SPATIAL ATTENTION-MODULATED SURROUND SUPPRESSION ACROSS DEVELOPMENT: A PSYCHOPHYSICAL STUDY

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Abstract

Several studies have demonstrated that surrounding a given spatial location of attentional focus is a suppressive field (e.g., Hopf et al., 2006). Though several studies have provided psychophysical (e.g., Cutzu & Tsotsos, 2003) and neural evidence of this effect in young adults (e.g., Boehler et al., 2009), whether this phenomenon is also observed in development was not fully known.

Experiment 1 of the current study was therefore conducted to examine whether attention-modulated surround suppression was observed in younger age groups. Participants between the ages of 8 and 22 years were tested on a two-alternative forced choice task, in which their accuracy in discriminating between two red target letters among black distractor letters was measured. A spatial cue guided the participants' attention to the upcoming location of one of the target letters. As would be predicted for the young adults, their accuracy increased as the inter-target separation increased, suggesting that visual processing is suppressed in the immediate vicinity of an attended location. Pre-adolescents (12 to 13 years) and adolescents (14 to 17 years) also exhibited attentional surround suppression, but intriguingly their inhibitory surround appeared to be larger than that of young adults. The 8- to 11-year-olds did not exhibit attentional suppression.

In Experiment 2, when a central cue instead of a spatial cue was presented, surround suppression was no longer observed in an independent set of 8- to 27-year-olds, suggesting that the findings of Experiment 1 were indeed related to spatial attention.

In Experiment 3, yet another independent group of 8- to 9-year-olds were tested on a modified version of the Experiment 1 task, where the cue presentation time was doubled to provide them with more support and more time to complete their top-down feedback processes. With this manipulation, attention-modulated surround suppression was still not observed in the 8- to 11-year-olds.

Overall the current study findings suggest that top-down attentional feedback processes are still immature until approximately 12 years of age, and that they continue to be refined throughout adolescence. Protracted white matter maturation and diffuse functional connectivity in younger age groups are some of the potential underlying mechanisms driving the current findings.

Dedication

For my dad, whose only career advice for me was to follow a path that I am passionate about, full of challenges and continual learning. As I complete this dissertation project and my final year of studies, I finally understand the feeling of satisfaction and pride you spoke of many years ago. Satisfaction and pride that come with overcoming challenges that seem insurmountable and genuine hard work. I finally understand the personal merit of not taking the easy way out, and instead welcoming a challenge - of striving for and working towards my best.

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List of Abbreviations

Abbreviation	**Term**
2AFC	Two-Alternative Forced Choice Task
AIP	Anterior intraparietal area
ANT	Attention Network Model
ANOVA	Analysis of Variance
ASD	Autism Spectrum Disorder
Cg	Cingulate
CCR	Contingent-Capture Ratio
DAN	Dorsal Attention Network
DTI	Diffusion Tensor Imaging
BOLD	Blood Oxygen Level-Dependent
FEF	Frontal Eye Fields
FFA	Fusiform Face Area
fMRI	Functional Magnetic Resonance Imaging
IFJ	Inferior Frontal Junction
LGN	Lateral Geniculate Nucleus
LIP	Lateral intraparietal area
MEG	Magnetoencephalography
MT	Middle Temporal Area
N2	Negative 200
N2pc	Negative 200-posterior-contralateral
PD	Distractor Positivity

PMd	Dorsal premotor cortex
pRF	Population Receptive Field
RF	Receptive Field
RSVP	Rapid Serial Visual Presentation
SOA	Onset Asynchrony
ST	Selective Tuning Model
SSVEP	Steady-State Visual Evoked Potentials
TEO	Tectum Opticum
V1	Visual Area One (Primary Visual Cortex)
V2	Visual Area Two
V3	Visual Area Three
V3A	Visual Area Three Accessory
V4	Visual Area Four
VO1	Ventral Occipital 1
VAN	Ventral Attention Network
WTA	Winner-Take-All

1. Introduction

In our environment, there is an overabundance of available visual information. Our visual system has a limited processing capacity, and as a result it cannot process all the information it receives from our eyes (Carasco, 2011). Our brains must instead use attention to bring important information into focus, while filtering out irrelevant information (Driver, 2001). Attention is "the mechanism that turns looking into seeing" (p.1484, Carasco, 2011), because though our eyes are the organs that capture information, without our brain's ability to organize and filter such information, we would not be able to interpret any of it.

William James (1890), famously known as one of the earliest theorists of attention, described attention as "the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought." (p. 404, James, 1890). He described two types of stimuli, one that attracts attention because of their impression on the senses in a reflexive stimulus-driven manner, and the other capturing attention voluntarily, where the observer makes an effort to attend (James, 1890). In more recent times, psychological researchers have established this divide as a distinction between bottom-up or stimulus-driven versus top-down or goal-driven attention (e.g. Folk & Remington, 2010; Theeuwes, 2010).

Though much remains unknown about the functioning of attention in the brain, attention mechanisms are currently understood to involve the interaction of specific neural systems that allow for the control of information processing and action (Hopf, Boehler, Schoenfeld, Magun & Heinze, 2012). Within the visual domain, attention operates on different visual representations, such as spatial or location-, feature-, and object-based representations (Hopf et al., 2012). Spatial or location-based attention can be overt, in which the observers move their eyes to a location of interest, or covert, in which observers deploy their attention to a relevant location without moving their eyes (Carrasco, 2011). Feature-based attention can also be deployed overtly or covertly but to specific aspects of objects (i.e., colour, shape, orientation) in our environment (Carrasco, 2011), whereas object-based attention is guided by object structure (Olson, 2001). Regardless of the visual representations upon which it is operating, attention mechanisms optimize the visual system (Carrasco, 2011).

But how does attention optimize visual processing? Non-human primate and rodent studies have revealed direct evidence that the focus of spatial attention impacts activity in the visual areas of the brain, and facilitates the processing of relevant visual information. Sundberg and colleagues (2009), for example, recorded neurons in visual area 4 (V4) of rhesus macaques while they completed a multiple-object-tracking task. The authors found that where attention was allocated affected a given neuron's activity. If attention was allocated to a stimulus in the neuron's receptive field, the neuron remained activated. If attention was instead directed to a stimulus in the surround of the neuron's receptive field, the neuron's response to the now task-irrelevant stimulus was suppressed. Moreover, when attention was instead allocated to a distant stimulus, further away than the surround stimulus, less neural suppression was observed. In another study by Zhang and colleagues (2014), results revealed that the activation of the cingulate (Cg) area[1] of mice's frontal cortex exerted top-down modulation of visual processing. Optogenetic activation (using light to activate neuronal cells genetically modified to express light-

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[1] Mouse Cg is believed to be functionally similar to primate frontal eye fields (FEF) in its top-down attentional modulatory role on visual areas (Zhang et al., 2014).

sensitive ion channels) of Cg neurons enhanced neuronal activity in the primary visual cortex and improved visual discrimination in mice. Activations of Cg neurons also lead to the suppression of neuronal activity in nearby and task irrelevant locations. Not only do these animal studies suggest that attentional focus exerts top-down influence on the visual areas of the brain, they also highlight the influence of attention on the profile of activity in these visual areas. Attentional focus enhances visual processing by promoting the activation of the neurons that respond to information that is relevant, and inhibiting neighbouring neurons that respond to distractors (Sundberg, Mitchell & Reynolds, 2009). Additionally, greater levels of suppression are found for stimuli immediately surrounding an area of attention than for stimuli that are further away (Sundberg et al., 2009).

These non-human primate and rodent findings also converge well with psychophysical (e.g., Cutzu & Tsotsos, 2003) and imaging studies with humans (e.g., Hopf, Boehler, Luck, Tsotsos, Heinze & Schoenfeld, 2006), in which participants demonstrate reduced accuracy at discriminating between stimuli that fall close to the spatial location of attentional focus, as well as reduced neural activity for items appearing closer to the spatial location of attentional focus in comparison to items presented further away. There is both psychophysical and neural evidence, therefore, pointing to a zone of suppression or attenuation surrounding an attended item or spatial location. This attentional suppressive effect can be referred to as attention-modulated surround suppression and will be referred as such in the current study.

Though there is ample evidence of attention-modulated surround suppression in humans, it is currently not known whether it is also observed in development. Two questions that have yet to be fully answered are whether attention mechanisms optimize the visual system in a similar manner across development and how attentional mechanisms mature across development? These are important questions since attention processes are likely even more critical across development because of their potential impact on learning and day-to-day activities. For instance, attentional processes are thought to play a crucial role in directing children's focus to important events and items in their environment (Ruff & Rothbart, 2007; Weatherholt, Harris, Burns & Clement, 2006), and in attaining and maintaining an alert state, optimal for learning (Mullane, Lawrence, Corkum, Klein, McLaughlin, 2016). In adolescence, the inability to adequately allocate attention to road hazards is partially responsible for the increased number of driving accidents that occur in this age group (Romer, Lee, McDonald & Winston, 2014). Having a better understanding of how attention mechanisms mature and affect visual processing across development is not only important for practical reasons, it is also important for theoretical ones as well. To fully understand the functioning of attentional mechanisms in the adult brain, it is important to understand how these mechanisms manifest and mature in development such as in childhood or adolescence, a period of the lifespan where great change occurs.

Much of the theoretical literature on attentional development is influenced by Posner and Petersen's attention network model (ANT) and its framework for a dissociation between the networks of alerting, spatial orienting and executive attention (Petersen & Posner, 2012; Posner & Petersen, 1990). According to ANT, alerting is the generation of a state of arousal or readiness, which can be elicited by an external and unexpected cue, orienting is the shifting of attention to selected information in the environment (Posner & Petersen, 1990), and executive attention is the process of resolving conflict between competing inputs for the purpose of a goal driven task (Posner & Petersen, 1990). Previous studies have revealed that the alerting of attention is available very early in development, as even newborn babies are postulated to already have the capacity (Amso & Johnson, 2006). Attention-orienting shifts are functional between 3 and 6 months of age (e.g., Adler & Orprecio, 2006; Amso & Johnson, 2006; Johnson & Tucker, 1996) but are thought to continue developing during childhood and adolescence (Rueda, Fan, McCandliss, Halparin, Gruber, Lercari & Posner, 2004; Konrad, Neufang, Thiel, Specht, Hanisch, Fan, Herpertz-Dahlmann & Fink, 2005). Though executive attention, which is generally measured using an antisaccade task where participants are required to make an eye movement away from a cue (anti-saccades) rather than towards it (pro-saccades), is observed as early as in infancy (Johnson, 1995; Konrad et al., 2005), it does not become more adult-like until around 14 years of age (Luna, Garver, Urban, Lazar & Sweeney, 2000). While studies based on ANT are informative regarding the developmental trajectory of different attentional networks, they have not readily provided information about whether the influence of attentional mechanisms on visual processing as seen in adults, is the same across development.

From a different theoretical perspective, studies largely focusing on the development of top-down or bottom-up attentional processes have revealed differences in the maturation timeline of these processes. For instance, visual search tasks have shown that younger children tend to be slower and less accurate at finding a target among distractors, particularly on trials that are more difficult and presumably requiring more top-down attentional processes. In difficult cases where the target shares features with the distractors, such as in a conjunction search, children up to about 6 to 7 years of age have difficulty searching for the target (Donnelly, Cave, Greenway, Hadwin, Stevenson, & Sonuga-Barke, 2007; Trick & Enns, 1998; Woods, Göksun, Chatterjee, Zelonis, Mehta & Smith, 2013). Under conditions where the target is more salient, however, and obviously different from distractors, young children can accurately search and locate a target much like adults (Donelly et al., 2007; Merrill & Conners, 2013; Taylor, Chevalier& Lobaugh 2003; Trick & Enns, 1998; Woods et al., 2013). Across all of these studies, researchers typically attribute their findings as evidence that top-down control of attention improves during childhood but that bottom-up attention is relatively mature early in development.

Additional studies featuring different tasks have also revealed findings that confirm the interpretation of late developing top-down attentional processes. For example, Gaspelin and colleagues (2015) compared young children's (4-year-olds) and young adults' ability to voluntarily control the capture of spatial attention. Participants were required to search for "spaceships" of a specific colour, while ignoring salient precues that either matched or mismatched the colour they needed to focus on. Top-down attention control was computed by a contingent-capture ratio (CCR). The CCR value was scaled as a percentage of the age group cue validity effects, which therefore corrected for group differences and provided an estimate of overall top-down control over attentional capture. Results revealed that children were much more vulnerable to capture by irrelevant stimuli than adults, as evidenced by their lower CCRs. Using a similar precueing paradigm, Greenaway and Plaisted (2005) also found that older children aged between 11 and 12 years scored similar CCRs as reported in the young children of the Gaspelin et al. study (2015). Taking both their own findings and that of Greenway and Plastied's (2005) into consideration, Gaspelin and colleagues (2015) proposed that top-down attentional control likely continues to develop beyond the age of 11 years. However, taken altogether, similar to ANT based research, the studies focusing on the development of top-down attentional processes have also not provided information about whether developing attentional mechanisms influence visual processing as in adults.

Moreover, both ANT and top-down attention based developmental studies have also not resulted in a complete theory of attentional development (Ristic & Enns, 2015) and how attention mechanisms manifest and mature into an adult state. Part of the issue may lie in the design of the attentional tasks. For instance, in a recent review, Ristic and Enns (2015) argued that chronometric reaction time measures designed for adults are often outside the repertoire of toddlers and infants, and in cases where a given task is made more appropriate for the younger age groups, it becomes too simple for adults, who perform at ceiling as a result. Studies in which developmental groups and adults can directly be compared are therefore sparse. Adler and Orprecio (2005, 2006) have also commented in a similar vein suggesting that previous attentional research on infants using preferential looking or habituation paradigms cannot provide meaningful insight into the development of attention mechanisms, since those tasks are not comparable to adult research, and suggest instead that the use of eye movements can allow for a direct comparison between infants' and adults' attention performance. They further argued that looking time paradigms, such as the novelty-preference paradigm, cannot accurately measure selective attention because the time-frame of those paradigms require infants to accumulate a total of 5 seconds (or more) of looking, which is far longer than the time-frame needed for selectively allocating attention. One potential approach that might overcome methodological issues of comparability across age groups and that could provide more insight into how attentional mechanisms mature across development is to work backwards - to first successfully apply a paradigm with adults, and subsequently use the paradigm down through development with younger age populations, until differences in performance are observed. In doing so, comparing attentional performance across development would be more readily possible since all age groups would be tested on the same task and under similar conditions. By studying a wider age range incrementally, instead of just one younger age group in comparison to adults, finer grain differences can also potentially be uncovered and be much more informative about the development of attentional mechanisms.

If examining whether there are differences in the effect of attention mechanisms on visual processing across development is also of interest, the task used must not only be appropriate for a large age range, it must also include two specific features. First, it must involve the measurement of the processing of visual stimuli, such as visual discrimination accuracy, and second, the task must include a means by which attention to stimuli can be manipulated to influence their processing. Fundamentally, a more explicit and effective way to examine the influence of attentional mechanisms on visual processing across development is therefore to use a task that can directly manipulate the effect of attention on visual processing, and is suitable for all age groups in question. As a first step in attempting to provide some answers to the questions of how attentional mechanisms mature across development, this study examined whether attentional focus exerts the same effect on visual processing, as observed in adults, throughout development. More specifically, I examined whether surround suppression modulated by spatial attention is observed across younger age groups. Currently, no study has examined developmental differences in how surround suppression and visual processing is affected by attentional focus.

The neural processes that give rise to attention modulated surround suppression are fairly understood, therefore examining when it is observed in development can also potentially provide indirect insight into its neural development. Broadly, it is believed that voluntarily focusing attention leads to competitive stimulus interactions in the visual cortex, which in turn promotes preferential processing of relevant over irrelevant input (Tsotsos, 1990; Desimone, 1998; Duncan, Humphreys & Ward, 1997). Incoming visual stimuli from the retina projects in a feedforward (bottom-up) manner to visual area 1 (V1), passing through the lateral geniculate nucleus (LGN), and attentional feedback (top-down) projections from higher order cortical areas, such as the frontal and parietal areas, bias processing in the visual cortex (Miller & Buschman, 2013). Examining whether younger age groups also show or when they begin to show surround suppression and top-down attentional biasing can therefore provide insight into the development of attentional top-down projections that enable more efficient visual processing.

To this end, the current study consisted of three experiments. The first experiment examined whether attention-modulated surround suppression is observed in younger age groups. The second experiment served as a control for any findings from Experiment 1, in which a baseline measure of performance across age groups on the task without the biasing of attention was measured. Both Experiment 1 and Experiment 2 were broken down into six sub-experiments, in which each age group (8-9, 10-11, 12-13, 14-15, 16-17, 18+ years) was examined individually. Experiment 3 was broken down into 2 sub-experiments, where the youngest age groups (8-9 and 10-11 years) were tested on a slightly modified and more developmentally appropriate version of the task, which I predicted they might need. This last experiment was also intended to allow for a further examination of the developmental maturation of feedback processing.

The following sections provide a more detailed account of attention-modulated surround suppression and its neural substrates, the development of visual attention and the visual system, and the research objectives and predictions of this study.

1.1 Attention Modulated Surround Suppression

A vast number of theories and models have been offered to describe how attention mechanisms function in the brain to reduce incoming information to a manageable level. Highly influential psychological and descriptive accounts include feature integration theory (Treisman & Gelade, 1980) and the metaphor of a spotlight (Shulman, Remington & McLean, 1979; Posner, 1980).

As its name entails, the spotlight metaphor views the function of attention in a manner similar to a spotlight, shining a light on areas of interest, while keeping in the dark that which is not of interest (Posner, 1980; Eriksen & Yeh, 1985). Previous functional magnetic resonance imaging (fMRI) studies supported this description of attention, whereby blood oxygen level-dependent (BOLD) enhancements in visual cortex areas were activated retinotopically in correspondence to attended locations (Brefcynski & DeYoe, 1999; Müller, Bartelt, Donner, Villringer & Brandt, 2003). Findings from previous psychophysical studies also provided support for the spotlight theory, by demonstrating that the spatial focus of attention is a simple monotonic activity gradient, in which there is enhanced activity at an attended location that falls off gradually with increasing distance (e.g., Henderson & Macquistan, 1993; Handy, Kingstone & Mangin, 1996). Indeed, Henderson and Macquistan (1993), demonstrated that participants' response time was better at an exogenously cued location (a cue appearing at the target location prior to the target) than nearby locations within the same visual quadrant, and that performance was also affected by the spatial distance between the cued and target locations. Spatial distribution of exogenously oriented attention followed a simple gradient model, in that the response times for targets appearing further away from the cued location were slower than for targets appearing closer.

However, findings from more recent studies have revealed a more complex profile than a simple gradient, contesting the spotlight metaphor (Hopf et al., 2012). For instance, in addition to enhanced processing at an attended location, several studies have observed reduced perceptual processing at locations near an attended item in comparison to locations further away, suggesting that there is a zone of suppression or attenuation surrounding an attended item (Caputo & Guerra, 1998; Cutzu & Tsotsos, 2003; McCarley & Mounts, 2007). In Cutzu and Tsotsos' (2003) study, for example, participants were required to visually discriminate between two letter character targets of a different colour from distractors, and report whether the targets' identities were identical or different from each other in a two-alternative forced choice task (2AFC). In cases where the participants' spatial attention was cued to one of the letter targets, their accuracy increased as the distance between the target letters increased. The participants' accuracy was worst when the two letter targets were side by side. These findings indicated that the processing advantage allocated by the spatial cue was also accompanied with a suppressive ring surrounding the cued target letter.

As previously mentioned, neurophysiological studies in both monkeys and rodents have revealed a center-surround suppressive profile (Sundberg et al., 2009; Zhang et al., 2014). Remarkably, studies on humans using magnetoencephalography (MEG) have revealed a similar attention profile. For instance, using MEG, Hopf and colleagues (2006) required participants to search for a red target C among blue distractor Cs, while remaining fixated at the center of the screen. The red target C and blue distractor Cs were all presented at an equal distance from the center of the screen in the shape of a quarter circle on a given side of the screen. On half of the trials, a white ring, referred to as the probe stimulus, was flashed around the center C. On the other half of the trials, no probe was presented. Given that the probe position remained constant while the target position varied, there were five target-to-probe distances, ranging from PD0 (target presented at the probed location) through PD4 (target presented 4 items away from the probe). The magnetic response to the probe was analyzed as a function of the target-to-probe distance, by subtracting the MEG response of a search frame with and without a probe. When the target appeared at the probe location (PD0), the MEG response was highest, but interestingly, the response was significantly reduced when the target appeared at position next to probe (PD1). The response reduction observed at PD1 was also significantly less than the responses to attended positions farther away (PD2-PD4), suggesting that surrounding the focus of attention, there was indeed a region of suppression or neural attenuation (Hopf et al., 2006). In a second experiment, Hopf and colleagues confirmed that these MEG response differences were not due to simple low-level stimulus interaction and instead due to attentional focus. Having participants focus on another difficult rapid serial visual presentation (RSVP) task at fixation, in which they were required to detect a target in a presentation of rapidly and serially displayed stimuli, while concurrently presenting the stimuli (red and blue Cs and probe) from the first experiment, completely eliminated the spatial profile of surround suppression. The RSVP task was demanding and assured that attention was not on the peripheral stimuli. Conversely, if participants were asked to complete the search task again, while ignoring the RSVP stimuli presentation, the spatial profile of surround suppression was observed again. The authors believed that this provided strong evidence for their finding of surround suppression being a specific consequence of attentional focusing.

1.2 Neural Mechanism of Attention-Modulated Surround Suppression

But how can the previous findings showing a monotonic gradient be reconciled with the surround suppression findings of more recent studies? According to computational models of attention, such as Tsotsos' (1995) selective tuning model (ST), the answer lies in the degree to which feedback projection or top-down processes are needed to focus attention (Hopf et al., 2012). According to the ST, surround suppression arises as a consequence of top-down attentional selection in the visual processing hierarchy. Top-down attentional selection is suggested to mediate from higher cortical areas, pruning or suppressing forward-projecting units or neurons not representing relevant input (Tsotsos, 2005). The requirements of a given task determine the degree to which the top-down projections are needed. For instance, in cases where spatial resolution is not needed, such as the detection of a colour stimulus, enough information is provided from the initial feedforward processes (Boehler, Tsotsos, Schoenfeld, Heinze & Hopf, 2008). Surround suppression would therefore not be observed given that feedback projections are not needed. This rationale has been confirmed by behavioural (McCarley

& Mounts, 2007) and MEG studies (Boehler et al., 2008). Boehler and colleagues (2008), for example, instructed participants to either report a gap orientation of a pop-out target (orientation of the gap of the C target), or to just report the colour of the target (red or green), the latter, a task that they hypothesized does not require much top-down processing. Similar to the Hopf and colleagues (2006) study, a white ring probe was presented as the center stimulus on half the trials. The probe only influenced the participants' accuracy for the orientation discrimination task and not the colour discrimination task. Moreover, a surround suppressive profile of neural activity was only observed for the orientation discrimination task. In contrast, a simple gradient neural activity was observed for the colour discrimination task. This pattern of findings confirmed that attention-modulated surround suppression is only present in cases where recurrent or top-down processing is needed to complete a task.

Further evidence of attention-modulated surround suppression being an effect of recurrent top-down processing derives from its presentation in relation to time. Boehler and colleagues (2008), for example, also demonstrated that whether surround suppression was observed depended on time. Similar to their previous experiments, participants were instructed to report the orientation of a target stimulus, and a probe ring was presented on half the trials as the center stimulus. The time course of surround suppression was assessed by systematically varying the frame-probe stimulus onset asynchrony (SOA) between 100 to 400 msec. The MEG results revealed that surround suppression was only observed at a time delay of 175 to 250 milliseconds (msec) after a task image onset.
The fact that attention modulated surround suppression is only observed for tasks demanding top-down processing and for delays of time between 175 to 250 milliseconds,

strongly demonstrates that it is a result of top-down mechanisms. This lag is beyond the initial feedforward bottom-up sweep of information that is believed to take place within approximately the first 100 msec (Foxe & Simpson, 2002). The time course of surround suppression also aligns with the typical time range of recurrent activity modulations in the early visual cortex due to attention (Martinez, Di Russo, Anllo-Ventom Sereno, Buxton & Hillyard 2001; Noesselt, Hillyard, Woldoff, Schoenfeld, Hagner, Jäncke, Tempelmann, Hinrichs & Heinze, 2002). According to the ST model, surround suppression arises from a top-down propagating winner-take-all (WTA) process that is initiated after the feedforward bottom-up sweep of processing reaches higher levels of the visual hierarchy (Boehler et al., 2008). As the WTA process moves down the hierarchy, there is a delay before reaching back to earlier visual areas (Boehler et al., 2008). Figure 1 demonstrates the ST process of selection and suppression. Neurally, the sources of top-down attentional signals are hypothesized to be a network of frontoparietal regions (Zanto & Rissman, 2015), including the frontal eye fields (Couperus & Mangun, 2010; Seiss, Driver & Eimer, 2009), inferior frontal junction (IFJ) (Sylvester, Jack, Corbetta & Shulman, 2008), superior frontal and angular gyri (Ruff & Driver, 2006), and precuneus (Payne & Allen, 2011).

