoing tonic alpha (similar to 10 Hz) power supports successful phasic goal activation. European Journal of Neuroscience 25(3): 900-907.


Footnotes

1. Participants were run on one of two identical testing rooms. After data collection it became apparent that the interaction of the stimulus presentation software with the operating system installed on one of the systems resulted in a delay of the onset of the auditory S2 stimulus by 50 ms, as verified by a two channel oscilloscope (Tektronix TDS2012C, Beaverton, Oregon). In total, of the 20 participants in each diagnostic group, 11 ASD and 9 TD individuals were run on the experimental setup with the 50 ms delayed S2 auditory stimuli (see Figure 3.1). Diagnostic groups were similarly represented in each testing booth and there were no significant differences in participant characteristics as a function of ‘Booth’. We performed analyses to determine how 'Booth' might impact any of the dependent measures (RT, d-prime, and alpha power). We analyzed the data in precisely the same manner as reported below, but used Booth as the grouping variable in place of Diagnosis. Neither main effects of Booth or interactions with Booth approached significance for any of these analyses, suggesting that the small timing difference did not significantly influence any of the results reported below.
Figure legends

**Fig 3.1.** *Schematic of the experimental paradigm.* At time 0 participants received a pictorial cue (200 ms in duration) indicating which stimulus modality to attend. Next came a blank interval during which only the fixation cross was presented. This was followed by presentation of the S2 stimulus. For trials including auditory tone pairs, the first tone onset at 1300ms (*or 1350ms: for half of the participants the auditory stimuli were unintentionally delayed by 50 ms), and the onset of the second tone was at 1405 ms (*or 1455 ms for half the participants, again due to the delay in the auditory stimuli). For trials including the visual stimulus, visual stimulation always onset at 1355 ms.

**Fig 3.2.** *Behavioral data.* (A) Unisensory and bisensory d-prime data for the two diagnostic groups, collapsed across auditory and visual trials. (B) RT data for unisensory and bisensory S2s within the cue auditory and visual conditions. Asterisks indicate significant differences at $\alpha < 0.05$. The error bars indicate ±1 SE (standard error).

**Fig 3.3.** *Spectrograms.* Spectrograms of the subtraction of the cue-visual condition from cue-auditory condition, averaged over the left or right parieto-occipital electrodes used in the statistical analysis. Time zero indicates cue onset. The head map at upper right indicates the electrode positions. Units are baseline normalized z-scores.
**Fig 3.4.** *Alpha waveforms.* Alpha waveforms (8-14 Hz) for cue-auditory and cue-visual conditions, averaged across left or right parieto-occipital electrodes used in the statistical analyses. Head map at upper right indicates the electrode positions. Units are baseline normalized z-scores. The semi-transparent color represents ± 1 SE.

**Fig 3.5.** *Topographies.* (A) Topographic representation of alpha power for the two cued attention conditions and their subtraction, averaged over the 200 ms before S2 onset. Units are baseline normalized z-scores. (B) Topographies representing t-scores of significant electrodes resulting from paired t-tests of cue-auditory versus cue-visual alpha power in the 200 ms window prior to S2 onset across all electrodes, FDR corrected for multiple comparisons.

**Fig 3.6.** *Correlations and distribution of effects.* (A) Scatter plots depict the relationship between alpha power modulation (cue auditory minus cue visual) and behavioral performance (d-prime) on the auditory task. Solid lines represent the least squares fit of the data. (B) Scatter plots depict the relationship of average alpha power on auditory and visual trials for each participant in the ASD group (left) and the TD group (right). Solid lines delineate equality between conditions.
Figure 3.1.
Figure 3.2.
Figure 3.3.
Figure 3.4.
Figure 3.5.
Figure 3.6.

A

Left Hemisphere

ASD: $r = 0.32$, $p = 0.17$
TD: $r = -0.21$, $p = 0.38$

Right Hemisphere

ASD: $r = 0.56$, $p = 0.001^*$
TD: $r = -0.25$, $p = 0.29$

B

ASD

TD
Table 1. Means and standard deviations (in parentheses) for the demographic data of the participants (A) and excluded participants (B).

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Table 2. Behavior means and standard deviations (in parentheses). (A) d-prime and (B) RT data for all conditions and the two diagnostic groups.