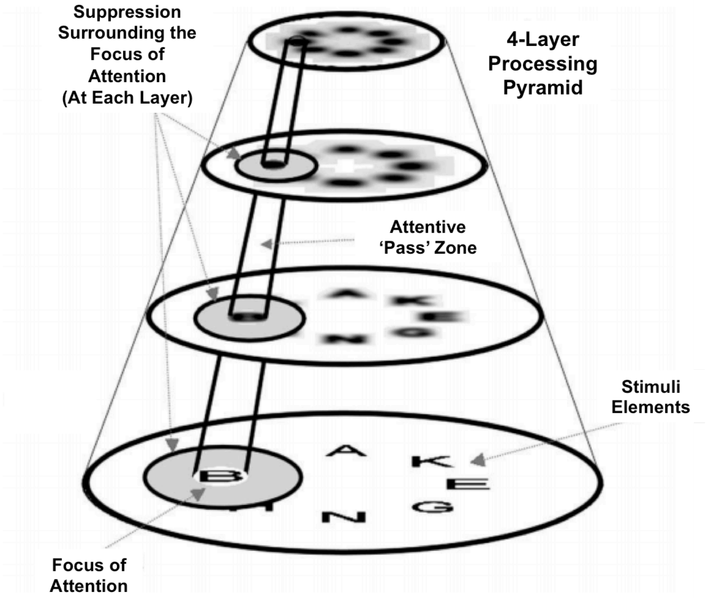

Figure 1. Selective tuning process of attentional selection and suppression. ST views the visual processing architecture as a pyramid in which units within the network receive both feedforward (top-down) and feedback (bottom-up) connections. The WTA process initially localizes the units or neurons with the largest response. All of the connections of the units or neurons that do not contribute to the winner are inhibited. This strategy of finding the winners, layer by layer, and then pruning away irrelevant connections is applied recursively. The remaining connections can be considered as the pass zone of attentional focus, while the pruned connections form the suppressive surround. Adapted from Tsotsos, Rodríguez-Sánchez, Rothenstein & Simine (2008).

1.3 Development of Visual Attention

Are there developmental differences in attention-modulated surround suppression in children and adolescents? Currently, there is not much developmental data to answer this question. Though the effect of top-down attentional mechanisms on visual processing has not readily been examined in development, visual attention has been studied extensively.

As previously mentioned, studies in the cognitive development literature have mainly centered on the ANT model (Petersen & Posner, 2012; Posner & Petersen, 1990), and have revealed that the three ANT networks of attention (spatial orientation, alerting and executive attention) are present as early as in infancy, but continue to develop well into childhood and adolescence (Johnson, 1995; Konrad et al., 2005; Luna et al., 2000). The developmental timeline for the development of each ANT network is relatively well understood and agreed upon across studies; however, it is unclear how these processes interact as they become more functional (Amso & Scerif, 2015) or how these networks emerge.

From a more visual and neurodevelopmental perspective, visual attentive behaviour across development is determined by the functional maturation of visual pathways (Johnson, 1990; Atkinson, 1984; 2000). For instance, in Johnson's (1990) model of attention development in infancy, visual attentive behaviour and eye movement characteristics early in development were reasoned to be governed by the maturity of vision related cortical pathways. Johnson organized known visual pathways into four categories and deduced that perceptual abilities throughout infancy were a result of which of the specific groups of pathways were mature. The first pathway, believed to mature early in infancy, is the direct pathway from the retina to the superior colliculus, which Johnson suggested is involved in rapid input-driven or stimulus-driven reactive eye movements. The second pathway is a cortical pathway connecting the superior colliculus directly to the primary visual cortex and also via middle temporal area (MT), and is involved in motion processing. The third pathway is considered by Johnson to combine processing streams in the frontal eye fields (FEFs) and to be involved in the detailed and complex analysis of visual stimuli, as well as the temporal sequencing of eye movements and anticipatory eye movements. Finally, the fourth pathway is involved in the control of eye movements through tonic inhibition, via the substantia nigra and basal ganglia.

Johnson (2002) stressed that the pathways were not rigid and did not develop in a sudden-onset fashion. Rather, he considered the observed onset of the pathways as snapshots of a constantly changing visual system. His model explains several changes in infant eye movement and visual attention behaviour from newborns into the first year of life. For instance, by 3 months of age, the pathway involving FEFs has begun dendritic growth and further myelination is taking place in the primary visual cortex (Johnson, 2002). These changes can readily account for how infants between the ages of 3 and 4 months can make anticipatory eye movements and even form expectations about visual stimuli, as first observed by Haith and colleagues (1988) in a series of experiments and in other more recent infant studies (e.g., Wong-Kee-You & Adler, 2016; Baker, Tse, Gerhardstein & Adler, 2008).

Similar to Johnson, Atkinson (1984; 2000) hypothesized in her model of visual development that the cortex takes over executive visual control from subcortical regions that are operational early at birth. At birth, the newborn uses their subcortical system to orient their eyes to abrupt changes in their environment. The functional onset of cortical systems involved in the processing of size, shape, pattern, colour, depth and movement subsequently takes place, maturing at varying rates. Visual attention is hypothesized by Atkinson (1984; 2000) to initially be a process that allows infants to integrate information from different cortical visual systems and to disengage processing of one object within the same depth plane and switch to the processing of another. As infants begin to reach, grasp at 5 to 6 months and become more mobile at 12 months of age, attention processes allow for the integration of manual action and visual space.

Beyond infancy, however, how do attentional mechanisms mature?

In a recent review of visual attention development spanning from infancy to adolescence, Amso and Serif (2015) used a similar hierarchical framework as Johnson's (1995) and Atkinson's (1984; 2000) to map out visual attention development. They reviewed studies examining the different attention networks of the ANT model but interpreted and organized the findings from a visual neurodevelopmental perspective. Amso and Scerif also applied principles of visual neuroscience and computational vision to their attentional framework.

The literature has well established that vision is organized hierarchically (Grill-Spector & Malach, 2004). Visual information is transmitted from the eyes to the LGN and then to other cortical areas that process the incoming visual information in parallel before feeding it forward to other cortical areas of the hierarchy for further complex processing (Maunsell & Newsome, 1987). There are separate hierarchical streams in the visual system for the analysis of motion and location (dorsal pathway), and object recognition and form representation (ventral pathway) (Goodale & Milner, 1992). And again, just as visual input is sent in a feedforward manner from lower visual areas to higher more specialized ones, top-down or feedback signals from high-level regions modulates functional activity in lower visual areas (Miller & Buschman, 2013). Amso and Scerif's (2015) proposed framework suggests that this hierarchical organization matures into a stable state over the course of development, which gives rise to a visual attentive system (Figure 2). Top-down modulation of visual pathways take place in response to the cumulative development of visual areas feeding forward to higher-level regions (Amso & Scerif, 2015). Accordingly, top-down attentional modulation also results in the improved quality of early vision, acuity, contrast sensitivity, and overall perceptual processing of attended information (Carrasco, Ling & Read, 2004). Disruption to the lower level visual organization or top-down feedback connection in development would therefore result in changes in functional connectivity and attentional network integration, and could potentially lead to developmental disorders (Amso & Scerif, 2015).

Amso and Scerif (2015) noted that their overall framework fit well with the development of the brain. Visual development is characterized with an increase of feedforward projections competing for attention allocation (Amso, Haas, Markant, 2014), and as a consequence top-down signals begin to tune the visual areas and the hierarchical organization is set in motion in the first postnatal year (Amso & Scerif, 2015). This visual attention framework also fits with connectomics research (identification of functional coupling of brain regions to form networks from fMRI analyses), demonstrating that infant brains are more generally best characterized by short-range sensorimotor connections, whereas long-range, more top-down, connections become more functional throughout development (Fransson, Skiöld, Horsch, Nordell, Blennow, Lagercrantz & Åden, 2007). Organization of cortical long-range connections involving increasingly frontal cortical areas continues to develop into childhood and adolescence (Fair, Cohen, Power, Dosenbach, Church, Miezin, Schlaggar & Petersen, 2009; Sepekar, Musen & Menon, 2009). Other imaging studies also support this short-range and long-range connection developmental timeline, in that they report increases in long-range region connectivity that continues late in development, including increased myelination and white matter integrity that facilitates long-range communication (Raznahan, Shaw, Lerch, Clasen, Greenstein, Berman, Pipitone, Chakravarty & Giedd, 2014; Vandekar, Shinohara, Raznahan, Roalf, Ross, DeLeo, Ruparel, Verma, Wolf, Gur, & Gur, 2015).

Collectively, therefore, Johnson's and Atkinson's model, and Amso and Scerif's framework, suggest that early in development the visual feedforward and low-level orienting mechanisms are more dominant and throughout development top-down feedback processes are strengthened. Pertinently, a question that should be asked is what would these developmental frameworks predict regarding the manifestation of attention-modulated surround suppression across development? Since attention-modulated surround suppression is largely a by-product of feedback tuning of the visual system (Boehler et al., 2008), it should be possible to reason when in development attention-modulated surround suppression would be observed by examining when feedback processes are believed to mature.

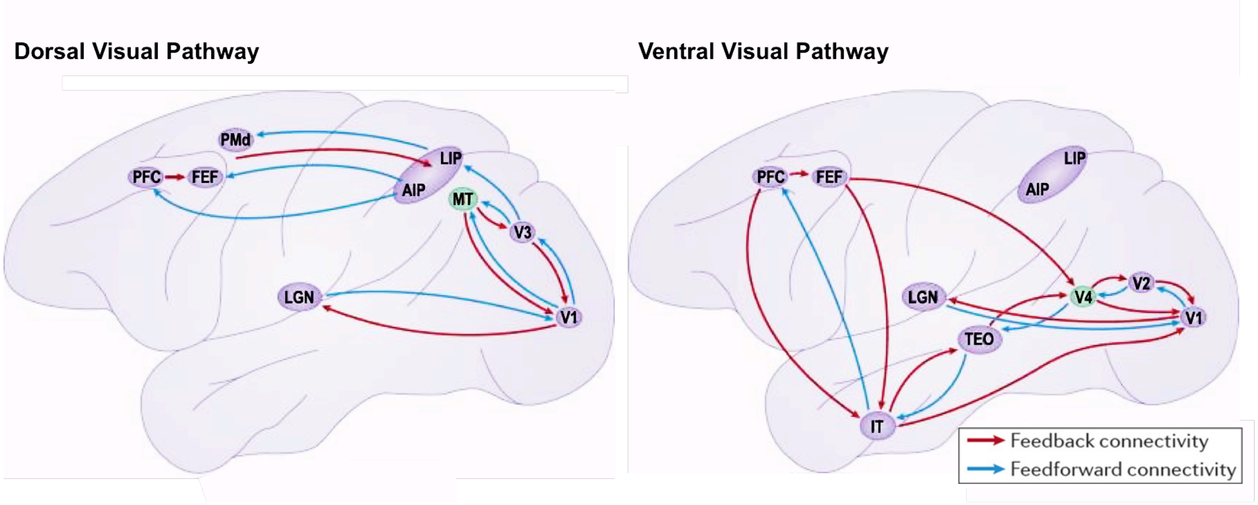

Figure 2. Amso and Scerif's (2015) framework of visual attention. This figure is a simplified overview of feedforward and feedback connectivity between visual areas and more-rostral cortical areas, including parts of the parietal, frontal and temporal cortices

involved in visual attention processes. The framework includes the distinction between the dorsal visual pathway, processing location and motion, and a ventral pathway, processing object recognition and form representation. PFC, prefrontal cortex; FEF, frontal eye fields; PMd, dorsal premotor cortex; LIP, lateral intraparietal area; AIP, anterior intraparietal area; MT, medial temporal area; TEO, tectum opticum; LGN, lateral geniculate nucleus; V1, visual area 1; V2, visual area 2; V3, visual area 3; V4; visual area 4. Figure adapted from Amso & Scerif (2015).

1.4 Development of the Visual System

An important factor to consider when studying attentional development, is the possibility that developmental differences in visual attention observed in previous studies are simply due to immature visual processing mechanisms. In order to rule out this possibility, it is important to examine when the visual system in the brain begins to function adult-like. In adulthood, the visual system follows two main principles: hierarchical processing and functional specialization (Grill-Spector & Malach, 2004). The visual system is hierarchical in the sense that visual perception is achieved through a stage-wise process where information is first represented in a localized and simple form, and is transformed, via a sequence of processes, into more abstract and holistic representations (DeYoe & VanEssan, 1988; Biederman, 1987; Marr, 1982). The principle of functional specialization, proposes that specialized brain areas and neural pathways process different aspects of a visual scene, such as: motion and depth in the dorsal pathway, and colour and shape in the ventral pathway (Grill-Spector & Malach, 2004, Goodale & Milner, 1992). The primary visual cortex (V1) is the first cortical area to receive input for processing (Grill-Spector & Malach, 2004). V1, also known as the striate cortex, is organized retinotopically in that mapping from the retina to V1 is topographic, whereby nearby areas on the retina project as nearby regions in V1 (Engel, Gloover & Wandell, 1997). Processing output from V1 is then sent to V2, V3, V3a dorsally, and V2, V3 and V4 ventrally, finally ending in object-related areas (Grill-Spector & Malach, 2004), such as the face selective fusiform gyrus FFA (fusiform face area) (Kanwisher , McDermott & Chun, 1997), all the while maintaining the hierarchical nature of the processing. The prestriate (V2) and extrastriate (V3, V3a, V4) are also organized retinotopically (Engle et al. 1997).

Psychophysical studies have revealed that the maturation of the visual system depends extensively on postnatal experience (Conner, Sharma, Lemieux & Mendola, 2004). Though most of the maturation of the visual systems takes place in the first year of life, some abilities take longer to mature (Conner et al., 2004). For instance, for the first 6 to 7 years of life, there are significant improvements in visual capacity for tasks involving second-order motion (Wandell, Brewer & Dougherty, 2005), grating acuity discrimination (Ellenberg, Lewis, Liu & Maurer, 1999), form from motion (Ellemberg, Lewis, Dirks, Maurer, Ledgeway, Guillemot & Lepore, 2004), and orientation discrimination (Lewis, Kingdon, Ellemberg & Maurer, 2001). Other aspects of vision take longer to develop. For example, spatio-chromatic (differences in chromaticity such as saturation or hue color in space) processing of low-spatial frequency isoluminant stimuli do not reach an adult-like state until around 12 to 13 years (Ellemberg et al., 2004) and face perception doesn’t reach adult levels until around 16 years of age (Mondloch, Geldart, Maurer & Le Grand, 2003). Another example of a late developing visual process is spatial contour integration. Spatial integration performance, as measured by the ability to detect a closed figure embedded among randomly positioned and oriented distractors, significantly improves from childhood into adolescence (5 years to 14 years) and is thought to rely on long-range projections (Kovács, Kozma, Fehér & Benedek, 1999)

Neuroimaging research has also revealed differences in the maturation of specific visual areas and the importance of postnatal experience on visual development. For instance, in an imaging study, Conner and colleagues (2004) demonstrated that the retinotopic organization of the striate (V1), prestriate (V2) and extrastriate (V3, V3a, VP and V4) cortex in children older than 9 years and adults are similar; however, the extrastriate cortex appears to increase in size past the age of 12 (Conner et al., 2004). In a more recent study, Deen and colleagues (2017) found that the extrastriate cortex in infants as young as 4 to 6 months of age is spatially organized much like in adults. Even here, however, the response profiles and patterns of activity across different visual categories were different between infants and adults, indicating that though the organization of the visual cortex is adult-like early in infancy, subsequent refinement occurs throughout development (Deen, Richardson, Dilks, Takahashi, Keil, Wald, Kanwisher & Saxe, 2017).

Overall, the majority of the maturation of the visual system takes place during early development. This is evident from cataract reversal studies, which indicate that there are differences among sensitive periods for normal visual development, sensitivity to deprivation and recovery from deprivation (Lewis & Maurer, 2005; Fuhrmann, Knoll & Blackemore, 2015). For instance, for visual acuity, individuals are sensitive to deprivation until around 10 years of age (Maurer & Lewis, 2013). On the other hand, the period of visually driven normal development is over by 5 to 7 years of age and the sensitive period for recovery lasts until about age 7 for low spatial frequencies but only until about age 5 for higher spatial frequencies (Lewis & Maurer, 2005). With regard to visual attention studies, it is therefore unlikely that attention performance differences observed in younger children on attentional tasks (ANT, visual search, etc.) are due to immaturity in visual acuity or in the processing of simple visual stimuli, particularly for children older than 5 to 7 years. Performance differences are instead likely a result of immature attentional processes or differences in the effect of attentional focus on visual processing. Of relevance to the current study, it can therefore be argued that top-down mechanisms in adults, adolescents and older school-aged children can be tested on an attentional visual discrimination task to examine potential differences in top-down attentional processes. Potential performance differences will likely be driven by differences in the maturity of top-down attentional processing and not simply low-level visual processing.

1.5 Research Objectives and Predictions

In the current study, there were two goals. The first was to examine whether younger age groups exhibit attention-modulated surround suppression. Accordingly, mapping the developmental timeline of surround suppression was undertaken. As a secondary goal, the current experimental findings were evaluated collectively with the aim to provide some answers of how attentional mechanisms mature, namely, how top-down processing matures across development. Attention-modulated surround suppression was used as a general measure of the effectiveness of top-down tuning on the visual system.

Taking the principles of the attentional development frameworks into consideration, visual and feedback pathway will likely dictate whether attention-modulated surround suppression is observed in a particular age group. Specific details about the study task and design will be highlighted in the methods sections, but broadly, the task used for this dissertation involved a 2AFC task in which participants needed to visually discriminate between 2 targets (replication of Cutzu & Tsotsos (2003)). One of the targets was spatially cued, which typically results in that cued target being highly visually discriminable. This attentive advantage, however, is predicted to be accompanied with a suppressive ring surrounding the cued and attended target. This means that as the second target is presented further away from the cued target, the participants' visual discrimination accuracy of both targets is expected to increase. Accuracy is expected to increase linearly as the inter-target separation increases, because the second target begins to fall outside of the surrounding suppressive ring. Given that top-down feedback processes continue to develop into early adolescence, we hypothesized that older adolescents (16-17 years) would exhibit a similar presentation of surround suppression modulated by attention as adults, whereas younger adolescents (14-15 years) will demonstrate the pattern but in a less precise manner. More specifically, we hypothesized that the older adolescents would exhibit a strong linear relationship between inter-target separation and accuracy. For younger adolescents we hypothesized that inter-target separation would also affect their accuracy but not in a clearly strong linear pattern, given that their top-down feedback processes are still maturing.

For the pre-adolescents (12-13 years) and younger children (under 12 years) it was difficult to hypothesize whether they will demonstrate the effect or not. Previous studies have suggested that top-down attentional processes are developing in infancy, childhood and even early adolescence (Amso & Scerif, 2015), but it is unclear exactly how the immaturity of these processes at specific ages impact tuning of the visual system. The answer, however, may partially lie in the findings of imaging work of known attentional networks in the developing brain. There are two partially segregated attention networks in the human brain: the dorsal and ventral attention networks (Corbetta & Shulman, 2002). Each network includes different brain areas that are believed to play a different role in attention. The dorsal attention network (DAN) shows activation when attention is focused, and is believed to be responsible for goal-driven top-down processing (Corbetta & Shulman, 2002). The ventral attention network (VAN) is generally activated in cases where bottom-up processing is taking place, such as when an unexpected event occurs and breaks an observer's attention from a given task (Corbetta & Shulman, 2002). Of relevance, the frontoparietal regions in the DAN are believed to be sources of attention biases onto the sensory cortex (i.e., visual cortex) (Desimone & Duncan, 1995; Corbetta & Shulman, 2002; Reynolds & Chelazzi, 2004). In a recent study, Farrant and Uddin (2015) used resting state fMRI to examine the development of DAN and VAN in children aged between 7 and 12 years. Farrant and Uddin (2015) found that for the DAN, children exhibited greater within network connectivity (short-range functional connectivity) in comparison to adults. In adults, long-range functional connectivity between DAN and regions outside the network is believed to enable greater top-down attentional capacities in adulthood (Rubia, 2013). For VAN, children showed greater functional connectivity than adults (Farrant & Uddin, 2015). The authors speculated that this over-connectivity in the VAN can perhaps explain why children are susceptible to interruption by environmental stimuli and are less able to maintain activities requiring top-down attentional control (Gaspelin, Margett-Jordan & Ruthruff, 2015; Bunge, Dudukovic, Thomason, Vaidya & Gabrieli, 2002).

Though informative for the current study, Farrant and Uddin's study did include a wide age range (7 to 12 years) all grouped together in their analyses. As such, a clear developmental timeline of top-down processes is difficult to determine. Nevertheless, it can be concluded from their findings that for children under the age of 12 years, top-down processes are not as functionally connected to farther regions such as the visual cortex. As such, I hypothesized that children under the age of 12 years would not exhibit attention-modulated surround suppression. I hypothesized that inter-target separation would not affect their visual discrimination accuracy. For our pre-adolescent group of 12 to 13 years, predicting whether they will exhibit surround suppression is difficult given there is not as much research to guide predictions. Nevertheless, I hypothesized that 12- to 13-year-olds would likely exhibit attention-modulated surround suppression, but in a weaker and less precise manner than the older age groups.

The following sections outline the methodological and data analysis procedures of the experiments that were undertaken.

2. Experiment 1: Attention-Modulated Surround Suppression Across Development

This study was designed to examine whether a ring of suppression surrounding an attended item is observed in younger age groups. In order to examine this question, the first experiment of Cutzu and Tsotsos' (2003) psychophysical study was replicated with younger age groups. Participants were required to detect two letter character targets of a different colour from distractors and report whether the identity of the targets were identical or different. Participants' spatial attention was cued to one of the two letter targets. All age groups were examined individually in six sub-experiments. The results of a mixed-effects ANOVA, with the data combined across age group, can be found in Appendix A.

2.1 Experiment 1A: Young Adults (18+ years)

Prior to testing younger age groups, young adults were first tested to assure that the version of the task used in the current study replicates previous findings in the literature. That is, whether, as predicted, young adults' target discrimination accuracy increases as a function of inter-target separation, as a consequence of surround suppression modulated by attention, was examined.

2.2.1 Methods

Participants

Twenty-eight young adults were recruited to participate in the study. Young adult participants were recruited from Undergraduate Research Participant Pool and the Ontario Science Center. For the participants tested at the Ontario Science Centre, the lab set up was replicated at the Science Centre. The mean age of the participants was 19.75 years (age range = 18.00 to 27.34 years; 17 = female, 11 = male). All participants reported their vision as normal and had no history of psychiatric or neurological disorders.

Stimulus and Procedure

The experimental session began with participants first reading through and filling out a consent form and a demographic questionnaire.

Participants were seated in front of a mounted laptop. The laptop was mounted in order for the screen to be at the participants' eye level. To maintain the distance from the screen equal for all participants and to minimize head movements, a chin rest was used. Participants were instructed to comfortably sit and rest their head on the chin rest and ready their fingers on the response keys of a connected external keyboard.

The experimental sequence began with the cue, a light gray disk was briefly displayed and anticipated the location of the first target. The cue was presented for a duration of 100 msec and was valid on all trials. Following the cue, the visual array was displayed and consisted of 6 randomly oriented Ls and 6 randomly oriented Ts, arranged in the shape of a circle centered on a fixation point at the center of the screen. The radius of the circle was 4º and the character size was 0.6º visual angle. The items in the visual array were displayed in a circle to make sure that all items have equivalent retinal resolution. The letter characters were equally spaced out and were overlaid on top of a circular light disk, identical in size and colour to the cue disk. Two of the letter characters were red, one of which was cued target, Target 1, whose location was cued, while the remainder of the characters were black. The distances between the two target letters, Target 1 and Target 2 varied among six values of inter-target separation distances. The inter-target separation distances varied from where targets were neighbours, to where two targets were diametrically opposite, with five distracter characters between them. The inter-target distances were measured as a line segment between Target 1 and Target 2. At the largest inter-target separation distance, the distance was considered as 1.00. The smaller inter-target distances were considered as a fraction of the largest inter-target distance that it represents. The orientation of the line segment connecting Target 1 and

Target 2 was random across all trials. Figure 1 depicts the 6 inter-target separation distances included in this experiment.

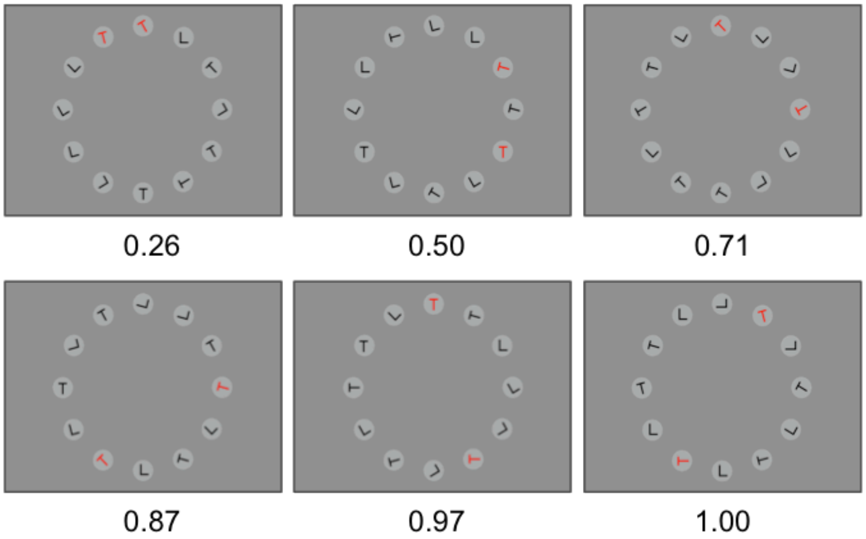
0.26 0.50 0.71
0.87 0.97 1.00

Figure 3. Inter-target separations included in the experiment. At the largest inter-target separation distance, the distance was considered as 1.00. The smaller inter-target distances were considered as a fraction of the largest inter-target distance that it represents.

Participants were instructed to respond to the visual array as accurately and quickly as possible. A 2AFC method was used in which the participants were required to decide by pressing one of two keys on the keyboard connected to the mounted laptop whether Target 1 and Target 2 were identical (L-L or T-T) or different (T-L or L-T). Throughout the entire task there was a white cross, the size of 0.6 degrees in eccentricity, at the center of the screen. Participants were instructed to maintain fixation on the cross while they completed the task.

The visual array was presented for 175 msec, followed by a mask consisting of multiple randomly coloured and oriented Ls and Ts scattered on the screen. The role of the mask was to prevent a potential after-image of the visual array, and to erase any iconic memory of the target letters and visual array. While the mask was on the screen, participants made their response. Given that the measurement of eye movements was not possible in the current testing setup, the visual array was presented for 175 msec to minimize the participants' ability and likelihood of making eye movements while the array was on the screen. Eye movements are known to be closely related to attention (e.g., Adler, Bala & Krauzlis, 2002) and without being able to measure eye movements, it would not be possible for us to assure that differences in eye movements were not a confound across the inter-target separations. Once the participants responded, the next trial was initiated. Figure 2 provides a visual depiction of the temporal sequence.

Participants were given 3 blocks of practice trials. For the first block, the visual array was on for 500 msec, for the second 250 msec and finally for the third 175 msec. The decreasing duration of the visual array presentation during practice was found in pilot testing to greatly help younger age groups understand the task. In order to maintain consistency among all age groups, older participants, including adults, also underwent the practice blocks and were instructed in a similar manner to the younger groups.

Participants completed a total of 144 trials, in which each six inter-target separations were presented a total of 24 times, with 12 of those times being in the identical targets condition (LL or TT, 6 times each) and 12 times in the different targets condition (LT or TL, 6 times each). Trials were divided into 3 blocks. This provided the participants a short break in between each block and assured that all the participants remain focused on the task throughout the entire experiment. This breakdown was particularly critical for the younger participants who were tested in the next experiments.

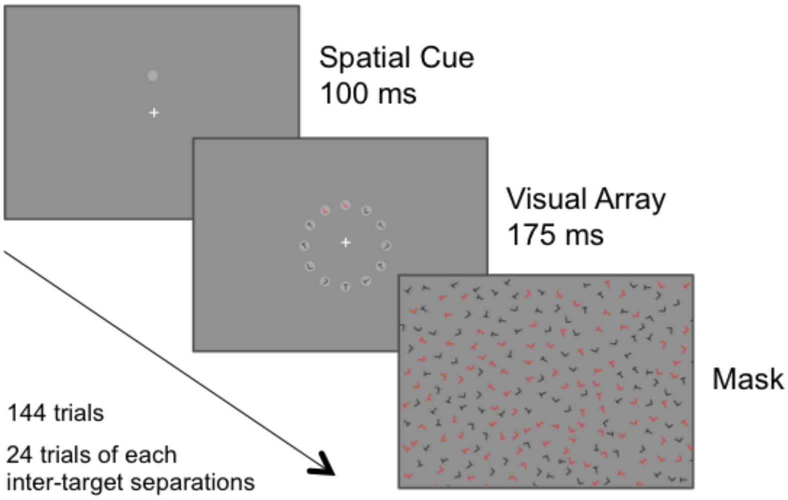

Figure 4. Visual depiction and temporal sequence of Experiment 1.

2.1.2 Results

The young adults' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 5 depicts the adults' accuracy as a function of inter-target separation. Accuracy improved with increasing inter-target separation, increasing from approximately 60% when the targets were immediate neighbors to about 72% when diametrically opposite. The young adults' mean accuracy across inter-target separation can be found in Table 1.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R statistical software (R Core Team, 2013). Inter-target separation was set as a fixed variable and subject as a random variable. The mixed effects model accounted for 40% of the variance in the adults' accuracy (pseudo-$R^2 = 0.402$). There was a significant main effect of inter-target separation on accuracy, $F(5,135) = 8.75$, $p < .0001$. Bonferroni corrected post-hoc tests revealed that adults' accuracy was significantly lower at the minimum inter-target separation of 0.26 (M = .60, SD = .07) compared to separations of 0.71 (M = .67, SD = .10), 0.87 (M = .70, SD = 0.11), 0.97 (M

= .71, SD = .11) and 1.00 (M = .72 SD = .11) (*p* < .001 for 0.26 compared to 0.71 and *p* < .0001 for all other comparisons). Adults' accuracy was also lower at inter-target separation 0.50 (M = .62, SD = .11) compared to 0.87 (M = .70, SD = 0.11), 0.97 (M = .71, SD = .11) and 1.00 (M = .72 SD = .11) (*p* < .01). Accuracy for the smaller inter-target separations of 0.26 and 0.50 were not significantly different from one another. Similarly, accuracy for the larger inter-target separations of 0.81, 0.97 and 1.00 were not significantly different from one another.

To further examine the hypothesis that accuracy is affected, and in fact improves as a function of inter-target separation, a linear regression analysis of the dependence of accuracy on inter-target separation was performed. The linear regression model was significant $F(5,162) = 6.20$, $p < .0001$, indicating that the null hypothesis of all the slope coefficients being equal to 0 can be rejected. The *R*-squared statistic of the linear regression model was $R^2 = 0.16$, which as an index of effect size represents a medium to large effect (Cohen, 1988).

Table 1. Accuracy across inter-target separation for young adults age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.60	0.07
0.50	0.62	0.11
0.71	0.67	0.10
0.87	0.70	0.11
0.97	0.71	0.12
1.00	0.73	0.11

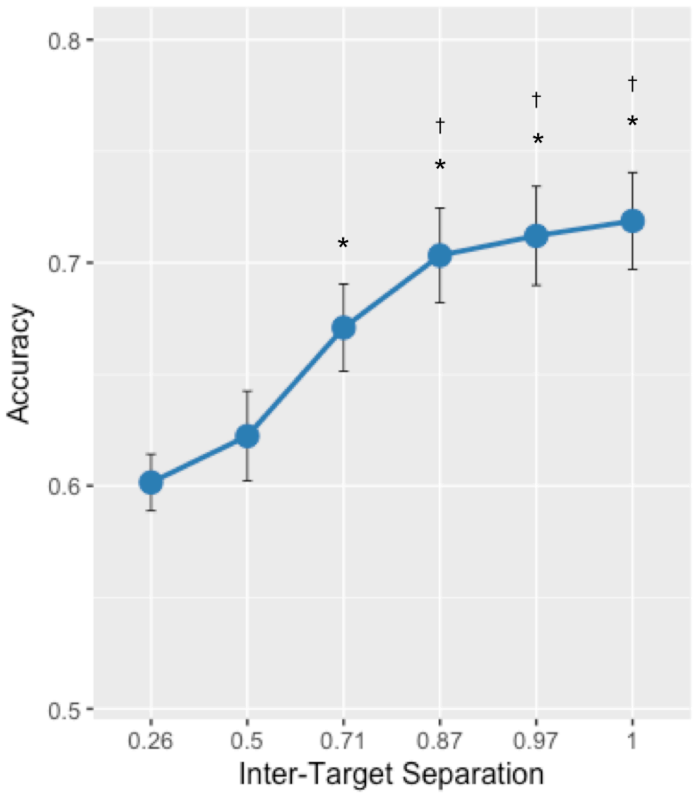

Figure 5. Accuracy as a function of inter-target separation in young adults. * = Accuracy significantly greater than at inter-target separation 0.26. † = Accuracy significantly greater than at inter-target separation 0.50. The error bars indicate standard errors.

2.1.3 Discussion

The young adults' accuracy significantly improved as inter-target separation increased. With the exception of one inter-target separation greater than itself, the adults' accuracy at 0.26 and 0.50 was significantly lower compared to all of the larger inter-target separations. These results generally replicate the findings of Cutzu and Tsotsos (2003) and provide further evidence of a ring of suppression surrounding a spatially attended location. The results of this experiment also suggest that the current version of the task can be appropriately used to study attention-modulated surround suppression in the subsequent sub-experiments.

2.2 Experiment 1B: Older Adolescents (16-17 years)

2.2.1 Methods

Participants

Thirty-one 16- to 17-year-olds were recruited at the Ontario Science Centre to participate in the study. The mean age of the participants was 16.95 years (age range = 16.05 to 17.84 years; 21 = female, 10 = male). All participants reported their vision as normal and had no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1A, with the exception that testing took place at the Ontario Science Centre. The set-up replicated that from the lab.

2.2.2 Results

Similar to Experiment 1A, target discrimination accuracy was computed for all 6 inter-target separation values for each participant. Figure 6 depicts the participants' accuracy as a function of inter-target separation. Accuracy in 16- to 17-year-olds improved with increasing inter-target separation, increasing from approximately 58% when the targets were immediate neighbors to 70% when diametrically opposite. The 16- to 17-year-olds' mean accuracy across inter-target separation can be found in Table 2.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The mixed effects model accounted for 45% of the variance in the 16- to 17-year-olds' accuracy (pseudo-$R^2 = 0.447$). There was a significant main effect of inter-target separation on accuracy, $F(5,150) = 9.50$, $p < .0001$. Bonferroni corrected post-hoc tests revealed that the 16- to 17-year-olds' accuracy was significantly lower at the minimum inter-target separation of 0.26 (M = .58, SD = .12) compared to separations of 0.97 (M = .69, SD = .13) and 1.00 (M = .70 SD = .12) ($p < .0001$). Accuracy was lower at inter-target separation 0.50 (M = .59, SD = .11) compared to 0.97 (M = .69, SD = .13) and 1.00 (M = .70 SD = .12) ($p < .001$). Accuracy was also lower at 0.71 (M = .59, SD = 0.13) compared to 0.97 (M = .69, SD = .13) and 1.00 (M= .70 SD = .12) (all p-values < .001). No significant accuracy differences were found between the smaller inter-target separations of 0.26, 0.5 and 0.71. Similarly, accuracy for the larger inter-target separations of 0.81, 0.97 and 1.00 were not significantly different from one another.

A linear regression analysis of the dependence of accuracy on inter-target separation was performed to examine whether accuracy improves as a function of inter-target separation. The linear regression model was significant $F(5,180) = 6.12$, $p < .0001$, indicating that the null hypothesis of all the slope coefficients being equal to 0 can be rejected. The R-squared statistic of the linear regression model was $R^2 = 0.15$, which as an index of effect size represents a medium to large effect (Cohen, 1988).

Table 2. Accuracy across inter-target separation for 16-17 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.58	0.12
0.50	0.59	0.11
0.71	0.60	0.13
0.87	0.64	0.11
0.97	0.70	0.13

1.00	0.70	0.12

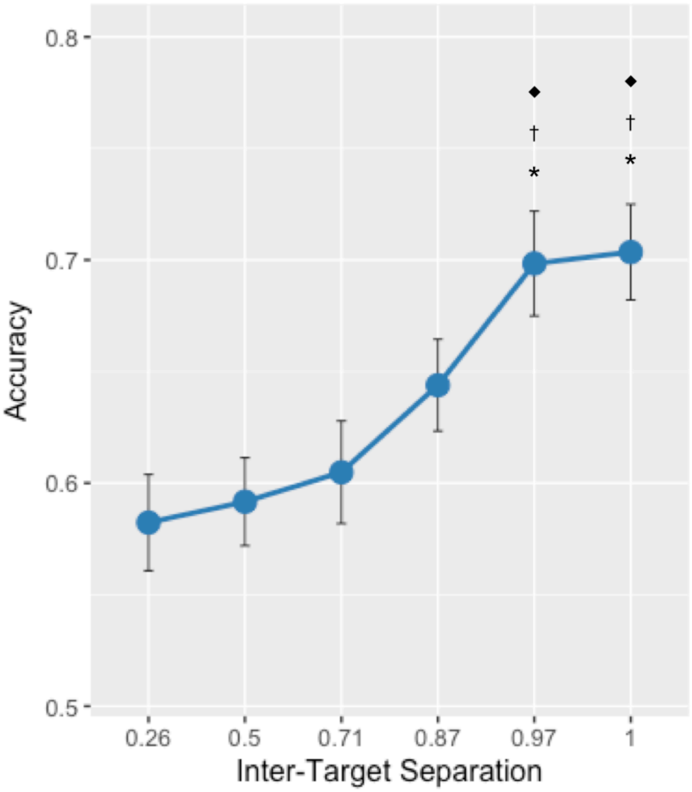

Figure 6. Accuracy as a function of inter-target separation in 16- to 17-year-olds. * = Accuracy significantly greater than at inter-target separation 0.26. † = Accuracy significantly greater than at inter-target separation 0.50. ◆ = Accuracy significantly greater than at inter-target separation 0.71. The error bars indicate standard errors.

2.2.3 Discussion

Similar to the young adults, the 16- to 17-year-olds' accuracy increased as a function of inter-target separation. However, their accuracy at 0.26 and 0.50 was only significantly lower compared to the two largest inter-target separations of 0.97 and 1.00. In contrast to the young adults, 16- to 17-year-olds' accuracy at 0.71 was also significantly lower compared to accuracy at 0.97 and 1.00. Accuracy gains in 16- to 17-year-olds were not observed until much larger inter-target separations, pointing to the possibility that attentional surround suppression in this age group is larger than in young adults.

2.3 Experiment 1C: Younger Adolescents (14-15 years)

2.3.1 Methods

Participants

Twenty-five 14- to 15-year-olds were recruited and tested at the Ontario Science Centre to participate in the study. The mean age of the participants was 14.75 years (age range = 14.10 to 15.89 years; 7 = female, 18 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1B with the exception of participants' parents providing consent for their child's participation and filling out a demographic questionnaire. Verbal assent was also obtained for each participant.

2.3.2 Results

Target discrimination accuracy was computed for all 6 inter-target separation values for each participant. Figure 7 depicts the 14- to 15-year-olds' accuracy as a function of inter-target separation. Accuracy in 14- to 15-year-olds improved with increasing inter-target separation, increasing from 60% when the targets were immediate neighbors to about 69% when diametrically opposite. The 14- to 15-year-olds' mean accuracy across inter-target separation can be found in Table 3.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The mixed effects model accounted for 43% of the variance in the participants' accuracy (pseudo-$R^2 = 0.428$). There was a significant main effect of inter-target separation on accuracy, $F(5,120) = 9.32$, $p < .0001$. Bonferroni corrected post-hoc tests revealed that participants' accuracy was significantly lower at the minimum inter-target separation of 0.26 (M = .59, SD = .09) compared to separations of 0.97 (M = .72, SD = .10) and 1.00 (M = .69 SD = .09) ($p < .001$). Accuracy was lower at inter-target separation 0.50 (M = .57, SD = .10) compared to accuracy at 0.97 (M = .72, SD = .10) and 1.00 (M = .69 SD = .09) ($p < .05$). Accuracy was lower at 0.71 (M = .64, SD = .11) compared to 0.97 (M = .71, SD = .10). Accuracy was also lower at 0.87 (M = .61, SD = 0.13) compared to 0.97 (M = .72, SD = .10) and 1.00 (M = .69 SD = .09) ($p < .05$). No significant accuracy differences were found between the smaller inter-target separations of 0.26 and 0.50. Similarly, accuracy for the larger inter-target separations of 0.97 and 1.00 were not significantly different from one another.

A linear regression analysis of the dependence of accuracy on inter-target separation was also performed to examine whether accuracy increased as a function of inter-target separation. The linear regression model was significant $F(5,120) = 7.85$, $p < .0001$, indicating that the null hypothesis of all the slope coefficients being equal to 0 can be rejected. The R-squared statistic of the linear regression model was $R^2 = 0.25$, which as an index of effect size represents a medium to large effect (Cohen, 1988).

Table 3. Accuracy across inter-target separation for 14-15 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation

0.26	0.60	0.09
0.50	0.58	0.11
0.71	0.64	0.01
0.87	0.61	0.13
0.97	0.72	0.10
1.00	0.69	0.09

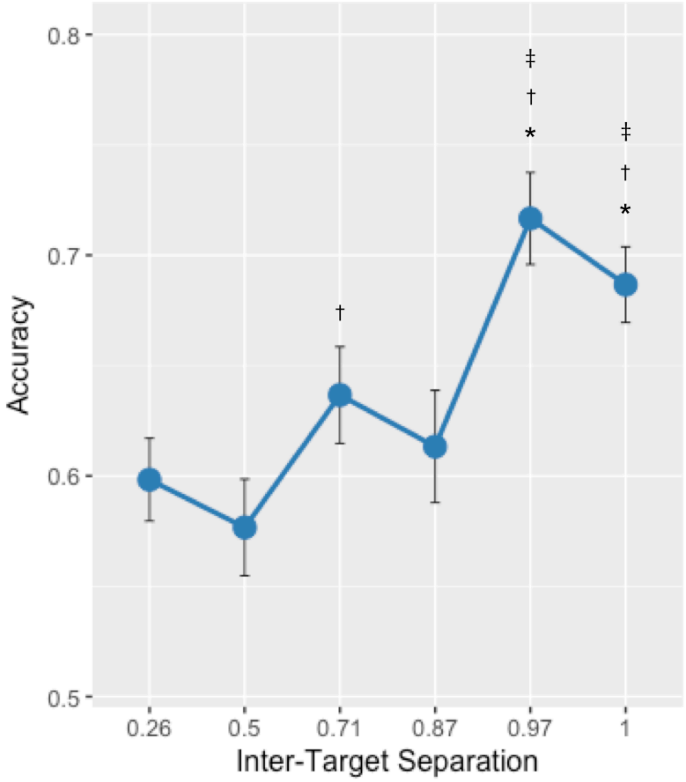

Figure 7. Accuracy as a function of inter-target separation in 14- to 15-year-olds. * = Accuracy significantly greater than at inter-target separation 0.26. † = Accuracy significantly greater than at inter-target separation 0.50. ‡ = Accuracy significantly greater than at inter-target separation 0.87. The error bars indicate standard errors.

2.3.3 Discussion

Similar to the 16- to 17-year-olds, the 14- to 15-year-olds' accuracy increased as a function of inter-target separation, and accuracy at 0.26 and 0.50 was only significantly lower than the two largest inter-target separations of 0.97 and 1.00. However, in contrast to the 16- to 17 year-olds, accuracy at 0.50 in 14- to 15-year-olds was significantly lower than at 0.71 and accuracy 0.87 was also significantly lower than accuracy at 0.97 and 1.00. This finding possibly indicates that attention-modulated surround suppression in 14- to 15-year-olds is noisier and larger than that of both adults and 16- to 17-year-olds.

2.4 Experiment 1D: Pre-Adolescents (12-13 years)

2.4.1 Methods

Participants

Thirty-six 12- to 13-year-olds were recruited and tested at the Ontario Science Centre to participate in the study. The mean age of the participants was 12.80 years (age range = 12.05 to 13.89 years; 15 = female, 21 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1C.

2.4.2 Results

Target discrimination accuracy was computed for all 6 inter-target separation values for each participant. Figure 8 depicts the 12- to 13-year-olds' accuracy as a function of inter-target separation. Accuracy in 12- to 13-year-olds improved with increasing inter-target separation, increasing from 54% when the targets were immediate neighbors to about

65% when diametrically opposite. The 12- to 13-year-olds' mean accuracy across inter-target separation can be found in Table 4.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The mixed effects model accounted for 35% of the variance in the participants' accuracy (pseudo-$R^2 = 0.353$). There was a significant main effect of inter-target separation on accuracy, $F(5,175) = 7.26$, $p < .0001$. Bonferroni corrected post-hoc tests revealed that the 12- to 13-year-olds' accuracy was significantly lower at the minimum inter-target separation of 0.26 (M = .54, SD = .10) compared to separations of 0.97 (M = .63, SD = .14) and 1.00 (M = .65 SD = .11) ($p < .001$ for both comparisons). Accuracy was lower at inter-target separation 0.50 (M = .56, SD = .10) compared to of 0.97 (M = .63, SD = .14) and 1.00 (M = .65 SD = .11) (both at $p < .001$). Accuracy was also lower at 0.71 (M = .57, SD = 0.11) compared to 1.00 (M = .65 SD = .11) ($p < .01$). No significant accuracy differences were found between the smaller inter-target separations of 0.26, 0.5 and 0.71. For the larger inter-target separations of 0.87, 0.97 and 1.00, they were also not significantly different from one another.

A linear regression analysis of the dependence of accuracy on inter-target separation was performed. The linear regression model was significant $F(5,210) = 5.27$, $p < .001$, indicating that the null hypothesis of all the slope coefficients being equal to 0 can be rejected. The R-squared statistic of the linear regression model was $R^2 = 0.11$, which as an index of effect size represents the lower bounds of a medium effect (Cohen, 1988).

Table 4. Accuracy across inter-target separation for 12-13 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.54	0.10
0.50	0.55	0.12
0.71	0.57	0.12
0.87	0.58	0.12
0.97	0.63	0.15
1.00	0.65	0.11

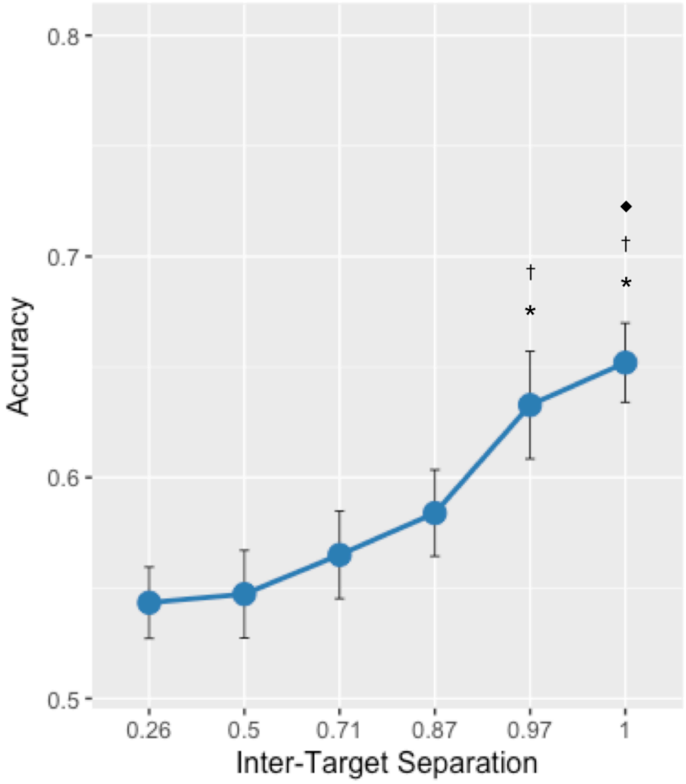

Figure 8. Accuracy as a function of inter-target separation in 12- to 13-year-olds. * = Accuracy significantly greater than at inter-target separation 0.26. † = Accuracy

significantly greater than at inter-target separation 0.50. ◆ = Accuracy significantly greater than at inter-target separation 0.71. The error bars indicate standard errors.

2.4.3 Discussion

The 12- to 13-year-olds performed less accurately overall compared to the older age groups. However, accuracy in this age group similarly increased as a function of inter-target separation. The 12- to 13-year-olds' accuracy at 0.26 and 0.50 was significantly lower than the two largest inter-target separations of 0.97 and 1.00. Similar to the 16- to 17-year-olds', their accuracy at 0.71 was also significantly lower than accuracy at 0.97 and 1.00, possibly indicating that attention-modulated surround suppression in this age group is larger than that of young adults but smaller than that of 14- to 15-year-olds. Notably, for 12- to 13-year-olds, the effect of inter-target separation appears to be weakened in comparison to the older age groups, as indicated by the smaller R^2 of the linear regression.