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<td><strong>B. RT (ms)</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><strong>A</strong></td>
<td><strong>Cue Auditory</strong></td>
<td><strong>Cue Visual</strong></td>
<td></td>
<td></td>
<td><strong>Cue Auditory</strong></td>
<td><strong>Cue Visual</strong></td>
<td></td>
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<tr>
<td><strong>ASD</strong></td>
<td>Repeat</td>
<td>1.80(0.89)</td>
<td>1.44(0.96)</td>
<td>1.62</td>
<td>Repeat</td>
<td>1.83(0.67)</td>
<td>1.59(0.85)</td>
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<tr>
<td></td>
<td>Switch</td>
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<td>1.45(0.94)</td>
<td>1.72</td>
<td>Switch</td>
<td>1.89(0.78)</td>
<td>1.66(0.82)</td>
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<tr>
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<td>Switch</td>
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<td><strong>RT (ms)</strong></td>
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<td><strong>Cue Auditory</strong></td>
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<td>889(183)</td>
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<td></td>
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<td>Switch</td>
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<tr>
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<td>899(196)</td>
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General Discussion

In Chapter 1 we investigated the effect of task switching on intersensory alpha biasing signals in young adults. In previous work it has been shown that alpha amplitude is relatively increased over parieto-occipital regions in the preparatory interval after an individual is cued to attend to the auditory modality as opposed to the visual modality (Foxe et al., 1998; Fu et al., 2001). This has largely been interpreted as an increase in alpha amplitude during cue auditory trials, reflecting the deployment of top-down suppression of task-irrelevant information. We hypothesized that switching to a task that required selectively attending to the auditory modality in the face of irrelevant (but previously relevant) visual stimuli would result in increased alpha amplitude over parieto-occipital regions above and beyond that observed during a repeat of the same task. We additionally hypothesized that these relative alpha amplitude differences would extend over prefrontal cortices, reflecting the reweighting of task-sets in prefrontal cortices. Added to this, we posited that perhaps this frontal differentiation would dissociate among task switches and repeats but not between the two tasks themselves, since presumably both task-sets are maintained in this region. We did indeed find increased alpha amplitude differences between the two tasks on switch trials compared to repeat trials as well as a suggestion of the involvement of more frontal regions on switch trials. However, upon further investigation it became apparent that these differences were driven by strong alpha desynchronization on cue visual switch trials relative to cue visual repeats. Meanwhile, switch and repeat cue auditory trials exhibited statistically identical alpha profiles.
Behaviorally, participants did not exhibit classical switch costs, although we did find evidence for mixing costs, suggesting that performing the two tasks together did indeed stress cognitive control mechanisms. It is important to point out that the probability of a switch trial occurring during a block was equal to that of a repeat. Previous work has shown that decreasing the probability of a switch, such that participants receive several task repeat trials prior to a switch trial increases the switch cost (Monsell & Mizon, 2006). Future work manipulating the probability of a switch trial either in a blocked fashion or across participant groups may provide further insight into the dynamics of alpha amplitude modulation as it pertains to a switch of task.

In Chapter 1, we further discussed the possibility that, when faced with relatively continuous switching, the system is unlikely to expunge one task-set and instantiate the switched-to task-set de novo. This idea was most notably formulated by Goschke (2000), who suggested that when alternately switching among two tasks, it may be most beneficial for the system to maintain both of these task-sets at relatively high levels of activity, and then ‘tip’ the balance towards one or the other. One possibility when decreasing the probability of a switch, is that the dormant task becomes progressively more suppressed, or rather that there is a cumulative effect over many successive trials, such that the reinstatement of this neglected task-set requires a higher level of top-down control. If this is the case, alpha oscillations acting as biasing signals may be observed to show greater amplitude modulation if the probability of a switch is parametrically decreased.

In Chapter 2 we investigated intersensory selective attention and task switching in school-aged children, adolescents and young adults. It is noteworthy to point out here that the probability of a switch was reduced in this case from 50% in Chapter 1 down to 30%. In this
experiment we observed robust behavioral switch costs. In the adults, we found a similar pattern of alpha modulation to that found in Chapter 1. It is worth pointing out that perhaps the most striking aspect of alpha modulation in the adult group was the extremely small amplitude of this modulation on repeat trials. This could imply that as an adult participant successively repeats the same task, a ‘just enough’ principle is at play so that the differential deployment of costly top-down biasing signals (e.g., alpha), are titrated down to a point where the task can be performed at some acceptable criterion with as little effort as possible. This is a tantalizing idea, and it remains to be directly tested, but it is already somewhat at odds with what we generally observe in task-switching. That is, if top-down biasing is relaxed towards an optimal state, why do we observe increased switch costs when the probability of switching is decreased? That is, the relaxation of top-down biasing after several task repeats should result in a more equal playing field for competition among the task-sets. It follows that this more level playing field would allow for a less effortful task switch, but in fact we see just the opposite after many task repeats.