2.5 Experiment 1E: Older School-Aged Children (10-11 years)

2.5.1 Methods

Participants

Twenty-nine 10- to 11-year-olds were recruited and tested at the Ontario Science Centre to participate in the study. The mean age of the participants was 10.76 years (age range = 10.03 to 11.88 years; 6 = female, 23 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1C and 1D.

2.5.2 Results

Target discrimination accuracy was computed for all 6 inter-target separation values for each participant. Figure 9 depicts the 10- to 11-year-olds' accuracy as a function of inter-target separation. Accuracy in 10- to 11-year-olds remained at around 55% (range = 52% to 59%). The 10- to 11-year-olds' mean accuracy across inter-target separation can be found in Table 5.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,140) = 1.81$, $p > .05$.

Similar to the previous experiments, a linear regression analysis of the dependence of accuracy on inter-target separation was performed. The linear regression model was not significant $F(5,168) = 1.23$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 could not be rejected. The *R*-squared statistic of the linear regression model was $R^2 = 0.04$.

Table 5. Accuracy across inter-target separation for 10-11 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.54	0.13
0.50	0.53	0.12
0.71	0.52	0.10
0.87	0.53	0.13
0.97	0.56	0.11
1.00	0.59	0.13

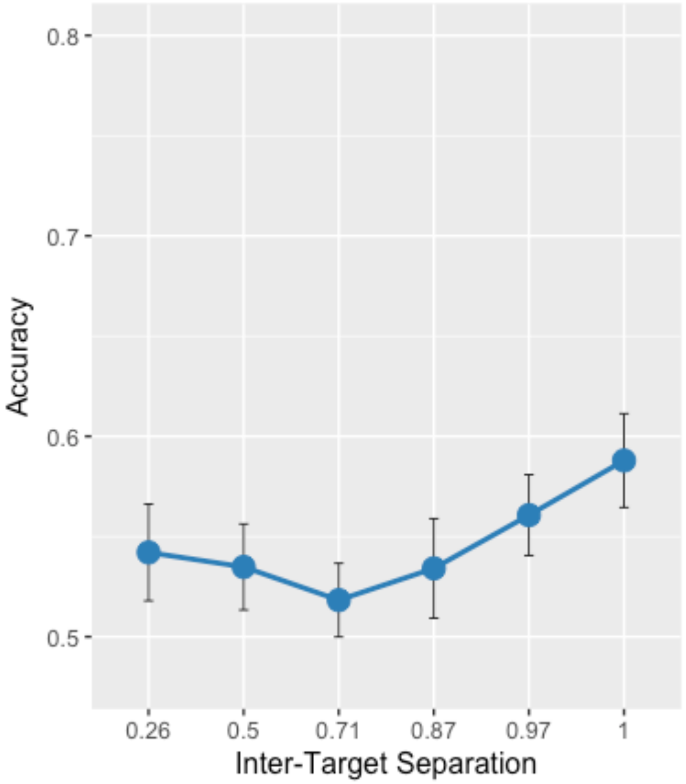

Figure 9. Accuracy as a function of inter-target separation in 10- to 11-year-olds. The error bars indicate standard errors.

2.5.3 Discussion

Similar to the 12- to 13-year-olds, the 10- to 11-year-olds performed less accurately overall compared to the older age groups. However, in contrast to the 12- to 13-year-olds, accuracy in the 10- to 11-year-olds did not increase as a function of inter-target separation from the separation of 0.26. This suggests that 10- to 11-year-olds do not exhibit attention-modulated surround suppression as observed in the older age groups. However, it is possible that top-down attentional processes are modulating visual processing in this age group but need more time to complete. This possibility was examined in Experiment 3.

2.6 Experiment 1F: Younger School-Aged Children (8-9 years)

2.6.1 Methods

Participants

Thirty-one 8- to 9-year-olds were recruited and tested at the Ontario Science Centre to participate in the study. The mean age of the participants was 8.81 years (age range = 8.01 to 9.90 years; 16 = female, 15 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiments 1C to 1E.

2.6.2 Results

Target discrimination accuracy was computed for all 6 inter-target separation values for each participant. Figure 10 depicts the 8- to 9-year-olds' accuracy as a function of inter-target separation. Accuracy in 8- to 9-year-olds remained at around 53% (range = 51% to 55%) did not improve with increasing inter-target separation. The 8- to 9-year-olds' mean accuracy across inter-target separation can be found in Table 6.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,150) = 0.58$, $p > .05$.

Similar to the previous experiments, a linear regression analysis of the dependence of accuracy on inter-target separation was performed. The linear regression model was not significant $F(5,150) = 1.80$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected. The R-squared statistic of the linear regression model was $R^2 = 0.01$.

Table 6. Accuracy across inter-target separation for 8-9 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.53	0.11
0.50	0.51	0.11
0.71	0.52	0.11
0.87	0.51	0.11
0.97	0.55	0.10
1.00	0.54	0.10

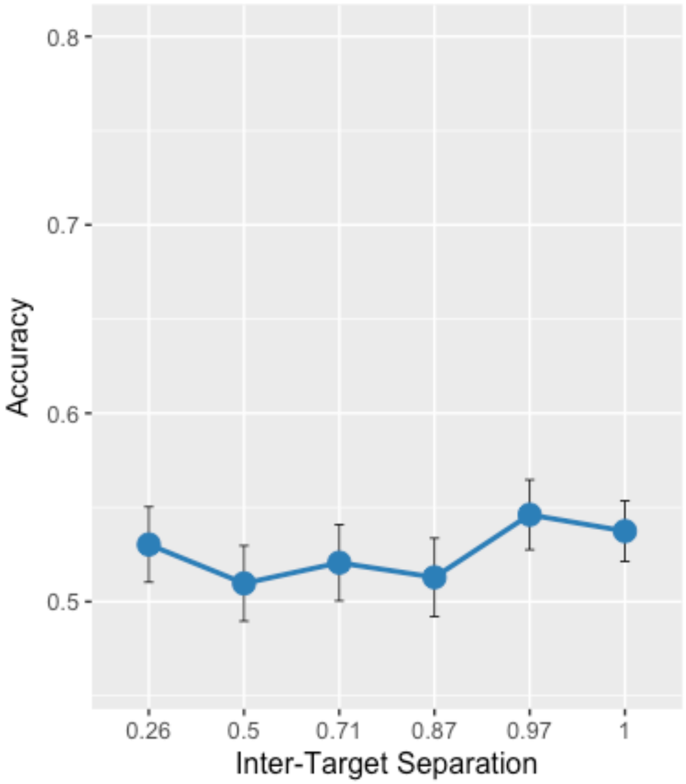

Figure 10. Accuracy as a function of inter-target separation in 8- to 9-year-olds. The error bars indicate standard errors.

2.6.3 Discussion

The 8- to 9-year-olds' accuracy was lower than all of the older age groups. Their performance across all the inter-target separation was essentially at floor (near chance - 50%). Accuracy in the 8- to 9-year-olds did not increase as a function of inter-target separation. Much like in the 10- to 11-year-olds, it is also possible that top-down attentional processes need more time to complete and modulate visual processing in the 8- to 9-year-olds. This possibility will be examined in Experiment 3.

3. Experiment 2: Control Experiment

It was possible that the effect of inter-target separation on accuracy found in Experiment 1 was unrelated to spatial attention modulation and instead simply due to the stimuli characteristics. Experiment 2 was therefore included to assess whether the spatial cue in Experiment 1 did in fact direct attention to the location of Target 1. This experiment served as a control experiment to verify whether the results of Experiment 1 actually provided a measurement of the attentional field and its limits or whether performance differences across inter-target separation was unrelated to attentional biasing. Participants performed the same task as in Experiment 1 with the exception that the spatial cue appeared at the center of the screen rather than at the Target 1 location and thus did not spatially cue attention. Similar to Experiment 1, all age groups were examined individually in six sub-experiments. The results of a mixed-effects ANOVA, with the data combined across age group, can be found in Appendix A.

3.1 Experiment 2A: Adults (18+ years)

3.1.1 Methods

Participants

Nineteen Undergraduate Research Participant Pool students were recruited to participate in the study. Young adult participants were also recruited from and tested at the Ontario Science Center. The lab set up was replicated at the Ontario Science Centre. The mean age of the participants was 23.31 years (age range = 18.01 to 23.31 years; 10 = female, 9 = male). All participants reported their vision as normal and had no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1A, with the exception of the cue being presented at the center of the screen.

3.1.2 Results

The young adults' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 11 depicts the adults' accuracy as a function of inter-target separation. Accuracy did not change across inter-target separation. The young adults' mean accuracy across inter-target separation can be found in Table 7.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,90) = 2.01$, $p > .05$. A linear regression analysis of the dependence of accuracy on inter-target separation was also performed to examine whether there was a linear relationship between accuracy and inter-target separation. The linear regression model was not significant $F(5,108) = 1.07$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected.

Table 7. Accuracy across inter-target separation for young adults age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.62	0.08
0.50	0.60	0.13
0.71	0.64	0.12

0.87	0.65	0.10
0.97	0.68	0.14
1.00	0.66	0.15

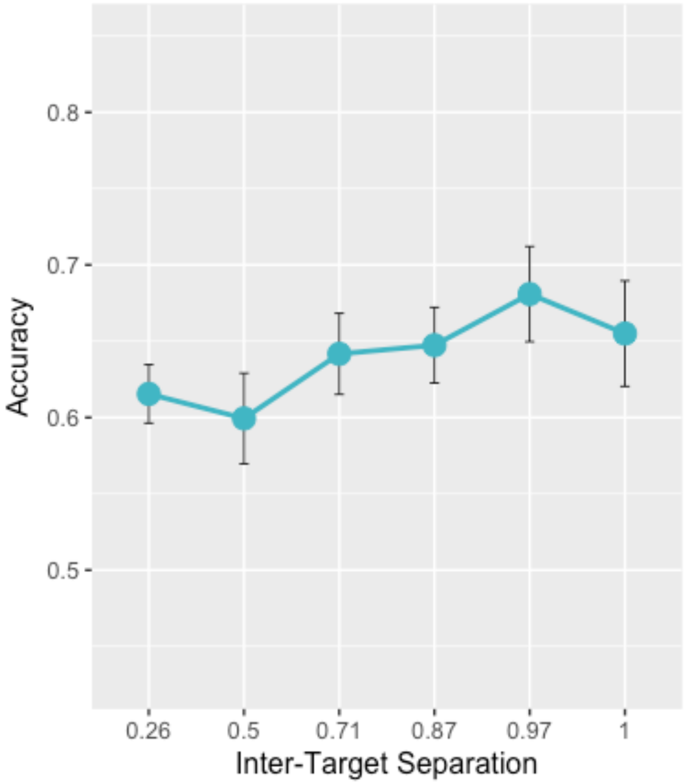

Figure 11. Accuracy as a function of inter-target separation in young adults. The error bars indicate standard errors.

3.1.3 Discussion

The young adults’ accuracy did not significantly differ across inter-target separation. Accuracy remained at around 64% (range = 60% to 68%) for all separations. This indicates that under similar methodological circumstances as in Experiment 1, with the exception of no spatial attentional cue, the effect of inter-target separation disappears. Accuracy increasing as a function of inter-target separation in Experiment 1 was therefore likely a result of attention-modulated surround suppression. More specifically, the results of Experiment 1 can be interpreted in the following manner. When the spatial cue focuses attention to one of the targets, enhanced processing of the cued target is accompanied by a suppressive surround. Therefore, when the second target is presented close to the attended target, as in case of inter-target separation 0.26, the second target falls in the suppressive surround, and as a result it becomes difficult to visually discriminate it. Since the cue is presented centrally in the current experiment, the targets are therefore equally slightly suppressed (since ring of suppression is around the center of the screen) and suppression is not varied across inter-target separation.

3.2 Experiment 2B: Older Adolescents (16-17 years)

3.2.1 Methods

Participants

Twenty-four 16- to 17-year-olds were recruited from the community or at the Ontario Science Centre to participate in the study. The mean age of the participants was 16.95 years (age range = 16.17 to 17.96 years; 11 = female, 13 = male). All participants reported their vision as normal and had no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1B, with the exception of the cue being presented at the center of the screen.

3.2.2 Results

The 16- to 17-year-olds' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 12 depicts the 16- to 17-year-olds' accuracy as a function of inter-target separation. Accuracy did not change across inter-target separation. The 16- to 17-year-olds' mean accuracy across inter-target separation can be found in Table 8.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,115) = 1.93$, $p > .05$. A linear regression analysis of the dependence of accuracy on inter-target separation was also performed to examine whether there was a linear relationship between accuracy and inter-target separation. The linear regression model was not significant $F(5,138) = 1.51$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected.

Table 8. Accuracy across inter-target separation for 16-17 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.56	0.11
0.50	0.56	0.12
0.71	0.56	0.08
0.87	0.59	0.11
0.97	0.61	0.11
1.00	0.62	0.12

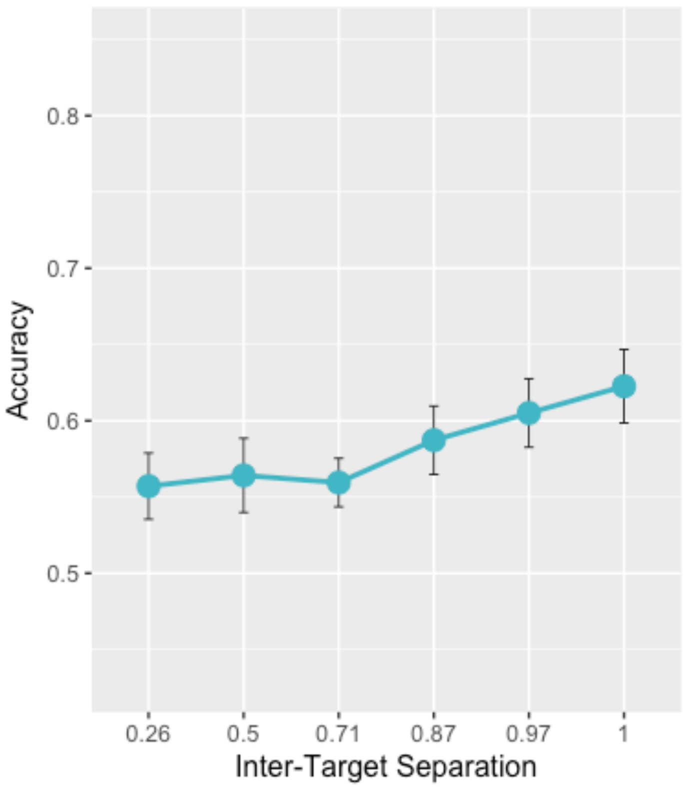

Figure 12. Accuracy as a function of inter-target separation in 16- to 17-year-olds. The error bars indicate standard errors.

3.2.3 Discussion

The 16- to 17-year-olds' accuracy did not significantly differ across inter-target separation. Accuracy remained at around 58% (range = 56% to 62%) for all separations. Similar to the young adult findings in Experiment 2A, the current findings suggest that performance in 16- to 17-year-olds' for Experiment 1 was a result of attention-modulated surround suppression. In Experiment 2, since the cue is presented centrally, the targets are therefore equally slightly suppressed (since ring of suppression is around the center of the screen) and suppression is not varied across inter-target separation, as evidenced by the separation not affecting accuracy.

3.3 Experiment 2C: Younger Adolescents (14-15 years)

3.3.1 Methods

Participants

Twenty-eight 14- to 15-year-olds were recruited from the community or at the Ontario Science Centre to participate in the study. The mean age of the participants was 14.68 years (age range = 14.05 to 15.93 years; 16 = female, 12 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1C, with the exception of the cue being presented at the center of the screen.

3.3.2 Results

The 14- to 15-year-olds' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 13 depicts the accuracy as a function of inter-target separation in the 14 to 15 years age group. Accuracy was lower at the smallest inter-target separation of 0.26 in comparison to the other separations, but accuracy did not increase as a function of inter-target separation. The 14- to 15-year-olds' mean accuracy across inter-target separation can be found in Table 9.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The mixed effects model accounted for 29% of the variance in the participants' accuracy (pseudo-$R^2 = 0.290$). The main effect of inter-target separation on accuracy was significant, $F(5,135) = 2.84$, $p < .05$. Bonferonni corrected post-hoc tests revealed that the main effect was only driven by the significantly lower accuracy at 0.26 (M= .51, SD = .07) in comparison to 1.00 (M = .59, SD = .11). No other inter-target separation accuracy comparison was significant.

A linear regression analysis of the dependence of accuracy on inter-target separation was also performed to examine whether there was a linear relationship between accuracy and inter-target separation. The linear regression model was not significant $F(5,162) = 2.15$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected.

Table 9. Accuracy across inter-target separation for 14-15 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.51	0.07
0.50	0.57	0.10
0.71	0.55	0.13
0.87	0.56	0.13
0.97	0.55	0.09
1.00	0.59	0.11

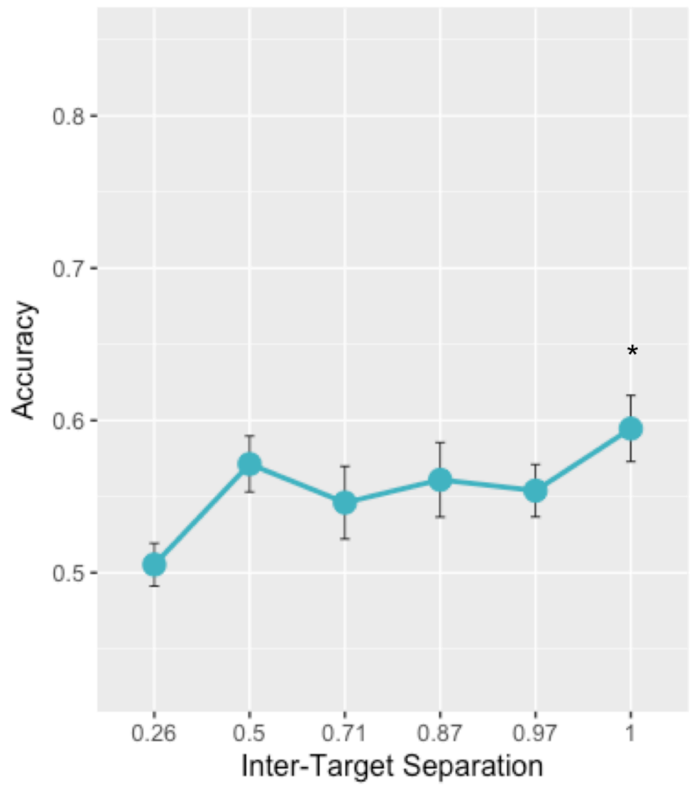

Figure 13. Accuracy as a function of inter-target separation in 14- to 15-year-olds. * = Accuracy significantly greater than at inter-target separation 0.26. The error bars indicate standard errors.

3.3.3 Discussion

Unlike the young adults and the 16- to 17-year-olds, the 14- to 15-year-olds performed significantly less accurately at the smaller inter-target separation of 0.26, in comparison to the largest separation of 1.00. However, no other inter-target separation comparison was significantly different from one another. For the separations of 0.50, 0.71, 0.87 and 0.97, accuracy was at around 56% (range = 51% to 59%). Unlike in Experiment 1, accuracy in the 14- to 15-year-olds in Experiment 2 did not significantly increase across inter-target separation. Therefore, the current findings thus suggest that performance in

14- to 15-year-olds' for Experiment 1 was likely a result of attention-modulated surround suppression.

3.4 Experiment 2D: Pre-Adolescents (12-13 years)

3.4.1 Methods

Participants

Thirty-one 12- to 13-year-olds were recruited at the Ontario Science Centre to participate in the study. The mean age of the participants was 12.85 years (age range = 12.01 to 13.95 years; 16 = female, 14 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1D, with the exception of the cue being presented at the center of the screen.

3.4.2 Results

The 12- to 13-year-olds' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 14 depicts the accuracy as a function of inter-target separation in the 12 to 13 years age group. Accuracy did not increase as a function of inter-target separation. The 12- to 13-year-olds' mean accuracy across inter-target separation can be found in Table 10.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,150) = 1.61$, $p > .05$.

A linear regression analysis of the dependence of accuracy on inter-target separation was also performed to examine whether there was a linear relationship between accuracy and inter-target separation. The linear regression model was not significant $F(5,180) = 1.39$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected.

Table 10. Accuracy across inter-target separation for 12-13 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.55	0.09
0.50	0.59	0.09
0.71	0.56	0.09
0.87	0.57	0.10
0.97	0.59	0.13
1.00	0.61	0.10

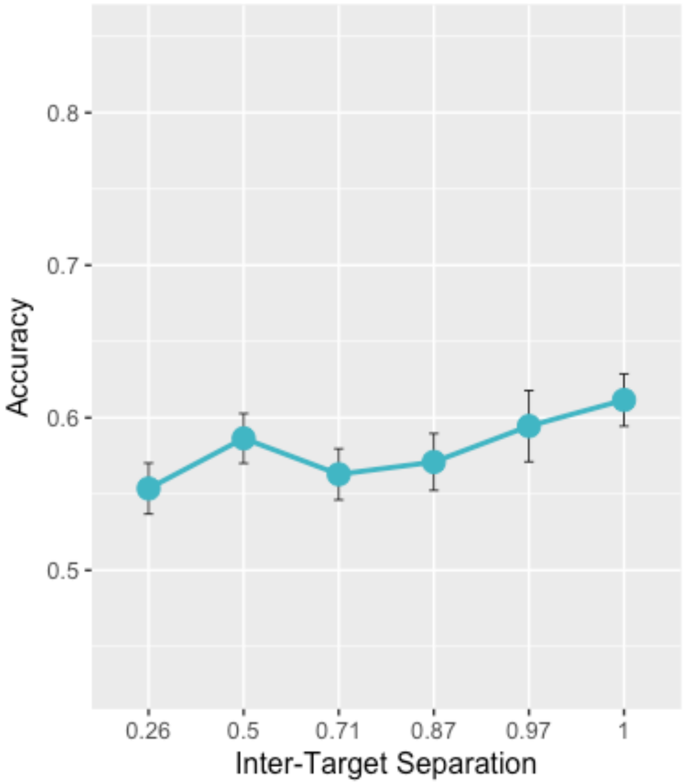

Figure 14. Accuracy as a function of inter-target separation in 12- to 13-year-olds. The error bars indicate standard errors.

3.4.3 Discussion

Similar to the young adults and the 16- to 17-year-olds, accuracy in the 12- to 13-year-olds did not significantly differ across inter-target separation. Accuracy remained at around 58% (range = 55% to 61%) for all separations. The current findings thus also suggest that performance in 12- to 13-year-olds' for Experiment 1 was a result of attention-modulated surround suppression.

3.5 Experiment 2E: Older School-Aged Children (10-11 years)

3.5.1 Methods

Participants

Thirty-seven 10- to 11-year-olds were recruited at the Ontario Science Centre to participate in the study. The mean age of the participants was 10.61 years (age range = 10.11 to 11.87 years; 16 = female, 21 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1E, with the exception of the cue being presented at the center of the screen.

3.5.2 Result

The 10- to 11-year-olds' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 15 depicts the accuracy as a function of inter-target separation in the 10 to 11 years age group. Accuracy did not increase as a function of inter-target separation, and performance was also at floor (at chance – 50%). The 10- to 11-year-olds' mean accuracy across inter-target separation can be found in Table 11.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,180) = 0.54$, $p > .05$. The linear regression model was not significant

F(5,216) = 0.51, *p* > .05, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected.

Table 11. Accuracy across inter-target separation for 10-11 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.53	0.13
0.50	0.52	0.11
0.71	0.55	0.11
0.87	0.53	0.13
0.97	0.55	0.13
1.00	0.52	0.11

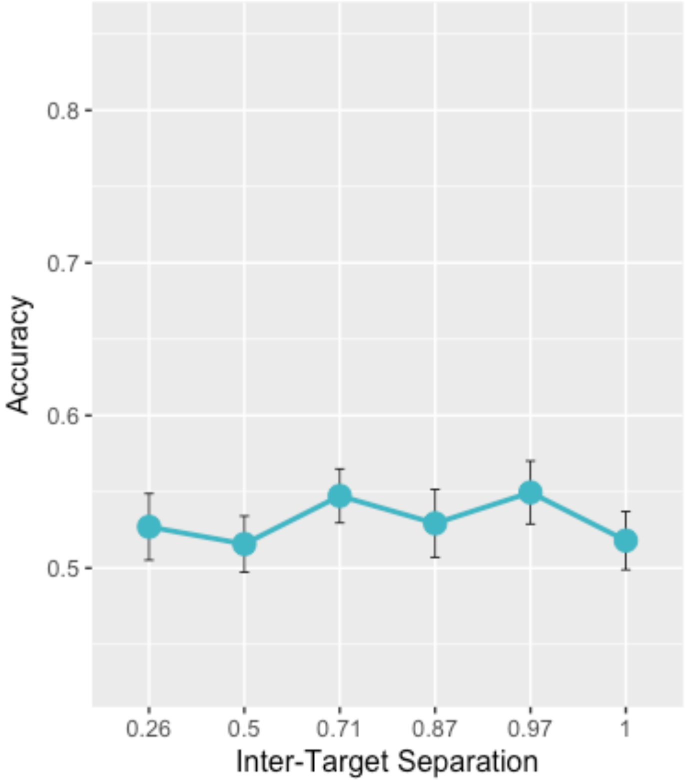

Figure 15. Accuracy as a function of inter-target separation in 10- to 11-year-olds. The error bars indicate standard errors.

3.5.3 Discussion

Similar to the young adults, 16- to 17-year-olds and 12- to 13-year-olds, accuracy in the 10- to 11-year-olds did not significantly differ across inter-target separation. Accuracy remained at around 53% (range = 52% to 55%) for all separation.

3.6 Experiment 2F: Younger School-Aged Children (8-9 years)

3.6.1 Methods

Participants

Twenty-five 8- to 9-year-olds were recruited from the community or at the Ontario Science Centre to participate in the study. The mean age of the participants was 8.73 years (age range = 8.12 to 9.99 years; 12 = female, 13 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1F, with the exception of the cue being presented at the center of the screen.

3.6.2 Results

The 8- to 9-year-olds' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 16 depicts the accuracy as a function of inter-target separation in the 8 to 9 years age group. Accuracy did not increase as a function of inter-target separation, and performance was also at floor (at chance – 50%). The 8- to 9-year-olds' mean accuracy across inter-target separation can be found in Table 12.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,120) = 1.10$, $p > .05$. A linear regression analysis of the dependence of accuracy on inter-target separation was also performed to examine whether there was a linear relationship between accuracy and inter-target separation. The linear regression model was not significant $F(5,144) = 0.99$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected.

Table 12. Accuracy across inter-target separation for 8-9 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.54	0.10
0.50	0.54	0.11
0.71	0.52	0.08
0.87	0.51	0.10
0.97	0.50	0.09
1.00	0.55	0.09

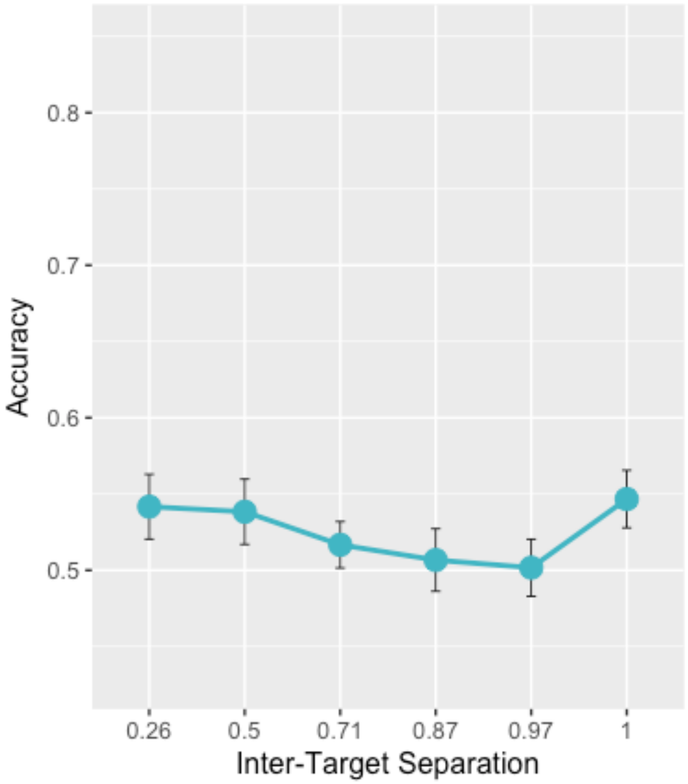

Figure 16. Accuracy as a function of inter-target separation in 8- to 9-year-olds. The error bars indicate standard errors.

3.6.3 Discussion

The 8- to 9-year-olds' accuracy did not significantly differ across inter-target separation. Accuracy remained at around 53% (range = 50% to 55%) for all separation. In comparison to the older groups, accuracy in the 8- to 9- year-olds was lower, especially at 0.71, 0.87 and 0.97 where they performed essentially at floor (50-51%).

4. Experiment 3: A Modified Task for The Younger Age Groups

One possible reason why the younger age groups performed poorly in Experiment 1 and did not exhibit surround suppression is that their visual system needs more time to process the spatial cue and subsequently more time to complete their feedback processes.

As a consequence, the younger age groups may not have exhibited the suppressive center-surround effect in Experiment 1 because their system was not given enough time to effectively tune their visual system. Experiment 3 therefore featured a longer cue presentation time in order to make the task more feasible by providing additional time for the feedback processes to reach an effective threshold for the younger age groups.

The same stimuli of Experiment 1 were used in this experiment, but the temporal parameters were modified. The spatial cue duration was increased from 100 msec to 200 msec, while the visual array duration remained at 175 msec. If younger age groups did in fact need more time for their feedback mechanisms to effectively modulate visual processing, a longer cue duration would allow them to not only complete the task more readily but perhaps also provide their attention processes more time to tune their visual system.

Both age groups were examined individually in two sub-experiments. The results of a mixed-effects ANOVA, with the data combined across age group, can be found in Appendix A.

4.1 Experiment 3A: Older-School Aged Children

4.1.1 Methods

Participants

Thirty 10- to 11-year-olds were recruited from the community or at the Ontario Science Centre to participate in the study. The mean age of the participants was 11.12 years (age range = 10.08 to 11.97 years; 15 = female, 16 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 1E, with the exception that the cue duration was increased from 100 msec to 200 msec.

4.1.2 Results

The 10- to 11-year-olds' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 17 depicts the accuracy as a function of inter-target separation in the 10 to 11 years age group. Accuracy did not increase as a function of inter-target separation. The 10- to 11-year-olds' mean accuracy across inter-target separation can be found in Table 13.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,145) = 0.19$, $p > .05$. A linear regression analysis of the dependence of accuracy on inter-target separation was also performed to examine whether there was a linear relationship between accuracy and inter-target separation. The linear regression model was not significant $F(5,174) = 0.13$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected.

Table 13. Accuracy across inter-target separation for 10-11 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.57	0.11
0.50	0.56	0.11
0.71	0.57	0.10

0.87	0.56	0.09
0.97	0.56	0.14
1.00	0.55	0.12

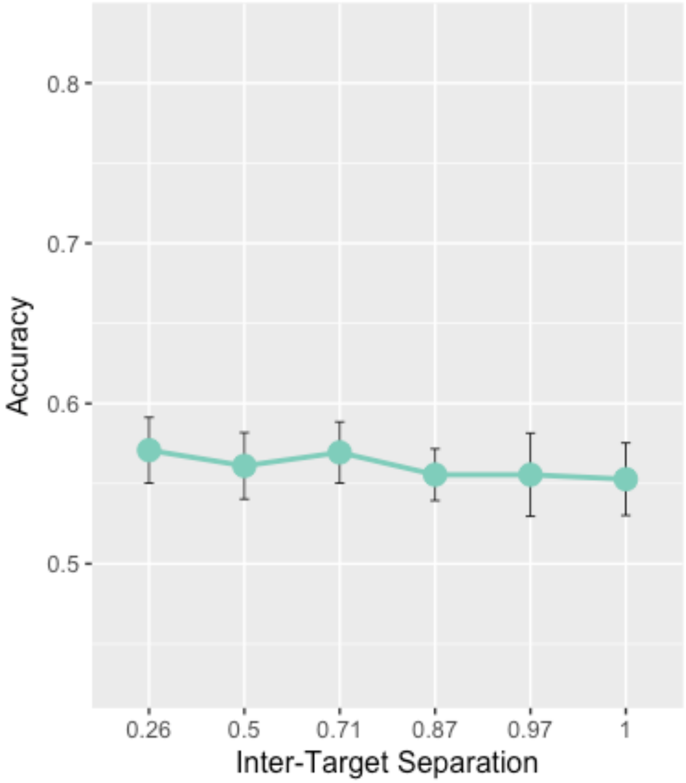

Figure 17. Accuracy as a function of inter-target separation in 10- to 11-year-olds. The error bars indicate standard errors.

4.1.3 Discussion

Similar to Experiment 1, the 10- to 11-year-olds in this experiment did not exhibit attention-modulated surround suppression. Their accuracy did not differ across inter-target separation. This suggests that increasing the cue duration with the goal of providing 10- to 11-year-olds with additional time to for their feedback processes to effectively modulate visual processing does not lead to the exhibition of a suppressive surround.

4.2 Experiment 3B: Younger School-Aged Children (8-9 years)

4.2.1 Methods

Participants

Twenty-seven 8- to 9-year-olds were recruited from the community or tested at the Ontario Science Centre to participate in the study. The mean age of the participants was 8.72 years (age range = 8.03 to 9.89 years; 18 = female, 9 = male). All participants were reported to have normal vision and no history of psychiatric or neurological disorders.

Procedure

The procedure was identical as in Experiment 3A.

4.2.2 Results

The 8- to 9-year-olds' target discrimination accuracy, defined as the proportion of correct responses, was computed for all 6 inter-target separation values. Figure 18 depicts the accuracy as a function of inter-target separation in the 8 to 9 years age group. Accuracy did not increase as a function of inter-target separation and they again performed close to floor (at chance – 50%). The 8- to 9-year-olds' mean accuracy across inter-target separation can be found in Table 14.

A repeated-measure analysis of variance (ANOVA) was conducted using the linear mixed-effects function in R. Inter-target separation was set as a fixed variable and subject as a random variable. The main effect of inter-target separation on accuracy was not significant, $F(5,130) = 1.20, p > .05$. A linear regression analysis of the dependence of accuracy on inter-target separation was also performed to examine whether there was a linear relationship between accuracy and inter-target separation. The linear regression model was not significant $F(5,156) = 1.13$, $p > .05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected.

Table 14. Accuracy across inter-target separation for 8-9 years age group.

Inter-Target Separation	Mean Accuracy	Standard Deviation
0.26	0.52	0.10
0.50	0.49	0.11
0.71	0.50	0.10
0.87	0.55	0.10
0.97	0.52	0.10
1.00	0.53	0.11

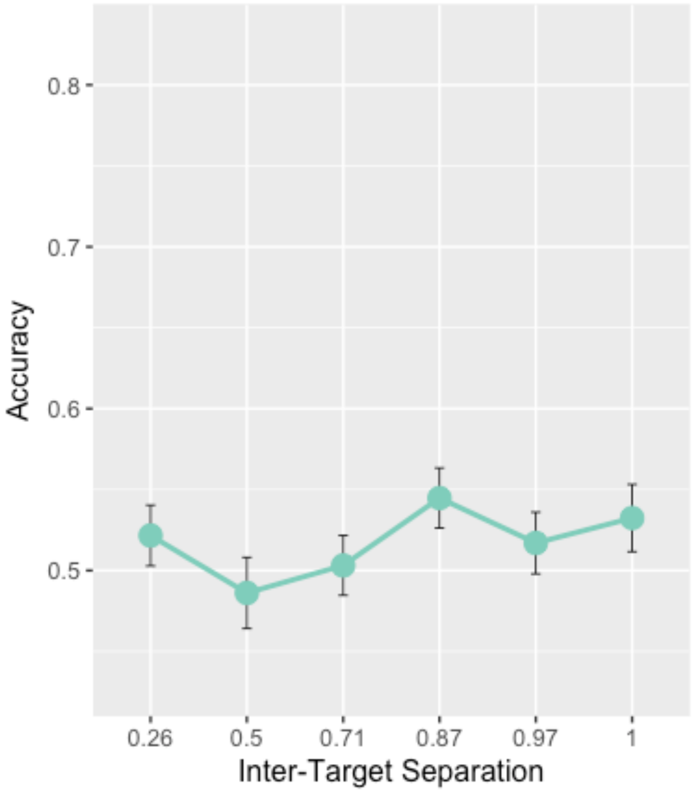

Figure 18. Accuracy as a function of inter-target separation in 8- to 9-year-olds. The error bars indicate standard errors.

4.2.3 Discussion

When additional time was provided to allow feedback processes to effectively modulate visual processing, accuracy in the 8- to 9-year-olds did not increase in comparison to the accuracy of the same age group in Experiment 1. Accuracy in the 8- to 9-year-olds across all the inter-target separations remained at floor (near chance - 50%) and did not increase as a function of inter-target separation. This suggests that providing 8- to 9-year-olds additional time to for their feedback processes to effectively tune visual processing does not lead to the exhibition of a suppressive surround.

5. General Discussion

5.1 Summary of the Experimental findings

In adulthood, previous research has well established that attentional feedback processes impact visual processing by modulating activity in the visual cortex (Hopf et al., 2012). Top-down attentional selection prunes and suppresses forward-projecting units or neurons not representing relevant input, which as a consequence gives rise to attention-modulated surround suppression (Tsotsos, 2005). Whether children and adolescents also exhibit attention-modulated surround suppression had never previously been examined. Therefore, the primary goal of the current study was to examine whether attention-modulated surround suppression is observed in younger age groups. Previous research has widely suggested that top-down control of attention improves during childhood but that bottom-up attention is relatively mature early in development (Amso & Scerif, 2015). However, these previous studies have not provided information about whether developing attentional mechanisms influence visual processing as observed in adults. Additionally, previous studies have also not produced a complete theory of attentional development (Ristic & Enns, 2015) and have not directly examined the effect of attentional mechanisms on the processing of visual information across development. In an attempt to tackle these limitations, the current study examined a large age range incrementally so that finer grain differences can potentially be uncovered and provide more detailed information about the development of attentional mechanisms. A task that can directly manipulate the effect of attention on visual processing was also used to truly examine whether attention affects visual processing similarly across development.

Experiment 1 was designed to assess whether a ring of suppression surrounding an attended item was observed in younger age groups. Experiment 1 replicated the first experiment of Cutzu and Tsotsos' (2003) adult psychophysical study with young adults and was then subsequently with younger participants aged between 8 and 17 years. Participants were required to detect two red letter character targets from black letter distractors and report whether the targets were identical (L-L and T-T) or different (L-T or T-L). Participants' spatial attention was cued to one of the two letter targets. Visual discrimination was expected to improve as a function of inter-target separation, as a consequence of a lessening of attention-modulated surround suppression with more distance from the attended location. More specifically, the spatial cue focusing attention to one of the targets was expected to not only enhance the processing of the cued target but also suppress surrounding stimuli. Therefore, when the second target is presented close to the attended target, as in the case of inter-target separation 0.26, the second target falls in the suppressive surround, and as a result it is expected that this second target would become difficult to visually process.

Findings of the current study demonstrated that spatial attention similarly influences visual processing in late development. The results of Experiment 1 showed that attention-modulated surround suppression was observed only in participants aged between 12 years and above. In the 12 to 26-year-olds of the current study, visual discrimination accuracy increased as a function of inter-target separation. As predicted, participants aged between 8 and 11 years did not exhibit attention-modulated surround suppression, as demonstrated by their accuracy not being affected by inter-target separation. Figure 19 depicts visual discrimination accuracy across inter-target separation for all of the age groups included in the Experiment 1.

Unlike in young adults where accuracy gradually increased as a function of inter-target separation, accuracy in the younger participants aged between 12 and 17 years did not increase until the largest separations of 0.97 and 1.00. The 12- to 17-year-olds performed relatively low for all separations smaller than 0.87 (from 0.26 to 0.71). This finding is surprising given that it suggests that the suppressive surround may encompass a larger area in 12- to 17-year-olds. A larger suppressive surround means that suppression would span over a larger distance from the attended target. As a consequence, the second target would need to be presented further away from the attended target to fall outside of the suppressive surround. A larger inhibitory surround therefore readily accounts for why accuracy in these younger participants did not increase until the larger inter-target separations. Figure 20 illustrates the hypothetical size difference in the inhibitory or suppressive surround across 12- to 27-year-olds.

Overall, the results of Experiment 1 provide further evidence that top-down feedback processes modulate visual processing in young adults. The findings of Experiment 1 also demonstrate that there is suppression or attenuation surrounding an attended item or spatial location, as predicted by the ST model of attention (Tsotsos, 1995). According to the ST model (Tsotsos, 1995), the role of attention is to locate and maximize the processing of a target stimulus in such a way that any interfering signals are minimized. The visual processing architecture is conceptualized to be pyramidal in which units within the network receive both feedforward and feedback connections. A given stimulus, for instance the spatial cue in Experiment 1, activates in a feedforward manner all of the units or neurons within the pyramid to which it is connected within the visual field. Selective attention is viewed as a process of winner-take-all (WTA), whereby a global winner is computed across the entire visual field and all of the connections of the visual pyramid that do not contribute to the winner are pruned (Figure 21). As a result, the selected stimulus in the input layer, for instance the spatial location of the cued target of Experiment 1, re-propagates through the network and is processed by the neurons without surrounding distracting stimuli. The eliminated or pruned projections of the neurons not representing the selected target stimulus form the suppressive surround.

In addition to providing further evidence of the existence of an attentional suppressive surround, the results of Experiment 1 uniquely demonstrate that attentional mechanisms also affect visual processing in pre-adolescents and adolescents, and that a larger window of attentional suppression is observed at these younger ages. Given that the younger age groups did not exhibit attention-modulated surround suppression, similar to previous studies on attentional development, the results of Experiment 1 also point to a protracted maturation of top-down attentional mechanisms in childhood.

In an effort to validate whether the findings of the Experiment 1 were indeed a manifestation of attention-modulated surround suppression as opposed to an effect simply arising from the stimuli characteristics, Experiment 2 was conducted. The cue was instead presented centrally in Experiment 2 and therefore no longer spatially cued attention to one of the target letters. If the findings of Experiment 1 were indeed related to spatial attention, inter-target separation would not be expected to affect visual discrimination accuracy in Experiment 2. Indeed, in most age groups, inter-target separation in Experiment 2 did not affect accuracy as it did in Experiment 1. Figure 22 depicts visual discrimination accuracy across inter-target separation for all of the age groups in Experiment 2. The lack of an inter-target separation effect on accuracy can be explained by the fact that a centrally presented cue leads to the suppressive surround manifesting around the center of the screen. Therefore, the targets and the distractors would be equally partially suppressed, and suppression would thus not vary across inter-target separation.

In the 14 to 15 years age group, accuracy at the smallest inter-target separation of 0.26 was significantly lower than accuracy at the largest separation of 1.00. Nonetheless, increases in accuracy across inter-target separation observed in the 14- to 15-year-olds in Experiment 1 were not observed in those of Experiment 2. This indicates that much like all the other age groups, a central cue did not have the same effect on visual processing and discrimination accuracy as the spatial cue did. The 8- to 11-year-olds in both experiments performed similarly. However, given that in Experiment 1 there was no effect of the spatial cue and inter-target separation on accuracy in the 8- to 11-year-olds, a lack of difference in performance in this age group across Experiment 1 and Experiment 2 has no impact on the result interpretations for the older age groups.

Given that in Experiment 1 the 8- to 11-year-olds performed poorly, in addition to not exhibiting attention-modulated surround suppression, the question could be asked whether they were even capable of completing the task under the original parameters. As a consequence, the possibility did exist that a modified task featuring parameters that are more age-appropriate would allow these younger participants to successfully complete the task and show improvements in their performance. Perhaps, for example, the younger age groups, due to slower neural processing systems, need more time to complete feedback processing. Therefore, a longer cue duration was hypothesized to potentially allow them to not only complete the task more readily but perhaps also provide their attention processes more time to tune their visual system. Experiment 3 was included in the current study to examine this possibility. The duration of cue presentation was increased from 100 msec to 200 msec.

Although overall accuracy increased in the 10 -to 11 year-olds with the longer cue duration, neither age group (10 to 11 years and 8 to 9 years) exhibited attention-modulated surround suppression. Accuracy remained the same at all inter-target separations, suggesting that the lack of attentional surround suppression in the 8- to 11-year-olds is not due to slower top-down feedback processes. Figure 23 depicts accuracy across inter-target separation for both of the age groups in Experiment 3.

Perhaps a greater increase in the cue presentation time is necessary for the 8- to 11-year-olds? This possibility, however, is very unlikely since cue durations of 100 msec have successfully been used with participants as young as 4-month-olds to spatially cue and speed their attentional orienting to a target (e.g., Johnson & Tucker, 1996). Therefore, it seems unreasonable that a cue duration of 100 or 200 msec would be too fast to spatially cue attention in 8- to 11-year-olds. Admittedly, however, the task used in the current study was much more perceptually challenging than the attentional orienting tasks used with infants. Consequently, perhaps the younger participants in the current study still needed more support. Other than increasing the cue duration, another manner in which the task could have been made more feasible for the 8- to 11-year-olds, is by increasing the visual array duration. This possibility will be further discussed in the limitations and future directions section.

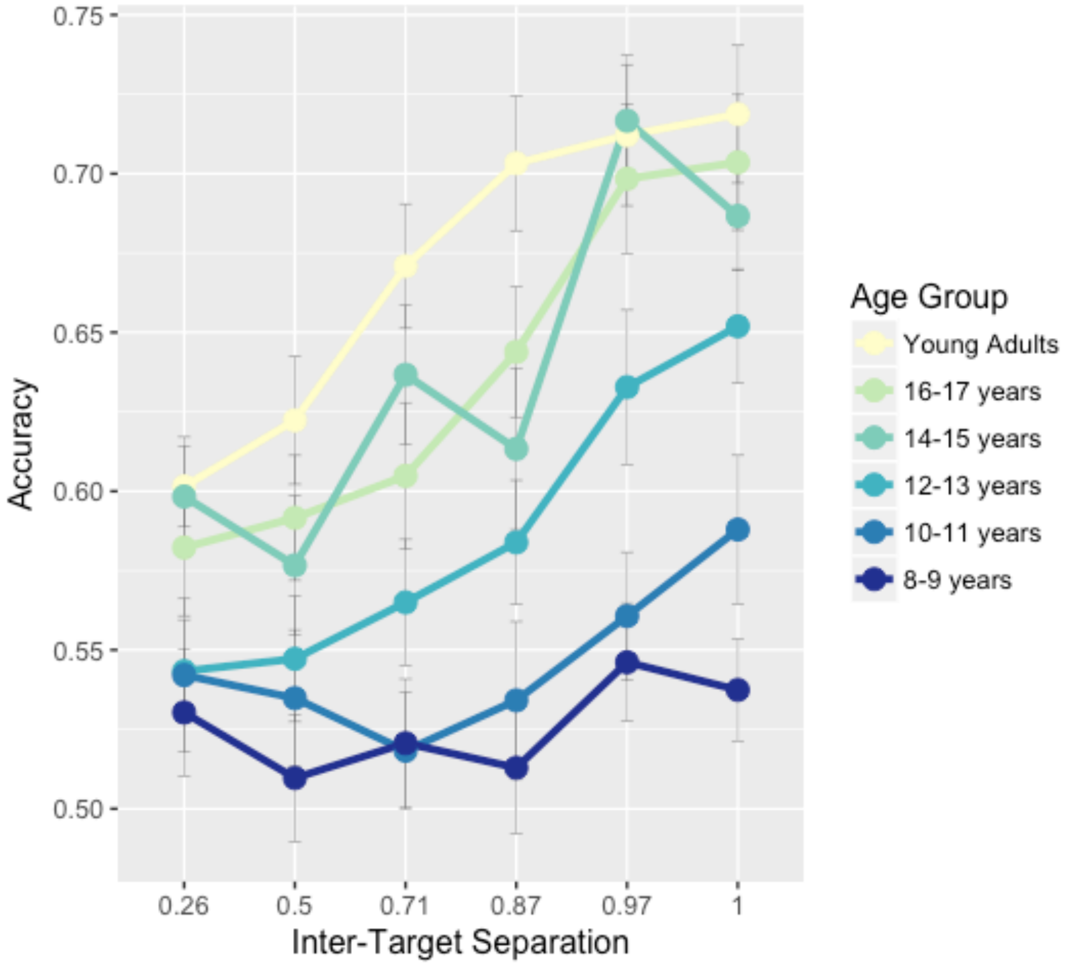

Figure 19. Visual Discrimination Accuracy of All Ages in Experiment 1. Visual discrimination accuracies for each inter-target separations are depicted by age group. Visual discrimination accuracy significantly increased as a function of inter-target separation in the 12 to 17 year-olds and the young adults. However, in the 12- to 17-year-olds accuracy improvements were mainly observed when the targets are largely separated

such as for the inter-target separations of 0.97 and 1.00. Inter-target separation did not affect accuracy in the 8- to 11-year-olds. The error bars indicate standard errors.