One possibility is that the neglected task-set degrades passively over time, and the relaxation of biasing signals occurs in response to the degradation of the competing task. When this long neglected, degraded task-set is called upon again a great deal of resources may be needed to bring it into a state at which it can compete with the switched-from task-set, and this could be expected to elicit a robust switch cost. Under this interpretation, alpha biasing signals decrease on task repetitions as a result of a degradation of the competing task-set.

In the youngest group (8-12 years) in Chapter 2, we found no evidence for the switch-related modulation of alpha amplitude, even when the well replicated divergence in alpha between cue visual and cue auditory trials was present in this young group. What does this
pattern of effects imply? It is noteworthy that the lack of a switch effect in the youngest age group was driven by a near zero microvolt difference in alpha amplitude between cue auditory and cue visual tasks on both task repeats and switches in the earlier portion of the preparatory period that we tested. That is, the lack of a difference in this group does not appear to have been driven by a robust, early cue-related alpha difference that was equal across task repeats and switches (see FIG 2.4, Chapter 2). If it were the case that early cue-driven amplitude differences were high in this group for both switches and repeats, one could argue that younger participants were establishing task-sets anew on each trial, or at least establishing the competitive balance among the tasks anew each time. Rather, it appears that children in the youngest age group simply failed to initiate this bias in the early time period whereas adolescents and adults exhibited this early amplitude difference on switches but not repeats. This was accompanied by behavioral deficits in the youngest group (i.e., higher switch costs on trials containing a task-incongruent distractor). I would argue that this reflects the underdeveloped state of the prefrontal cortices in these children. In the General Introduction, I discussed in detail the protracted development of the prefrontal cortices, specifically the protracted period of synapse elimination, which is thought to reflect a process of refinement and specialization of cortical ensembles.

It is possible that the switch related alpha comprises greater cognitive control processes, presumably arising from prefrontal areas, whereas the later and weaker differentiation of alpha on repeat trials reflects a state in which the performance of the task is de-coupled from cognitive control. This is perhaps reflected in the earlier divergence of cue-related alpha amplitude on switch trials relative to repeat trials, along with the more topographically widespread pattern of
alpha modulation on switches compared to the more focal pattern over parieto-occipital areas on task repeats.

The correlation computed between switch costs on cue visual trials when the auditory task was task-incongruent in Chapter 2 (FIG 2.6) is intriguing in that, topographically, alpha modulations on the cue visual switch trials versus repeat trials only correlate with switch costs over the left parieto-occipital scalp and right anterior frontal scalp. This is modestly suggestive of the involvement of prefrontal areas in mediating the switch specific aspect of alpha modulation that we have documented.

Both the increased modulation of alpha amplitude and greater spatial extent of this modulation occurred only within the cue visual condition, and this is true in the findings in adults in both Chapters 1 and 2, which utilized different participant cohorts, as well as in adolescents in Chapter 2. This is puzzling and presents a challenge for a hard-line interpretation of alpha as an active suppression mechanism. Why the incongruity between the senses? In all the experiments we made every effort to match the difficulty of the tasks performed in the two sensory modalities, and there is no strong evidence that one task was systematically more demanding than the other. There is, however, ongoing debate surrounding the ‘dominance’ of the visual modality (Colavita, 1974; Koppen et al., 2009; Spence, 2009). It has been observed in multiple studies that the presence of a visual stimulus asymmetrically impedes the detection of an auditory stimulus, as if the visual stimulus extinguishes the auditory stimulus. These findings along with the relatively large size of our visual cortices and our heavy reliance on vision for many day-to-day tasks have led some investigators to argue that vision is intrinsically dominant over the other sensory modalities (Colavita, 1974). Other researchers have argued more for the
so-called modality appropriateness hypothesis (Welch & Warren, 1986), which states that the modality that has the best perceptual machinery for a given task will dominate. Thus, vision would be expected to dominate during extra-personal localizations of stimuli, whereas judgments of timing may be performed more accurately in the auditory modality.