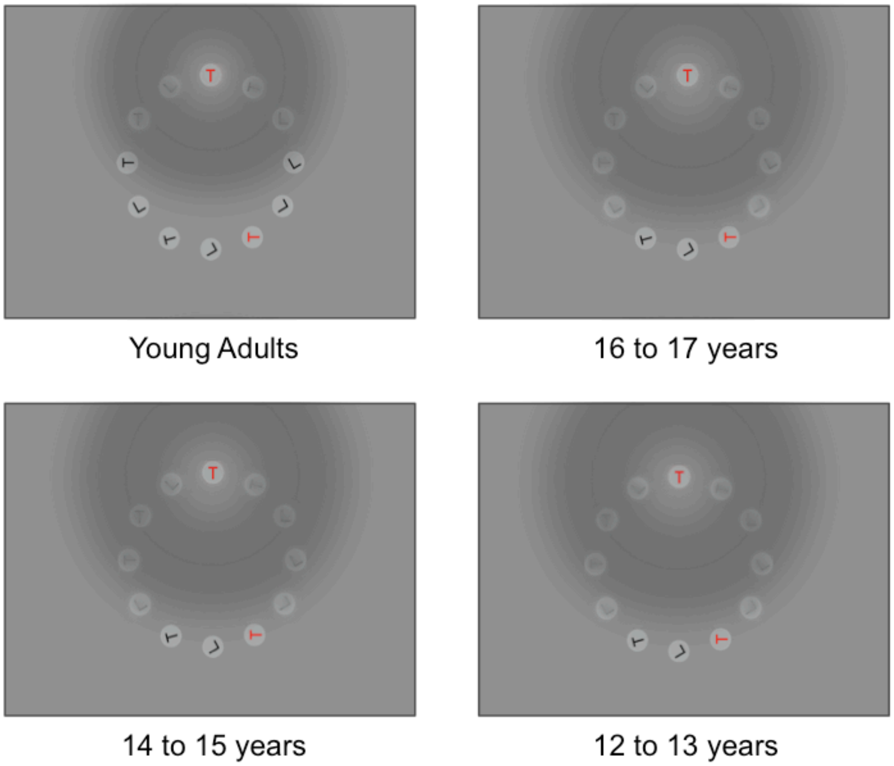

Figure 20. Attention-Modulated Surround Suppression in Young Adults, Adolescents and Pre-Adolescents. The suppressive surround is depicted as a dark gray ring. Letters that fall within the boundaries of the dark gray ring are noisy and difficult to discriminate. This figure is a hypothetical depiction that was conceptualized by examining accuracy across inter-target separation in all age groups. For inter-target separations where accuracy was low (nearly at chance), it was hypothesized that the second target falls in the suppressive surround. For example, in young adults accuracy at both 0.26 and 0.50 was significantly lower than the larger separations. This would suggest that when Target 2 was beside the focus of attention (0.26) or when there was only one distractor between it and Target 1 (0.50), Target 2 was within the boundaries of the suppressive surround

and difficult to process, resulting in lower discrimination accuracy. For pre-adolescents and adolescents whose discrimination accuracy did not significantly increase until the larger inter-target separation of 0.97 and 1.00, it was hypothesized that Target 2 had to be much further from the focus of attention (Target 1), with 4 distracters (0.97) or 5 distractors (1.00) in between it and Target 1, to be outside of the suppressive surround. Surround suppression is therefore depicted as a larger dark ring in the 12- to 17-year-olds. A larger suppressive surround in these younger participants can account for why their accuracy does not significantly increase until the targets are largely separated such as for the inter-target separations of 0.97 and 1.00.

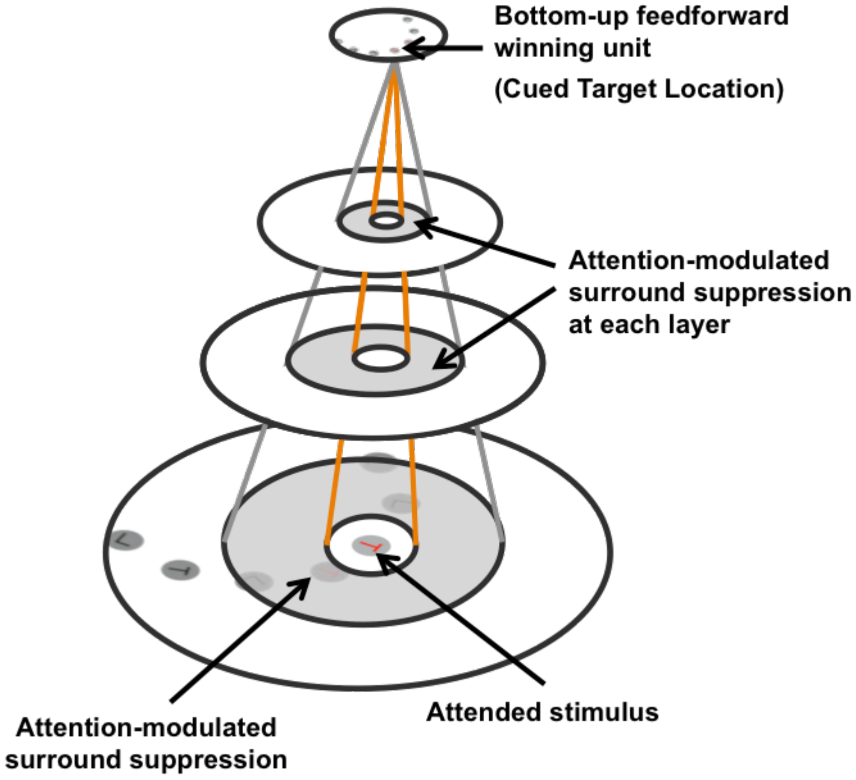

Figure 21. The ST process of selection and suppression for Experiment 1.

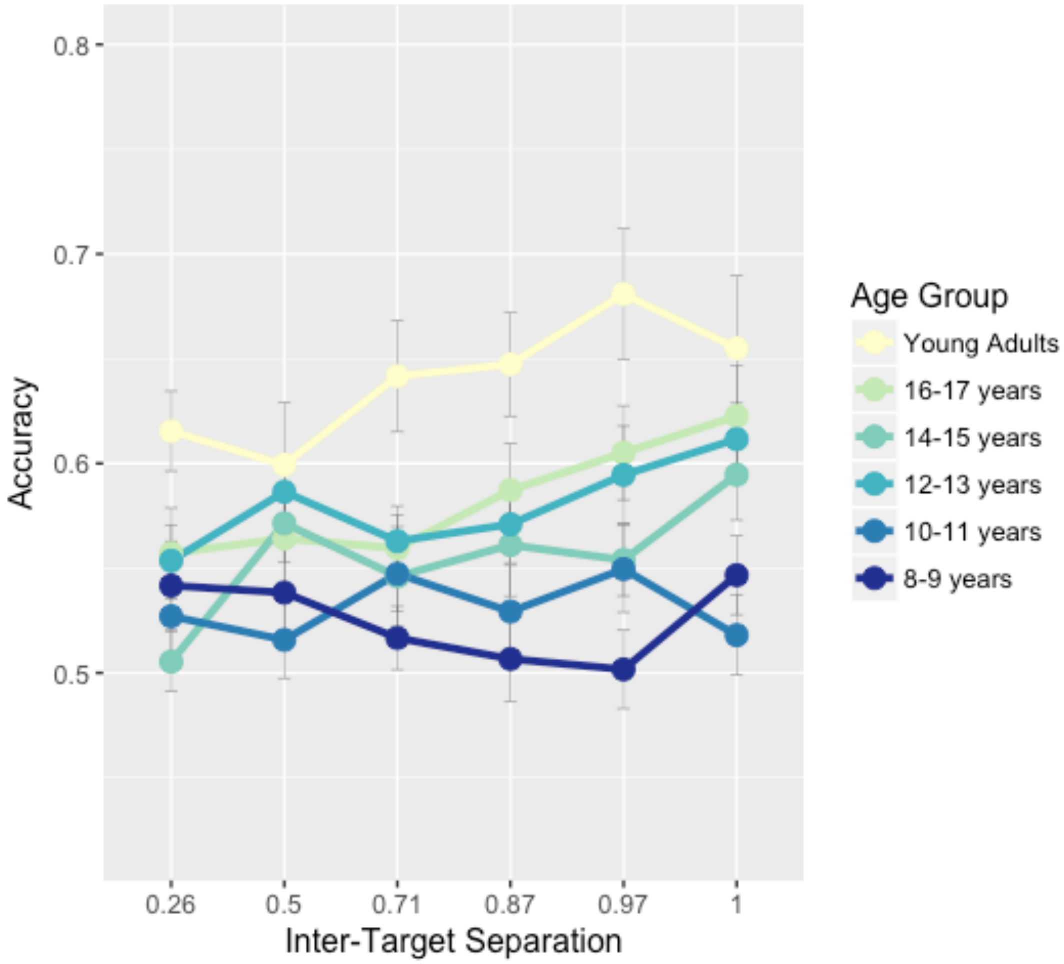

Figure 22. Visual Discrimination Accuracy of All Ages in Experiment 2. Visual discrimination accuracies for each inter-target separations are depicted by age group. Unlike in Experiment 1, visual discrimination accuracy did not increase as a function of inter-target separation. The error bars indicate standard errors.

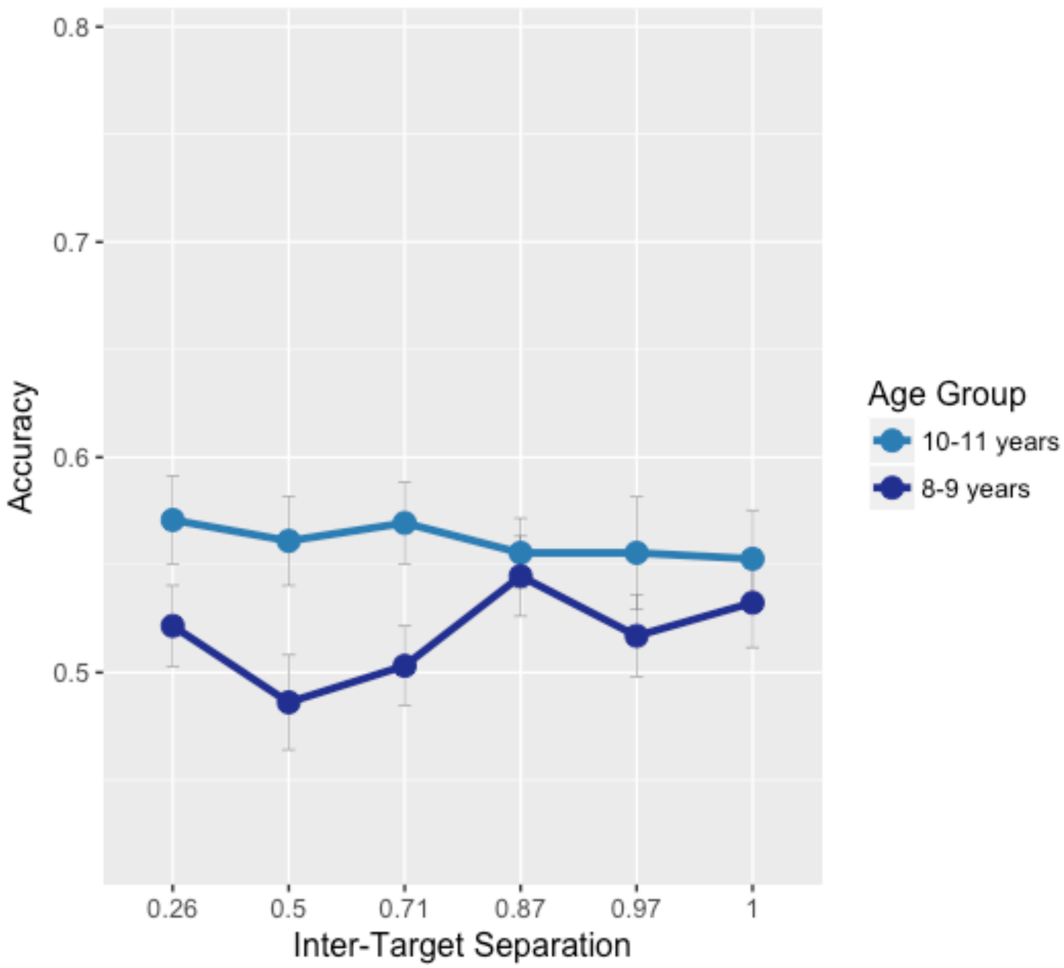

Figure 23. Visual Discrimination Accuracy of the 8- to 11-year-olds in Experiment 3. Visual discrimination accuracies for each inter-target separations are depicted by age group. Visual discrimination accuracy was not affected by inter-target separation. The error bars indicate standard errors.

5.2 Neural Development and Visual Attention

As previously discussed, attention-modulated surround suppression arises as a consequence of top-down attentional selection in the visual processing hierarchy (Hopf et al., 2012). Top-down selection is suggested to mediate from higher cortical areas, pruning or suppressing forward-projecting units or neurons not representing relevant input (Tsotsos, 2005). However, in early development, visual feedforward and low-level orienting mechanisms are thought to be more dominant, while top-down feedback processes continue to be strengthened (Amso & Scerif, 2015). It is therefore not surprising that in the current study surround suppression was only observed in the participants over the age of 12 years.

In adults, long-range functional connectivity between DAN and regions outside the network is believed to enable greater top-down attentional capacities (Rubia, 2013). The lack of surround suppression in the 8- to 11-year-olds is therefore likely a consequence of their immature top-down feedback projections that are not as strongly connected to further cortical regions. Indeed previous research has demonstrated that in children under the age of 12 years, the DAN, a neural network activated when top-down attention is focused, is not as functionally connected to farther regions such as the visual cortex (Farrant & Uddin, 2015).

Studies examining the maturation of structural connectivity, that is the physical connections of long-range connections formed by white matter tracts (Khundrakpam, Lewis, Zhao, Chouinard-Decorte & Evans, 2016), have shown that the maturity of structural connectivity is also protracted, continuing into adulthood. In a longitudinal study, Lebel and Beaulieu (2011) used diffusion tensor imaging (DTI) to examine developmental changes in white matter in healthy participants aged from 5 to 32 years. Continued maturation was observed from childhood to adulthood for all 10 major white matter tracts, but notably, maturation of the inferior and superior longitudinal and frontal-occipital fasciculi continued into the twenties (Lebel & Beaulieu, 2011). In a cross-sectional DTI study, Giorgio and colleagues (2008) similarly demonstrated that the maturation of the superior longitudinal fasciculus continued during young adulthood. The inferior and superior longitudinal fasciculi connect the temporal to the occipital cortex, and, the parietal to the frontal cortex, respectively. The frontal-occipital fasciculus connects the frontal cortex with both the temporal and occipital cortex. These association tracts connecting the frontal areas to other brain regions support complex cognitive function such as inhibition, executive function and importantly, attention (Lebel & Beaulieu, 2011; Moll, Zahn, de Oliveira-Souza, Krueger & Grafman, 2005; Blakemore and Choudhury, 2006; Jung and Haier, 2007). Thus, in the context of the current study, it can be speculated that these DTI findings support the idea that developmental differences in the manifestation of attention-modulated surround suppression are related to reduced connectivity between frontal brain areas and other regions of the brain.

The changes in white matter and connectivity from childhood to adulthood are believed to reflect increases in myelination and the axonal density (Khundrakpam et al., 2016). Cortical myelination occurs initially in the sensory tracts, followed by the motor tracts and finally the association tracts (Huttenlocher, 2009). White matter volume continues to increase with age during childhood and adolescence, and even continuing through adulthood (Lebel & Beaulieu, 2011), and importantly, the rate of volume increase varies by brain regions. For instance, in development, white matter increases in the occipital cortex are about 2.14% per year, whereas increases in the frontal cortex is only about 1.37% per year (Sowell, Peterson, Thompson, Welcome, Henkenius & Toga, 2003). This suggests that while white matter integrity in the sensory regions may be adult-like earlier in development, it takes far longer for white matter to completely mature in the frontal cortex, which in turn would likely affect the efficiency of top-down feedback modulation in development.

Indeed, white matter volume and myelination gain, particularly within frontal regions, has been found to be associated with improvements in cognitive processes (Khundrakpam et al., 2016). For instance, white matter volume in the frontal-striatal circuits is associated with better inhibitory control (Liston, Watts, Tottenham, Davidson, Niogi, Ulug & Casey, 2006). The fronto-striatal circuit is also believed to play a significant role in mediating attention (Wu, Gau, Lo & Tseng, 2012). Myelination facilitates interactions between brain regions, which leads to more efficient recruitment of the target neural population (Knyazeva, Fornari, Meuli & Maeder, 2006). Therefore, reduced myelination in the younger age groups, particularly in the frontal regions, likely leads to less efficient signal propagation from the frontal areas to the visual areas, resulting in less attentional modulation. Reduced attentional modulation would lead to reduced or no attentional surround suppression, which is what was indeed observed in the 10- to 11-year-olds and 8- to 9-year-olds of the current study.

But, for the pre-adolescents and adolescents, why did they exhibit a greater area of attentional-modulated surround suppression?

In adolescence functional activation is more spatially diffuse across frontal and parietal regions, whereas in adults activation is more focal and fine-tuned within the fronto-parietal network (Konrad, Neufang, Thiel, Specht, Hanisch, Fan, Herpertz-Dahlmann & Fink, 2005; Durston, Davidson, Tottenham, Galvan, Spicer, Fossella & Case, 2006). In adulthood, focal instead of diffuse activation is believed to represent reorganization in cortical areas, allowing for more efficient processing (Ungerleider, Doyon & Karni, 2002). In development, a change towards more focal functional activation is believed to be a result of synaptic pruning, which improves signal to noise ratio in the neural system and strengthens relevant connections (Durston, Davindson, Tottenham, Galvan, Spicer, Fossella & Casey, 2006). In the current study, perhaps a greater area of attentional surround suppression was observed in pre-adolescents and adolescents because functional connectivity between their frontal regions and visual cortex is not focal but rather more diffuse. Unlike in adulthood, attentional modulation of visual cortex activity in adolescence would therefore not be as specific and focal, and as a consequence, surround suppression would unnecessarily span over a larger spatial region. The suppression of visual processing surrounding the focus of attention would be expected to be more noisy in adolescence and this is indeed what was found in the 14- to 15-year-olds in the current study.

Protracted white matter maturation, particularly in the frontal regions, likely leads to inefficient signal propagation from the frontal areas to the visual areas in younger age groups. However, if the lack of attention-modulated surround suppression in younger children was simply due inefficient signal propagation, why would providing them with more time to complete their feedback processes, as in Experiment 3, not result in the effect being observed in their age group?

Incomplete myelination and reduced connectivity of the top-down feedback processes likely leads to a reliance on feedforward mechanisms in younger children. This reliance can explain why the 8- to 11-year-olds did not exhibit attention-modulated surround suppression, even when they were provided more time to complete their feedback processes. As the maturation of white matter continues during adolescence and into adulthood, more focal instead of diffuse activation results in more efficient top-down feedback processing (Ungerleider et al., 2002), which allows for the proper use of these top-down mechanisms and thus attentional modulation.

Importantly, the protracted maturation process of white matter, and its potential effects on attentional modulation, can also explain other development findings, lending support to its relevance in attentional development. For instance, children tend to be more susceptible to interference and less able to inhibit responses in comparison to young adults (Bunge et al., 2002). An over-reliance on feedforward bottom-up mechanisms can readily account for this finding. Moreover, as previously discussed there is an over-connectivity within the VAN and less connectivity between the DAN and farther regions such as the visual cortex in children (Farrant & Uddin, 2016). The DAN shows activation when attention is focused, and is believed to be responsible for goal-driven top-down processing (Corbetta & Shulman, 2002), whereas the VAN is generally activated in situations when bottom-up processing is taking place, such as when an unexpected event occurs and breaks an observer's attention from a given task (Corbetta & Shulman, 2002). Over-activity in the VAN would result in an increase of susceptibility of being interrupted by environmental stimuli and a reduced ability in maintaining tasks requiring greater top-down attentional control (Bunge et al., 2002). One possibility as to why a reliance of VAN in children is beneficial or necessary at younger ages is that it allows for the detection of salient stimuli, important for survival (Farrant & Uddin, 2015). As children mature, connectivity between the regions of the DAN and farther regions such as the visual cortex grows stronger. This maturation in turn allows for greater top-down attentional modulation.

5.4 Task Difficulty and Distractor Suppression

For pre-adolescents and adolescents, an additional possible explanation accounting for why they exhibited greater surround suppression involves task difficulty or task demands. In adults, greater suppression of unattended stimuli is typically observed under conditions of high attentional demands[2] (Parks, Beck & Kramer, 2013). Behavioural studies have shown that distractors cause less interference when the attentional demands, or perceptual load, of a task increases (Lavie & Tsal, 1994; Lavie, 1995). Neurophysiological studies have also demonstrated that high perceptual load decreases visual cortical responses to distractor stimuli (e.g., Rauss et al., 2009, 2012; Parks et al., 2011, Parks et al., 2013). For example, Rauss and colleagues (2009) showed that an increase in attentional load reduces activity of spatially surrounding locations in the early visual cortex. In another study by Parks and colleages (2013), the amplitude of the distractor steady-state visual evoked potentials (SSVEPs) was decreased under conditions of high attentional and perceptual load (i.e., when participants had to bind features).

For the pre-adolescents and adolescents, it is certainly conceivable that the current task was more difficult for them than it was for the young adults. As a consequence,

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[2] In Parks et al. (2013) study attention load was considered high when participants had to bind features of colour and orientation, whereas when attention load was low participants simply had to discriminate by colour)

perhaps greater suppression was exerted in the younger age group in order to manage the demands of the task. In fact, findings of a recent developmental electrophysiology study by Sun and colleagues (2018) support this possibility. In their study, children and adolescents between the ages of 9 and 15 years exhibited amplitude differences in target-elicited N2pc (N2-posterior-contralateral) and PD (distractor positivity) components in comparison to adults when completing a visual search additional-singleton paradigm (Sun, Wang, Huang, Zhao, Guo, Li, Sun, Du, Ding & Song, 2018).

The N2pc component is believed to reflect attentional selection, whereas the PD component is believed to reflect active suppression (Sun et al., 2018). More specifically, the N2pc is an enhanced negative potential that is observed contralateral to an attended target and typically emerges over the posterior scalp 200-300 msec after the appearance of a search array (Eimer, 1996; Luck & Hillyard, 1994). The PD component, on the other hand, is an enhanced positive potential that is observed when the selective processing of a stimulus is to be avoided or terminated (Hilimire & Corballis, 2014; Hilimire, Mounts, Parks, & Corballis, 2011; Jannati, Gaspar, & McDonald, 2013; Kiss, Sawaki, Geng, & Luck, 2012). Sun and colleagues (2018) found that children and adolescents exhibited smaller target-elicited N2pc, suggesting that the younger participants deployed insufficient attentional selection resources to targets. For the PD component, the results were interestingly varied across children and adolescents who performed more accurately in comparison to those who performed worse. A lateral salient-but-irrelevant distractor elicited a large PD only in children and adolescents with low behavioural accuracy, while those who performed at higher accuracy exhibited a small and “adult-like” PD. Sun and colleagues (2018) attributed their overall findings to insufficient attentional selection resources to targets but “adult-like” or perhaps greater attentional suppression resources to resist irrelevant distractors in 9- to 15-year-olds.

In the current study, given that the task was likely more difficult and demanding for the pre-adolescents and adolescents, perhaps greater distractor suppression was used as a compensatory mechanism to overcome their insufficient attentional resources. As a result, greater attentional suppression could potentially account for why suppression spanned over a larger spatial region in the pre-adolescents and adolescents. In adulthood, when top-down feedback projections are mature and allow for more efficient attentional selection, less distractor suppression would be needed.

5.5 Visual Attention and Receptive Fields

Insofar, it has been established that under the conditions of the current study, attention-modulated surround suppression is only observed in pre-adolescents and adolescents aged between 12 to 17 years and young adults 18 years of age and above. This finding can be attributed to immature functional connectivity between the source regions of top-down feedback processes and the visual cortex in children under the age of 12. Differences in attentional demands of the task used in the current study and its effect on distractor suppression in development is another potential factor driving the developmental differences in attentional surround suppression, particularly with regard to the finding of a greater area of surround suppression in pre-adolescence and adolescence. But what has yet to be discussed is exactly how top-down attention affects visual processing.

A suggested account of how attention biologically influences visual processing is by altering cortical receptive fields in the visual cortex (Anton-Erxleben & Carrasco, 2014). The receptive field of the neuron is the part of stimulus space within which a stimulus elicits a response from the neuron (Lennie, 2003). In the visual domain, a given neuron responds to a stimulus presented in a region of space in its visual field, or receptive field, but not to the same stimulus when it is instead presented outside of this region (Anton-Erxleben & Carrasco, 2014). For instance, an on-center neuron's response is strongest when a stimulus is presented at the centre of its receptive field, with its response gradually declining as the stimulus is presented further away from its centre. Each receptive field at one stage of the visual hierarchy is made up of input from several neurons of the earlier stages. Consequently, the receptive field size increases along the visual hierarchy (Lennie, 1998). The size of a given receptive field also depends on eccentricity, or distance of the receptive field from the center of gaze (Kay et al., 2013).

Previous studies have demonstrated that attention modulates spatial resolution (Anton-Erxleben & Carrasco, 2014). For instance, attention has been found to alter the perception of spatial properties, such as spatial frequency (Gobell & Carrasco, 2005; Abrams, Barbot, & Carrasco, 2010), the shape of objects (Fortenbaugh, Prinzmetal & Robertson, 2011), size of objects (Anton-Erxleben, Henrich, & Treue, 2007) and the perceived spatial separation between objects (Suzuki & Cavanagh, 1997). For these findings, the mechanism by which attention modulates spatial resolution has been suggested to be through changing the size of receptive fields (Anton-Erxleben & Carrasco, 2014). Receptive fields overlapping the focus of attention shrink, leading to greater spatial resolution, whereas those nearby the focus of attention expand, leading to the worsening of spatial resolution (Anton-Erxleben & Carrasco, 2014). The suppressive surround observed around the focus of attention would therefore be the result of receptive fields expansion surrounding the focus of attention leading to lower spatial resolution.

Receptive fields also have specific implications in the ST model. As previously discussed the ST model conceptualizes selective attention as a top-down process of WTA, whereby a global winner is computed across the entire visual field and all connections not contributing to the winner are pruned. As it turns out, ST's WTA process specifically localizes the largest response within the receptive field of the global winner (Cutzu & Tsotsos, 2003). Finding the winner within each receptive field and subsequently pruning irrelevant connections, is applied recursively throughout the pyramid, layer by layer. Consequently, the global winner can eventually be traced back to its perceptual origin and the connections that remain become the pass zone of attentional focus, while the pruned connections form the suppressive surround. Spatial attention is believed to exert top-down attenuation of neurons whose receptive fields represent distractors (Hopf et al., 2012), while increasing the responses of neurons whose receptive fields overlap the attended location (Huang, Xue, Wang & Chen, 2016). As a result, the further processing of distractor information is halted, thereby allowing for full spatial focus of attention onto to the target and the processing of only the region of the attended input (Hopf et al., 2012).

Surprisingly little is known about the development of receptive fields. Generally, however, animal (Huberman, Feller, & Chapman, 2008; White & Fitzpatrick, 2007; Luo, & Flanagan, 2007) and developmental retinotopic mapping studies (Conner et al., 2004) have predicted that in humans, receptive field properties and visual field maps in the ventral stream are developed by age 5. Indeed, this prediction has recently been confirmed in an fMRI study by Gomez and colleagues (2018). Gomez et al. (2018) examined the development of population receptive fields (pRFs) in childhood (5 to 12 years) and adulthood. Given that neurons with similar receptive fields (RFs) are spatially clustered (Hubel & Wiesel, 1962), pRF of neurons in fMRI voxels can be measured (Gomez et al., 2018). Gomez et al. (2018) found no differences in pRF size, pRF eccentricity and visual field coverage in early and intermediate visual areas (V1 to ventral occipital 1 (VO1)) across children and adults. For higher-level regions, such as face-selective and character-selective regions, pRF properties were found to continue developing into adulthood, increasing in foveal coverage bias in the right hemisphere for faces and left for words. However, similar to the early and intermediate visual areas, there were qualitative similarities in the overall visual field coverage for face-selective and character-selective regions across children and adults.

In the current study, near foveal stimuli (requiring small visual field coverage) were used. It is therefore unlikely that developmental differences observed in attentional surround suppression were a result of developmental differences in receptive field properties and spatial resolution.

Attention is believed to affect visual processing by affecting spatial resolution through the modulation of the size receptive fields or their neural response (Anton-Erxleben & Carrasco, 2013). Developmental differences in the effect of top-down attention on visual processing could therefore possibly point to either differences in shrinkage of receptive field size or ineffective pruning of neurons whose receptive fields represent distractors in younger age groups. Inadequate reduction of distractor receptive field size could possibly explain why young children are more susceptible to distractors and also why they do not exhibit attention-modulated surround suppression in the current study. Ineffective pruning of neurons whose receptive fields represent distractors in younger age groups, could also possibly explain why young children do not exhibit attention-modulated surround suppression.

There are no reported studies on the development of receptive field properties in adolescence. However, given the similarities in receptive field properties between children and adults, it can reasonably be speculated that receptive field properties are adult-like in adolescents. Therefore, the larger suppressive surround observed in adolescents likely represents developmental differences in top-down attentional long-range modulation and pruning of unnecessary connections at these ages.

5.6 Limitations and Future Directions

In the current study, there were two goals. The first goal was to examine whether younger age groups exhibit attention-modulated surround suppression. The second goal was to provide more insight into the development of top-down attentional mechanisms and examine more specifically when these mechanisms mature and whether they affect visual processing throughout development. Having a better understanding of when and how attentional mechanisms develop and its effects on visual processing in development, is not just of theoretical importance, it also has practical relevance. For instance, from an educational perspective, highly decorated classrooms have been found to negatively impact children's learning, presumably because they are unable to inhibit salient distractors (Fisher, Godwin & Seltman, 2014). Other studies have demonstrated that attentional processes play a crucial role in directing children's focus to important events and items in their environment (Ruff & Rothbart, 2007; Weatherholt et al., 2006), and in attaining and maintaining an alert state, optimal for learning (Mullane et al., 2016). Having a better understanding of when top-down attentional processes develop and how immature attentional mechanism impacts visual and cognitive processes can therefore have major pedagogical impact.

From a clinical perspective, pervasive neurodevelopmental disorders such as Autism Spectrum Disorder (ASD) have been found to not only cause social-communicative and behavioural impairments (DMS-5 - American Psychiatric Association, 2013), but also sensory anomalies (Ronconi et al., 2018). For instance, individuals with ASD have been reported to exhibit visual sensory overload (Grandin, 2009) and more interference from irrelevant distractors (Adams & Jarrold, 2012; Remington, Swettenham, Campbell & Coleman, 2009).

In a recent study, Ronconi and colleagues (2018) examined whether visual sensory anomalies in ASD are partially due to differences in attention-modulated surround suppression. Remarkably, similar to the current findings, their psychophysical results showed that typically developing adolescents (mean age of 14) exhibit attention-modulated surround suppression. In comparison to the typically developing adolescents, the ASD adolescents exhibited weaker attentional surround suppression. In a second experiment, Ronconi and colleagues (2018) used dense-array electroencephalography (EEG) to examine the neurophysiological underpinnings of surround suppression in typically developing and ASD children (mean age of 11 and 12 years respectively). In the typically developing children, the N2, a part of the family of components that reflect attentional selection of relevant stimuli in space (Bocquillon, Bourriez, Palmero-Soler, Molaee-Ardekani, & Derambure & Dujardi, 2009) and time (Ronconi, Pincham, Cristoforetti, Facoetti & Szűcs 2016), was suppressed for targets appearing in the surround of the attentional focus. This attentional surround-modulated N2 effect was observed 300 msec after the attention probe. In contrast, the ASD children did not exhibit the attentional surround-modulated N2 effect, highlighting their deficits in inhibiting visual information outside the focus of attention. Ronconi and colleagues (2018) further found that the degree of inefficiency in inhibiting distracting visual information is associated ASD symptom severity, demonstrating the clinical relevance of better understanding the role of attention in visual processing in development.

In the current study, the 10- to 11-year-olds did not exhibit attention-modulated surround suppression. In Ronconi and colleagues' (2018) study, however, the typically developing children aged at around 11 years did exhibit suppressed N2 for targets appearing in the surround of the attentional focus. This finding would suggest that attention-modulated surround suppression is present in 11-year-olds, despite it not being observed in the current study. However, due to reasonable practical reasons, the children in Ronconi and colleagues' (2018) study did not complete all the conditions of their first psychophysical with adolescents. Therefore, it is currently unclear whether in contrast to my study findings their 11-year-old participants demonstrate attention-modulated surround suppression psychophysically, as would be expected in older age groups.

Notably, another factor to consider is that in Ronconi and colleagues' (2018) study, the attentional surround-modulated N2 effect in the 11-year-olds was observed 300 msec after an attention probe. This raises the question of whether the temporal parameters used in the current study made the tasks too difficult for the younger children to complete, admittedly one potential limitation of the current study. Increasing the cue time in Experiment 3 was meant to overcome this limitation by providing the younger participants with more time to complete their feedback processes, but instead, perhaps increasing the visual array duration is what is necessary to make the task more feasible. For instance, keeping the spatial cue duration at 100 msec and increasing the duration of the visual array from 175 msec to 250 msec would have perhaps been more appropriate for the younger children. This change could have arguably still provided the younger age groups with more time to complete their feedback processes. If the top-down feedback processes were elicited soon after the onset of the spatial cue, increasing the visual array time to 250 msec would allocate close to 300 msec for the top-down processes to complete by the response mask. Indeed, the attentional surround-modulated N2 effect in the 11-year-olds of Ronconi and colleagues' (2018) study was observed 300 msec after the attention probe. However, given that there were no means of including a portable eye-tracker to my experimental set up, it would have not been possible to increase the visual array duration and control for potentially confounding effects of eye movements. In a subsequent study, increasing the visual array duration of the current task in younger age groups while monitoring eye movements to assure that they remain fixated at the center of the screen would have great empirical and theoretical value. This manipulation would allow for an examination of whether attention-modulated surround suppression can indeed be observed in younger age groups.

Another possible future direction is to confirm the current study findings with other psychophysical tasks. This is important not only for validation purposes but also because again a more appropriate task for younger age groups may reveal different findings. For example, the task used in the Hopf and colleages' MEG study (2006) discussed in the introduction may be slightly simpler since there is only one target. In their study, participants were required to search for a red target C among blue distractor

Cs. On half of the trials an attention probe was flashed at the center C. Therefore, by comparing accuracy across the five target-to-probe distances, ranging from PD0 (target presented at the probed location) through PD4 (target presented 4 items away from the probe), attention-modulated surround suppression could be examined. Pertinently, a near identical task was used in Ronconi and colleagues' (2018) study, where children and adolescents were tested, suggesting that it may be a more developmentally appropriate task. Using this task with younger age groups could also allow for further examination of the attentional profile of attention across development.

With the use of neuro-techniques, possible neurophysiological mechanisms underlying the developmental differences in attentional surround suppression could be uncovered. For example, with a similar task and MEG methodology as Hopf and colleagues (2006), the spatial profile of attention across development could be accurately examined. With regard to the current study, it would be compelling to examine whether MEG results in adolescents would mimic the current psychophysical findings of greater suppression in this age group. More specifically, perhaps similar to adults, the magnetic response would be highest when the target appears at the probe location (PD0), but that the response would be more significantly reduced when the target appeared at position next to probe (PD1) in comparison to adults, demonstrating that there is indeed greater suppression or neural attenuation during pre-adolescence and adolescence. Moreover, perhaps the magnetic response would continue to be reduced at larger distances (e.g., PD2 and PD3) in pre-adolescents and adolescents, showing that attentional surround suppression spans over larger distances in these age groups.

Yet another relevant avenue for further research is the further examination of the DAN and VAN functional connectivity across development. Farrant and Uddin's (2015) fMRI study importantly highlighted functional connectivity differences in VAN and DAN between young adults and children aged from 7 to 12 years and demonstrated how and why children may rely more on bottom-up feedforward processes. What currently remains unclear is how the DAN and VAN functional connectivity is characterized in adolescence. It would also be of value to examine whether DAN and VAN connectivity changes continuously or incrementally across a wider age range, which could provide compelling insight into the mechanisms underlying developmental differences in attentional surround suppression or simply visual attention in general.

Other considerations include examining whether surround suppression would be observed in children with different stimuli properties, such as varying the size or salience of the visual array or the individual stimuli. There are no differences in receptive field size, eccentricity and visual field coverage in early and intermediate visual areas in children (5 to 12 years) and adults (Gomez et al., 2018). And, in the current study, the visual array fit in the parafovea, a region with no visual field coverage difference between adults and children. Previous research has also demonstrated that the fovea develops quite early in development (Hendrickson & Yuodelis-Flores, 1984), and that low level visual abilities such as spatial acuity (Norcia & Tyler, 1985; Lai, Wang & Hsu, 2011), contrast sensitivity (Almoqbel, Irving & Leat, 2017) and orientation discrimination (Lewis et al., 2007; Jeon, Hamid, Maurer & Lewis, 2010) are adult-like by the age of 8 years, the youngest age group featured in the current study. However, it is still possible that larger and more salient stimuli could have made the task more feasible for the younger children. Especially, since children up to 11 years of age show greater crowding effects, that is, impaired target recognition caused by surrounding contours, in comparison to adults (Jeon et al., 2010).

5.7 Conclusion

Overall, the results of the current study demonstrate that top-down attentional modulation affects visual processing in pre-adolescents and adolescents over the age of 12 years. With regard to attentional development and more specifically the development of top-down attention mechanisms, the findings of the current study provide further support to the notion that early in development visual feedforward and low-level orienting mechanisms are more dominant and that as development proceeds top-down feedback processes strengthen (Amso & Scerif, 2015).

In Experiment 1, attention-modulated surround suppression was only observed in participants aged 12 years and above. These findings suggest that top-down attentional feedback processes are not as dominant until 12 years of age, and that they continue to be refined throughout adolescence. In early childhood when top-down feedback processes are not as effective, bottom-up feedforward processes are relied on instead. An over-reliance on feedforward bottom-up mechanisms can readily account for other developmental findings in the literature, such as children being more susceptible to interference and less able to inhibit responses in comparison to young adults (Bunge et al., 2002). As children mature, connectivity between the regions of the DAN and farther regions such as the visual cortex grows stronger, which subsequently allows for greater top-down attentional modulation.

Given its specific predictions, the ST model has for allowed for the examination top-down attention development and its effects on visual processing in development. If top-down feedback processes are mature at a given age, ST would predict that these top-down processes would efficiently promote the processing of relevant visual information, while also leading to suppression surrounding the focus of attention. Indeed, in the current study, ST correctly predicted that young adults, adolescents and pre-adolescents, whose top-down attentional mechanisms are believed to be mature or nearly mature, would exhibit suppression surrounding the focus of attention. In adulthood, ST provides a solution for the coding problem of the visual system, whereby receptive fields converge in the visual hierarchy, consequently leading to parts of a scene that are represented by separate receptive fields at the lower levels becoming inseparable within larger receptive fields at higher visual areas (Hopf et al., 2006). Similar to Desimone & Duncan's (1995) biased-competition model, ST proposed that there must be competition among objects for representation within the visual system (Tsotsos, 1995). ST, however, uniquely provides a network mechanism to accomplish this biased competition (Tsotsos, 1995), and in the current study, can likely be applied to pre-adolescents and adolescents, who also exhibited attention-modulated surround suppression and whose top-down attentional mechanisms are believed to be nearly mature.

Attention is undoubtedly vital because without our brain's ability to organize and filter relevant information from the overabundance of all available information, we would not be able to interpret and make sense of our environment. Attention is a gateway for given information to access conscious perception and explicit memory (Shim, Alvarez & Jiang, 2008). In development, attention is even more critical because it is a time period during which an immense amount of learning and psychological change is taking place. It is therefore critical to understand the functioning of visual attention processes in younger age groups and how these processes change over development. Understanding the development of attentional top-down projections is therefore important to the pursuit of understanding how the typically developing brain processes visual information. The current study is an important step demonstrating that top-down projections similarly affects visual processing in pre-adolescence, adolescence and young adults, while additionally highlighting how visual attention processes indeed function differently in childhood.

6. References

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7. Appendices

7.1 Appendix A. Mixed-Effects ANOVA for Experiment 1 to 3

To further examine the effect of age group, and the interaction of age group and inter-target separation, mixed-effect ANOVAs were run with the data combined across age group for each experiment.

Experiment 1

A 6 x 6 mixed-effects ANOVA was conducted with age group (8-9, 10-11, 12-13, 14-15, 16-17 and 18+ years) and inter-target separation (0.26, 0.50, 0.71, 0.87, 0.97, 1.00) as factors, and accuracy as the dependent variable. The main effect of age group on accuracy was not significant, $F(5,174) = 2.23$, $p > .05$. The main effect of inter-target separation was significant, $F(5,870) = 7.26$, $p < .0001$. The interaction of age group and inter-target separation was also significant, $F(25,870) = 1.73$, $p < .05$.

Bonferroni corrected post-hoc analyses demonstrated that collapsed across age group, participants' accuracy at 0.26 (M = .57, SD = .11) was significantly lower than at 0.87 (M = .59 , SD = .13), 0.97 (M = .64, SD = .14), and 1.00 (M = .65, SD = .13) ($p < .01$). Participants' accuracy at 0.50 (M = .56, SD = .12) was significantly lower than at 0.87 (M = .59 , SD = .13), 0.97 (M = .64, SD = .14), and 1.00 (M = .65, SD = .13) ($p < .01$).

The breakdown of the significant interaction of age group and inter-target separation can be examined in the reported separate analyses for Experiment 1A to E (results section). The effect of inter-target separation was significant only for young adults (18+ years), the 16- to 17-year-olds, 14- to 15-year-olds, and 12- to 13-year-olds, indeed demonstrating how the effect of inter-target separation varied across age group.

Experiment 2

A 6 x 6 mixed-effects ANOVA was conducted with age group (8-9, 10-11, 12-13, 14-15, 16-17 and 18+ years) and inter-target separation (0.26, 0.50, 0.71, 0.87, 0.97, 1.00) as factors, and accuracy as the dependent variable. The main effect of age group on accuracy was significant, $F(5,158) = 2.57$, $p < .05$. The main effect of inter-target separation was not significant, $F(5,790) = 1.61$, $p > .05$. The interaction of age group and inter-target separation was not significant, $F(25,790) = 1.73$, $p > .05$.

Bonferroni corrected post-hoc analyses demonstrated that collapsed across inter-target separation, the young adults (M = .64, SD = .12) performed significantly greater than the 14- to 15-year-olds (M = .56, SD = .11) ($p < .05$). No other age group comparison was significant.

Experiment 3

A 2 x 6 mixed-effects ANOVA was conducted with age group (8-9 and 10-11 years) and inter-target separation (0.26, 0.50, 0.71, 0.87, 0.97, 1.00) as factors, and accuracy as the dependent variable. The main effect of age group on accuracy was not significant, $F(1,55) = 2.88$, $p > .05$. The main effect of inter-target separation was not significant, $F(5,275) = 0.19$, $p > .05$. The interaction of age group and inter-target separation was not significant, $F(25,275) = 0.95$, $p > .05$.

7.2 Appendix B. Consent Form – Young Adults (16 years and up)

YORK UNIVERSITÉ UNIVERSITY

Visual and Cognitive Development Project

Informed Consent Form (Adults)

Project: Visual Search Across Development

Principal Investigator: Scott Adler Ph.D., York University.

Overview:
You are being asked to participate in a research study by Dr. Scott Adler, an Associate Professor at York University. Your participation in this study is entirely voluntary. Please read the information below and ask questions about anything you do not understand before deciding whether or not to participate.

Purpose of Study:
This study is designed to examine factors that affect visual search and attention performance across development.

Procedure:
There is one session involved in this study. During this study, images will be presented to you on a screen and you will be asked to report what you saw by button press.

Anticipated Benefits to Participants and Society:
This study helps us to better understand the development of attention. This could lead to advances in other areas such as perception and general cognitive processing.

Potential Risks and Discomforts:
Participation in this study does not pose any foreseeable risks other than fatigue. **If new information related to the Benefits and Risks of the study is obtained, you will be informed.**

Compensation:
At the end of each session, you will receive 0.5 URPP course credit for your undergraduate introduction to psychology course.

Participation and Withdrawal
Your participation in this research is entirely voluntary. If you decide to participate, you are free to withdraw your consent and discontinue participation at any time without penalty or loss of rights. The information obtained from this study may be presented at scientific conferences or in scientific journals, but your name will never appear in any public document. In order to ensure confidentiality, your name and other identifying information will be filed separately from the experimental data.

Please turn over to complete signature section

YORK UNIVERSITÉ UNIVERSITY

Visual and Cognitive Development Project

Signature Section (Adults)

I have read and understood the description of the research project. I understand the purpose of the current study, the purpose of my participation, the procedures involved, potential benefits, and the potential risks to me if I am to participate. I have asked for and received a satisfactory explanation of any language or details of the study that I did not fully understand.

I understand that my participation in the study is voluntary. I may withdraw from the study at any point in time. It has been explained to me that the results of the study are confidential. I understand that I will receive credit in my undergraduate psychology course as compensation for participating in this study.

All my information will be kept confidential to the fullest extent allowed by law and securely stored in the locked offices of the Project and on password protected computers for a period of 5 years. After this time, all documents associated with me will be shredded and computer files will be deleted. I understand, however, that all analyzed data generated by my participation will be kept indefinitely, for the possibility of reanalysis at a later date.

I hereby consent to participate. I have been given a copy of this consent form and the attached information sheet.

If, at a later time, I have any questions, I may contact Scott Adler, Ph.D., at York University (416-736-5115, ext. 33389, or 416-736-2100 ext. 20036, or adler@yorku.ca) for additional information.

This research has received ethics review and approval by the Human Participants Review Sub-Committee, York University's Ethics Review Board and conforms to the standards of the Canadian Tri-Council Research Ethics guidelines. If you have any questions about this process, or about your rights as a participant in the study, please contact the Sr. Manager & Policy Advisor for the Office of Research Ethics, 5th Floor, Kaneff Tower, York University (telephone 416-736-5914 or e-mail ore@yorku.ca).

Participant: ______________________________

Signature: ________________________________ Date: ________________

7.2 Appendix B. Consent Form – Children (8-15 years)

Visual and Cognitive Development Project

Informed Consent Form (Children and Adolescents)

Project: Visual Attention Across Development

Principal Investigator: Scott Adler Ph.D., York University.

Overview:
Your child is being asked to participate in a research study by Dr. Scott Adler, an Associate Professor at York University. Your child's participation in this study is entirely voluntary. Please read the information below and ask questions about anything you do not understand before deciding whether or not allow your child to participate.

Purpose of Study:
This study is designed to examine factors that affect visual perception and attention performance across development.

Procedure:
There is only one session involved in this study. During the study session, images will be presented to your child on a screen. Your child will be asked to report what they saw by button press. All testing will take place at the school your child attends and will be carried out by fully trained personnel.

Anticipated Benefits to Participants and Society:
This study helps us to better understand the development of attention. This could lead to advances in other areas such as perception and general cognitive processing.

Potential Risks and Discomforts:
Participation in this study **does not pose** any foreseeable risks other than fatigue. If new information related to the Benefits and Risks of the study is obtained, you will be informed.

Participation and Withdrawal
Your child's participation in this research is entirely voluntary. If your give permission to have you child participant participate, you and your child are free to withdraw your consent and discontinue participation at any time without penalty or loss of rights. The information obtained from this study may be presented at scientific conferences or in scientific journals, but your child's name will never appear in any public document. In order to ensure confidentiality, your child's name and other identifying information will be filed separately from the experimental data.

Please turn over to complete signature section

YORK U UNIVERSITÉ UNIVERSITY

Visual and Cognitive Development Project

Signature Section (Children and Adolescents)

Project: Visual Attention Across Development

I have read and understood the description of the research project. I understand the purpose of the current study, the purpose of my child's participation, the procedures involved, potential benefits, and the potential risks to me if my child were to participate. I have asked for and received a satisfactory explanation of any language or details of the study that I did not fully understand.

I understand that my child and I can ask further questions during any stage of the study and that my child's participation in the study is voluntary. My child may withdraw from the study at any point in time. I am aware that the study may not benefit my child specifically but knowledge will be gained that may benefit others. It has been explained to me that the results of the study are confidential.

Neither my child's identity nor any personal information will be available to anyone other than the investigators. No personal information will be disclosed in any resulting publication or presentation. I have been given a copy of this consent form.