In all of the experiments in this work, attention was directed endogenously to two laterally presented visual stimuli, while the auditory stimuli were presented either over headphones (Chapter 1) or over a single loudspeaker hidden centrally behind the computer monitor on which the visual stimuli were presented (Chapters 2 and 3). Although the effect of headphones on the co-localization of the audio-visual stimuli is hard to determine, audio-visual stimuli were presented in the same general spatial vicinity in Chapters 2 and 3, and the audio-visual stimuli were closely temporally coincident in all of the experiments conducted. It has been argued persuasively that two fundamental rules for multisensory integration are spatial alignment and close temporal coincidence (Stein et al., 1988). Furthermore, in experiments using stimuli very similar to the ones reported here, but in which the task was simply to respond to any and all stimuli, superadditive effects were reported in the evoked potentials over sensory specific as well as heteromodal areas, suggesting that an auditory stimulus coupled with a visual stimulus actually enhances the activity in each sensory region (Giard & Peronnet, 1999; Molholm et al., 2002). It is therefore possible that the brain has a strong proclivity to integrate multisensory information that is spatially and temporally concordant. Such concordance would involve the formation of a multisensory ‘object’ or rather a multisensory landmark on higher-level saliency maps in frontal and parietal cortices, where inputs from both modalities have been shown to be coded in spatial maps (Cohen & Andersen, 2002; O'dhaniel et al., 2005; Smith et al., 2009; Tark
Given the tightly coupled nature of these regions to eye-movements as well as reaching and generally interacting with the surrounding environment (Schall & Thompson, 1999; Cohen & Andersen, 2002), it is unlikely that the integration of audio-visual inputs in these areas involves high level semantic details. It may rather function to map intersensory signals in a manner that is conducive to saccading, orienting or reaching towards multisensory sources in space.

Possibly the increases in alpha when attending the auditory modality in the presence of an interfering visual distractor represent an active suppression of an otherwise automatic binding of audio-visual inputs into one ‘object’. This integration would be maladaptive in cases where the components of the multisensory stimulus signal conflicting responses. This is an intriguing idea, but why would we see this gating of multisensory integration only when attending the auditory modality? Would the same process not also be of use when performing the visual task?

It could be argued that vision dominates these maps of space in the posterior parietal cortices. It seems that many neurons in and around the intraparietal sulcus are heteromodal, but respond more so to visual inputs, and moreover these spatial maps are often found to be coded in eye-centered coordinates. Thus, when performing the visual task, the visual stimulus dominates, and auditory inputs into this area present relatively little competition. Alternately, heteromodal areas of the parietal cortex may be ‘pulled’ towards the visual stimulus, even when it is task irrelevant and interferes with performance, necessitating the deployment of alpha to both parietal and occipital regions to gate the visual signal.

This begs the further question, why would such a mechanism be needed when the task performed in the auditory modality is one of pitch discrimination, as in the experiments reported
here? Pitch discrimination likely relies most heavily on right auditory cortex (Johnsrude et al., 2000). However, the relatively automatic integration of audio-visual inputs onto a common reference frame may reflexively orient the individual to the spatial position of these stimuli. This proposition is highly speculative, and not without problems. However, if it were the case that alpha prevents haphazard multisensory integration or even retroactively unbinds incorrectly co-registered sensory signals, what would it be like to lack this mechanism?

Behaviorally, ASD children and adolescents surprisingly did not show a clear deficit in switching, but rather exhibited modest behavioral differences relative to controls, such that they appeared subject to greater interference from task-irrelevant distractors in the alternate modality, regardless of whether the trial was a switch or repeat. This was accompanied by a complete lack of alpha differentiation on cue visual versus cue auditory trials, when this differentiation was quite robust in the control participants. Could such a deficit result in individuals with ASD misattributing multisensory inputs as belonging together, causing the experience of a highly chaotic and disordered world? Such a proposition is somewhat in-line with the intense world theory of autism (Markram et al., 2007; Markram & Markram, 2010). According to this theory, ASD individuals, who are often thought to exhibit hypo-cognitive function actually are in a state of intense hyperactivity, particularly at the local neuronal population level. This state results in the experience of the world as extremely intense, leading to social withdrawal, a need for the predictable, and a desire to fixate on simple, well known sensory stimuli.