I,_______________________________, give permission for my child,

_______________________________________ to participate in this study.

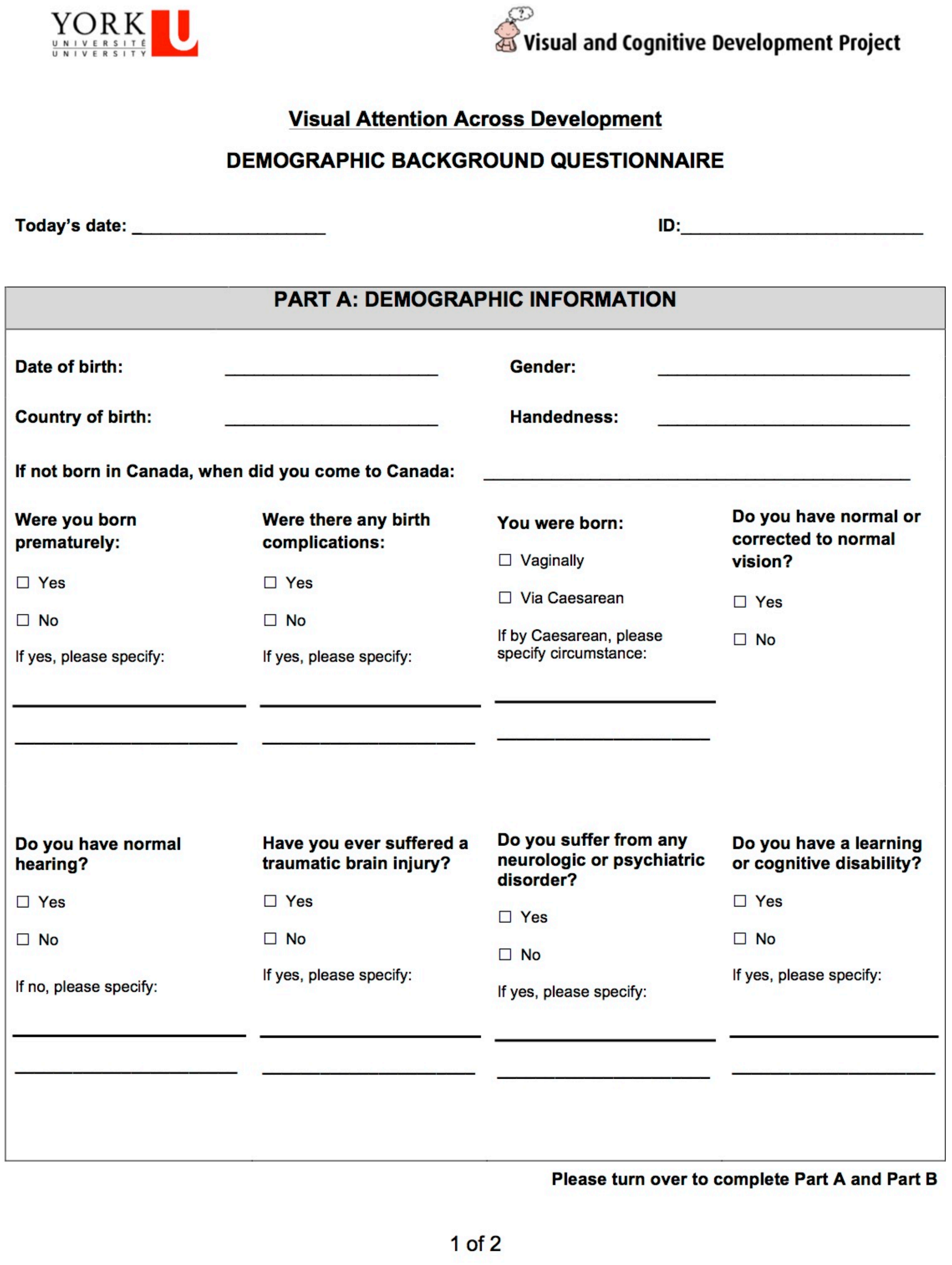
My child's information will be kept confidential to the fullest extent allowed by law and securely stored in the locked offices of the Project and on password protected computers for a period of 5 years. After this time, all documents associated with my child will be shredded and computer files will be deleted. I understand, however, that all analyzed data generated by my child's participation will be kept indefinitely, for the possibility of reanalysis at a later date.

If, at a later time, I have any questions, I may contact Scott Adler, Ph.D., at York University (xxx-xxx-xxxx, ext. xxxxx, or xxx-xxx-xxxx, ext. xxxxx, or xxxxx@yorku.ca) for additional information. If you have any concerns or complaints about how you were treated during the research sessions, please feel free to contact York University's Human Participants Review (Ethics) Sub-Committee at xxx-xxx-xxxx or xxxxxxx @yorku.ca.

________________________________ ________________________________

Signature of participant Date

7.3 Appendix C. Demographic Questionnaire – Young Adults (16 years and up)



YORK U UNIVERSITÉ UNIVERSITY

Visual and Cognitive Development Project

Visual Attention Across Development

DEMOGRAPHIC BACKGROUND QUESTIONNAIRE

Today's date: ____________________

ID: ________________________

PART A: DEMOGRAPHIC INFORMATION

Date of birth: ____________________

Gender: ________________________

Country of birth: ____________________

Handedness: ________________________

If not born in Canada, when did you come to Canada: ____

Were you born prematurely:

☐ Yes

☐ No

If yes, please specify:

____

____

Were there any birth complications:

☐ Yes

☐ No

If yes, please specify:

____

____

You were born:

☐ Vaginally

☐ Via Caesarean

If by Caesarean, please specify circumstance:

____

____

Do you have normal or corrected to normal vision?

☐ Yes

☐ No

Do you have normal hearing?

☐ Yes

☐ No

If no, please specify:

____

____

Have you ever suffered a traumatic brain injury?

☐ Yes

☐ No

If yes, please specify:

____

____

Do you suffer from any neurologic or psychiatric disorder?

☐ Yes

☐ No

If yes, please specify:

____

____

Do you have a learning or cognitive disability?

☐ Yes

☐ No

If yes, please specify:

____

____

Please turn over to complete Part A and Part B

1 of 2

PART A: DEMOGRAPHIC INFORMATION (Continued)

Please indicate your highest level of education and occupation:

☐ No high school diploma

☐ High school graduate

☐ Some college or college diploma

☐ Bachelor's degree

☐ Graduate or professional degree

Occupation: ____

PART B: VIDEOGAME EXPERIENCE OF THE CHILD

1. Have you ever played video games?

☐ Yes

☐ No

2. Do you currently play video games?

☐ Yes

☐ No

3. What type of video games do you mainly play?

☐ First person videogames

☐ Third person videogames

4. How long have you been playing video games?

☐ 6 months

☐ 1 year

☐ 2-5 years

☐ 5-10 years

☐ More than 10 years

☐ Not applicable

5. How often (approximately) do you play video games?

☐ Daily

☐ Weekly

☐ Once a month

☐ Once every 6 months

☐ Once a year

☐ Less than once a year

☐ Not applicable

6. How good do you feel you are at playing video games?

☐ Very good

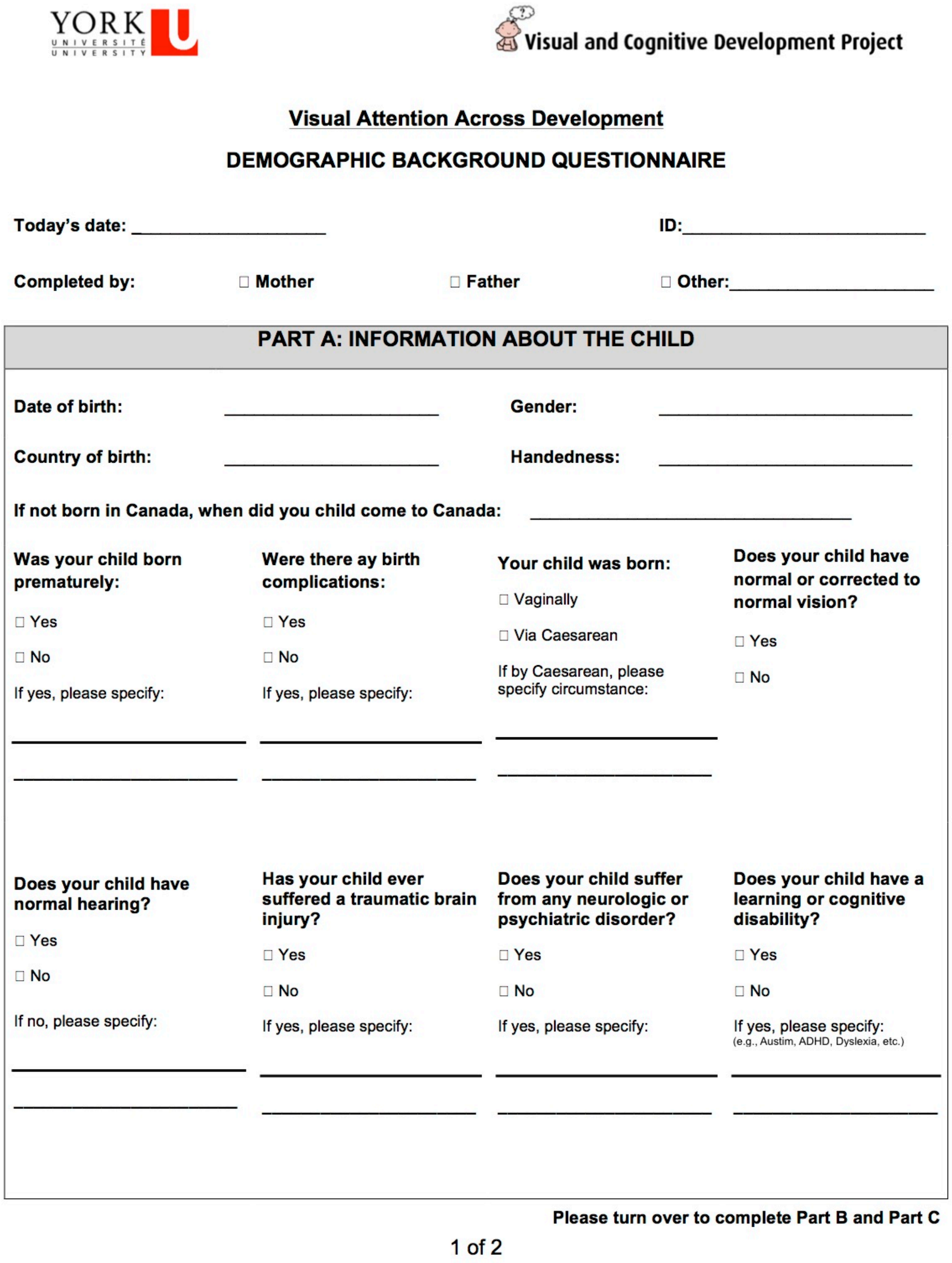
☐ Moderately good

☐ Not very skilled

☐ Not skilled

☐ Not applicable

7.4 Appendix D. Demographic Questionnaire – 8- to 15-year-olds



Visual and Cognitive Development Project

Visual Attention Across Development

DEMOGRAPHIC BACKGROUND QUESTIONNAIRE

Today's date: ____________________ **ID:**________________________

Completed by: ☐ **Mother** ☐ **Father** ☐ **Other:**____________________

PART A: INFORMATION ABOUT THE CHILD

Date of birth: ____________________ **Gender:** ________________________

Country of birth: ____________________ **Handedness:** ________________________

If not born in Canada, when did you child come to Canada: ______________________________

Was your child born prematurely:

☐ Yes

☐ No

If yes, please specify:

Were there ay birth complications:

☐ Yes

☐ No

If yes, please specify:

Your child was born:

☐ Vaginally

☐ Via Caesarean

If by Caesarean, please specify circumstance:

Does your child have normal or corrected to normal vision?

☐ Yes

☐ No

Does your child have normal hearing?

☐ Yes

☐ No

If no, please specify:

Has your child ever suffered a traumatic brain injury?

☐ Yes

☐ No

If yes, please specify:

Does your child suffer from any neurologic or psychiatric disorder?

☐ Yes

☐ No

If yes, please specify:

Does your child have a learning or cognitive disability?

☐ Yes

☐ No

If yes, please specify:
(e.g., Austim, ADHD, Dyslexia, etc.)

Please turn over to complete Part B and Part C

1 of 2

YORK UNIVERSITÉ UNIVERSITY

Visual and Cognitive Development Project

PART B: INFORMATION ABOUT THE PARENTS

PARENT 1:______________________

Country of birth: ___________________________

If not born in Canada, when did the mother come to Canada? (Month/Year):_____________________

What language(s) does the mother speak? **(please list):**

____

Please indicate the mother's highest level of education and occupation:

☐ No high school diploma

☐ High school graduate

☐ Some college or college diploma

☐ Bachelor's degree

☐ Graduate or professional degree

Occupation:_______________________________

PARENT 2:______________________

Country of birth: ___________________________

If not born in Canada, when did the father come to Canada? (Month/Year): _____________________

What language(s) does the father speak? **(please list):**

____

Please indicate the father's highest level of education and occupation:

☐ No high school diploma

☐ High school graduate

☐ Some college or college diploma

☐ Bachelor's degree

☐ Graduate or professional degree

Occupation:_______________________________

PART C: VIDEOGAME EXPERIENCE OF THE CHILD

1. Has your child ever played video games?

☐ Yes

☐ No

2. Does your child currently play video games?

☐ Yes

☐ No

3. What type of video games does your child mainly play?

☐ First person videogames

☐ Third person videogames

4. How long has your child been playing video games?

☐ 6 months

☐ 1 year

☐ 2-5 years

☐ 5-10 years

☐ More than 10 years

☐ Not applicable

5. How often (approximately) does your child play video games?

☐ Daily

☐ Weekly

☐ Once a month

☐ Once every 6 months

☐ Once a year

☐ Less than once a year

☐ Not applicable

6. How good do you feel your child is at playing video games?

☐ Very good

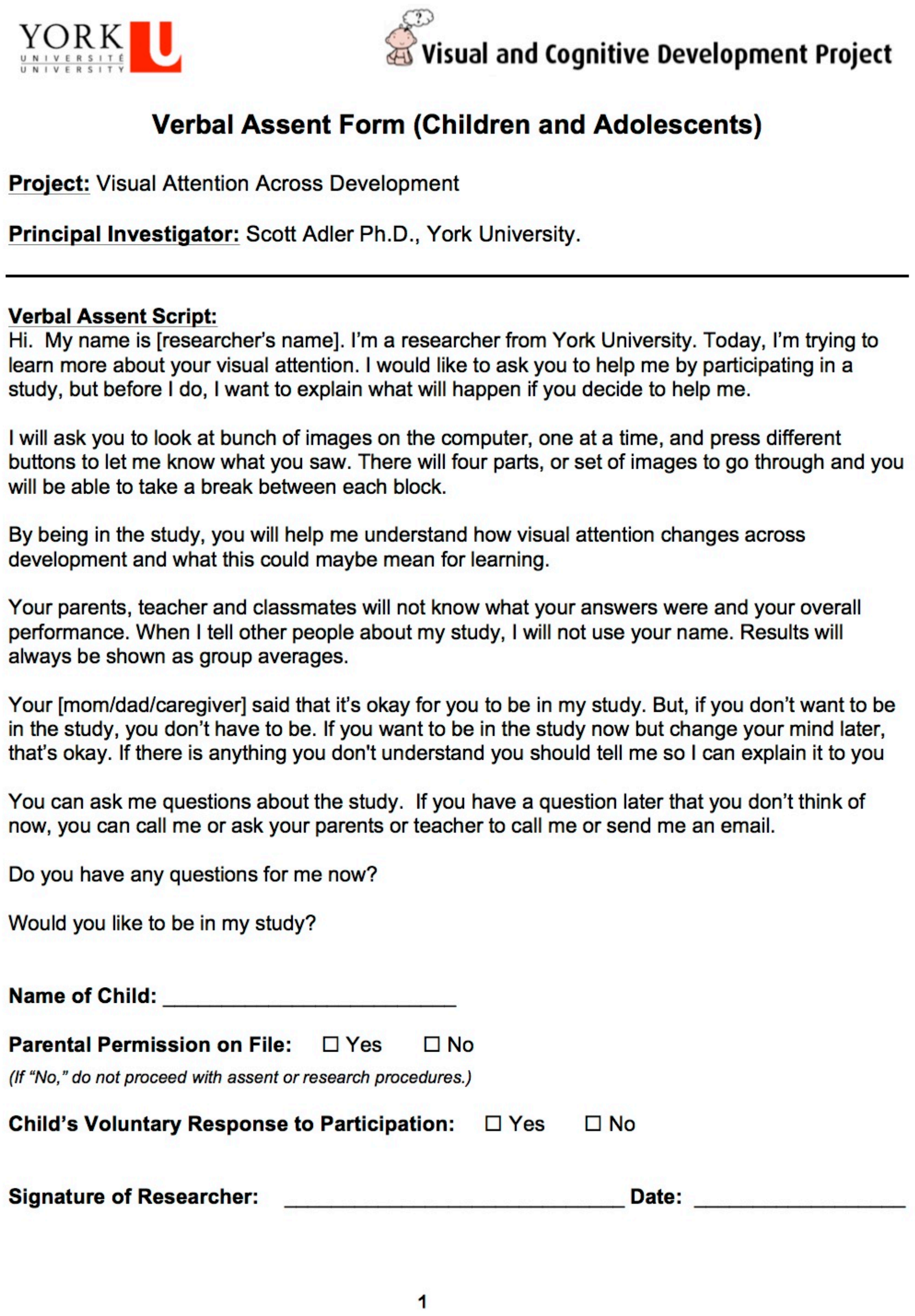
☐ Moderately good

☐ Not very skilled

☐ Not skilled

☐ Not applicable

7.5 Appendix E. Verbal Assent Form – 8- to 15-year-olds



YORK UNIVERSITÉ UNIVERSITY

Visual and Cognitive Development Project

Verbal Assent Form (Children and Adolescents)

Project: Visual Attention Across Development

Principal Investigator: Scott Adler Ph.D., York University.

Verbal Assent Script:
Hi. My name is [researcher's name]. I'm a researcher from York University. Today, I'm trying to learn more about your visual attention. I would like to ask you to help me by participating in a study, but before I do, I want to explain what will happen if you decide to help me.

I will ask you to look at bunch of images on the computer, one at a time, and press different buttons to let me know what you saw. There will four parts, or set of images to go through and you will be able to take a break between each block.

By being in the study, you will help me understand how visual attention changes across development and what this could maybe mean for learning.

Your parents, teacher and classmates will not know what your answers were and your overall performance. When I tell other people about my study, I will not use your name. Results will always be shown as group averages.

Your [mom/dad/caregiver] said that it's okay for you to be in my study. But, if you don't want to be in the study, you don't have to be. If you want to be in the study now but change your mind later, that's okay. If there is anything you don't understand you should tell me so I can explain it to you

You can ask me questions about the study. If you have a question later that you don't think of now, you can call me or ask your parents or teacher to call me or send me an email.

Do you have any questions for me now?

Would you like to be in my study?

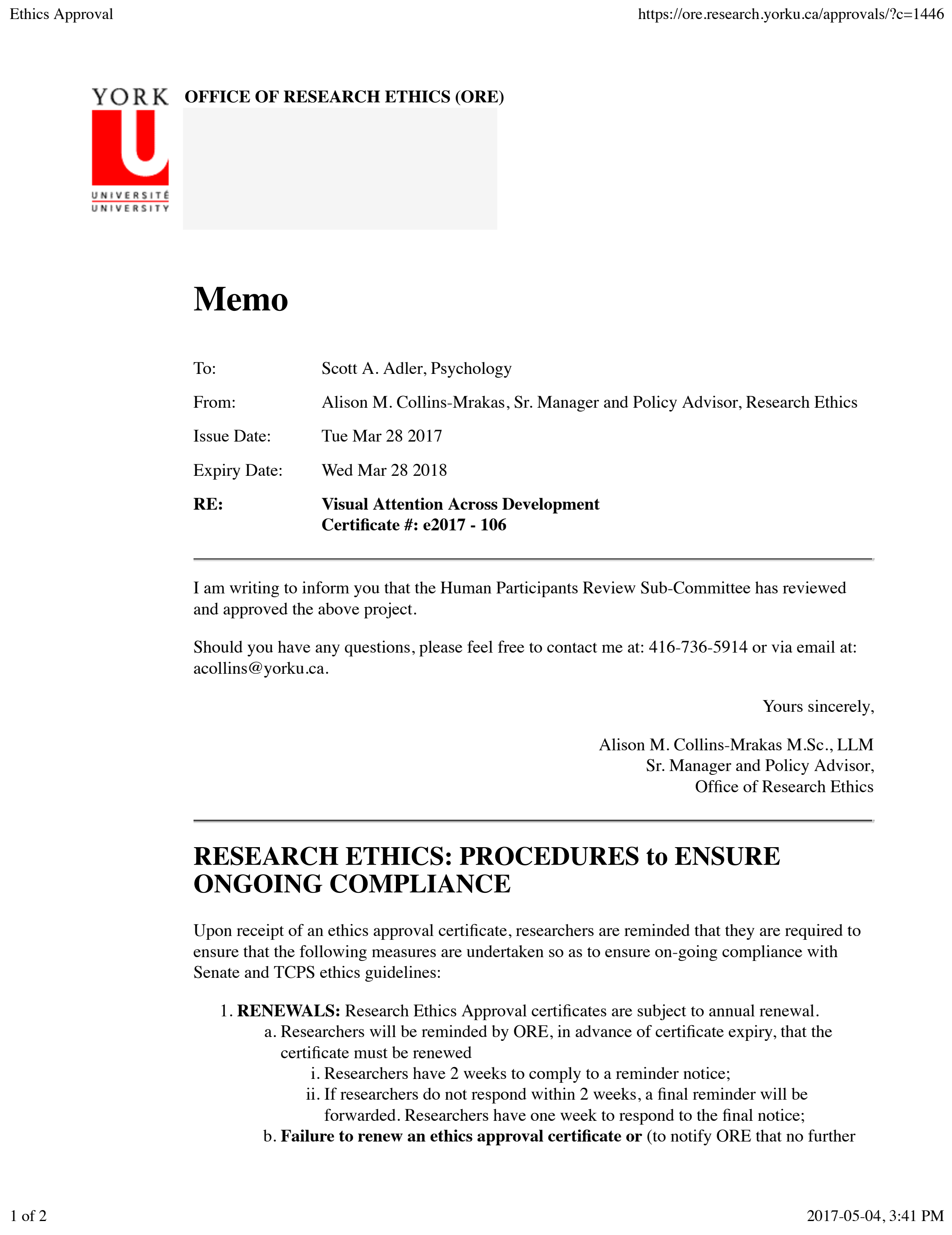
Name of Child: __________________________

Parental Permission on File: ☐ Yes ☐ No
(If "No," do not proceed with assent or research procedures.)

Child's Voluntary Response to Participation: ☐ Yes ☐ No

Signature of Researcher: ______________________________ **Date:** __________________

7.6 Appendix G. Ethics Approval



Ethics Approval https://ore.research.yorku.ca/approvals/?c=1446

OFFICE OF RESEARCH ETHICS (ORE)

Memo

To: Scott A. Adler, Psychology
From: Alison M. Collins-Mrakas, Sr. Manager and Policy Advisor, Research Ethics
Issue Date: Tue Mar 28 2017
Expiry Date: Wed Mar 28 2018
RE: **Visual Attention Across Development**
Certificate #: e2017 - 106

I am writing to inform you that the Human Participants Review Sub-Committee has reviewed and approved the above project.

Should you have any questions, please feel free to contact me at: 416-736-5914 or via email at: acollins@yorku.ca.

Yours sincerely,

Alison M. Collins-Mrakas M.Sc., LLM
Sr. Manager and Policy Advisor,
Office of Research Ethics

RESEARCH ETHICS: PROCEDURES to ENSURE ONGOING COMPLIANCE

Upon receipt of an ethics approval certificate, researchers are reminded that they are required to ensure that the following measures are undertaken so as to ensure on-going compliance with Senate and TCPS ethics guidelines:

1. **RENEWALS:** Research Ethics Approval certificates are subject to annual renewal.
    a. Researchers will be reminded by ORE, in advance of certificate expiry, that the certificate must be renewed
        i. Researchers have 2 weeks to comply to a reminder notice;
        ii. If researchers do not respond within 2 weeks, a final reminder will be forwarded. Researchers have one week to respond to the final notice;
    b. **Failure to renew an ethics approval certificate or** (to notify ORE that no further

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research involving human participants will be undertaken) **may result in suspension of research cost fund and access to research funds may be suspended/withheld ;**

2. **AMENDMENTS:** Amendments must be reviewed and approved **PRIOR** to undertaking/making the proposed amendments to an approved ethics protocol;
3. **END OF PROJECT:** ORE must be notified when a project is complete;
4. **ADVERSE EVENTS:** Adverse events must be reported to ORE as soon as possible;
5. **AUDIT:**
   a. More than minimal risk research may be subject to an audit as per TCPS guidelines;
   b. A spot sample of minimal risk research may be subject to an audit as per TCPS guidelines.

FORMS: As per the above, the following forms relating to on-going research ethics compliance are available on the Research website:

1. Renewal
2. Amendment
3. End of Project
4. Adverse Event