In the current case, if the world is experienced as a jumble of incorrectly co-registered sensory events because of the underperformance of top-down biasing, life would indeed be intense. Furthermore, social situations would be exceptionally challenging. For instance, at a
cocktail party, overlapping auditory speech signals would be haphazardly co-registered to surrounding talking faces. In this manner the world may be experienced as an unpredictable patchwork of sensory information. This would further undoubtedly hinder language acquisition and comprehension in so far as the visual modality would not be a reliable augmenting source of information for the auditory modality during speech comprehension in noisy situations. ASD individuals do indeed show a developmental delay in the utilization of visual information to augment auditory speech comprehension in noisy environments (Foxe et al., 2013). Quite a bit more work is needed before this proposition can gain traction.

Changing gears, the possible function of alpha oscillations as a top-down biasing signal that at times prevents the co-registration of stimuli from different modalities onto a common saliency map is well and good, but what do we make of the alpha desynchronization found specifically during cue visual switch trials? In the Discussion section of Chapter 2, we interpreted the pattern of alpha deployment, along with the behavioral findings, within the framework of asymmetrical switch costs and task-set inertia (Allport & Wylie, 2000). That is, because, as discussed above, vision may dominate in this context, alpha is deployed equally on switch and repeat cue auditory trials as a suppressive mechanism to overcome the strong bias in favor of the visual modality. Meanwhile, alpha desynchronization over parieto-occipital cortices, reflecting increased excitation in these areas, are minimal on cue visual task repeats, since by default the bias is in favor of vision. However, on visual switch trials, visual cortices have just been heavily suppressed in order to perform the auditory task, and this strong suppression lingers through into the next trial, resulting in the asymmetrical switch cost. In order to overcome this suppressed state, top-down biasing acts to desynchronize alpha over visual cortices.
How does desynchronization of alpha fit into a model in which increases in alpha synchronization are typically envisioned as suppressive signals? Can the same top-down biasing mechanisms synchronize and desynchronize alpha? Cortical ensembles in many cases exhibit alpha oscillations even when these ensembles are task relevant, as such desynchronization might be envisioned as the further withdrawal of this oscillatory state. That is, alpha may not be actively desynchronized but rather withdrawn to an even lower level, allowing for increased excitability in this region.

**Alpha oscillations and top-down biasing**

While inroads have been made into our understanding of the generation and functions of alpha oscillations, a great deal of work still remains to be done. For instance, the heterogeneity of attentional effects found across visual cortices reported by Bollimunta *et al.* (2008) are puzzling and a great deal of work needs to be performed to further explore the behavior of alpha oscillations in different regions using laminar intracortical techniques. It is noteworthy, that, to the best of my knowledge, no work has been performed in which alpha was investigated in this manner over dorsal stream visual areas, nor to my knowledge is there work on the nature of these oscillations in parietal regions that are central to visual selective attention.

Furthermore, while very detailed models of alpha generation were discussed in the **General Introduction**, very little is mentioned about the precise manner in which these rhythms might be modulated in a top-down manner. The study by Buschman *et al.* (2012), discussed throughout this work, provides a glimpse of the relevance of alpha for higher level task-sets in
prefrontal cortices. The researchers reported an increase in alpha coherence among neurons in
the macaque prefrontal cortex that was associated with the performance of a switched-from task.
The implication is that juggling multiple tasks is accompanied by the active suppression in
prefrontal cortex of the competing, currently irrelevant task-set through increases in coherent
alpha oscillations. Because the prefrontal cortex is exceptionally interconnected with other
regions of the brain (Miller and Cohen, 2001; Miller, 2000), perhaps the prefrontal cortex could
be a source for routing alpha oscillations in a top-down manner to regions of cortex that
represent the components of the irrelevant task-set. Future work, recording simultaneously from
multiple cortical locations is needed to further investigate this possibility.

The work presented here speaks to the dynamism and exceptional complexity of the
brain. Task switching and selective attention are constructs that aid our investigation of this
extremely complex system. Ultimately they may have to be revised, broken into subcomponents,
or even merged in order for us to make further progress. Likewise, alpha oscillations, as defined
within a strict frequency band and serving specific functions, guide our thinking now, but
ultimately oscillations in the brain may prove more fluid, necessitating a conceptual revision. We
employ these constructs as a window onto the brain, but a day will likely come when they have
to be abandoned or heavily overhauled as our understanding of the nervous system progresses.
We ought to embrace this rather than resist it.

The findings presented here highlight the great expanse of brain function that we still do
not understand, but we are making great leaps forward. This is exceptionally exciting, and
provides hope that individuals afflicted with disorders of the nervous system will find relief.
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