Development of spatial suppression surrounding the focus of visual attention

Audrey M. B. Wong-Kee-You
Smith-Kettlewell Eye Research Institute, San Francisco, CA, USA

Centre for Vision Research, York University, Toronto, ON, Canada

John K. Tsotsos
Department of Electrical Engineering and Computer Science, York University, Toronto, ON, Canada

Department of Psychology, York University, Toronto, Canada

Scott A. Adler
Centre for Vision Research, York University, Toronto, ON, Canada

In adulthood, research has demonstrated that surrounding the spatial location of attentional focus is a suppressive field, resulting from top-down attention promoting the processing of relevant stimuli and inhibiting surrounding distractors (e.g., Hopf et al., 2006). It is not fully known, however, how this phenomenon manifests during development. This is an important question since attention processes are likely even more critical in development because of their potential impact on learning and day-to-day activities. The current study examined whether spatial suppression surrounding the focus of visual attention, a predicted by-product of top-down attentional modulation, is observed in development. A wide age range separated in six incremental age levels was included, allowing for a detailed examination of potential differences in the effect of attention on visual processing across development. Participants between 12 and 27 years of age exhibited spatial suppression surrounding their focus of visual attention. Their accuracy increased as a function of the separation distance between a spatially cued (and attended) target and a second target, suggesting that a ring of suppression surrounded the attended target. Attentional surround suppression was not observed in 8- to 11-years-olds, even with a longer spatial cue presentation time, demonstrating that the lack of the effect at these ages is not due to slowed attentional feedback processes. Our findings demonstrate that top-down attentional processes exhibit functional maturity beginning around 12 years of age with continuing maturation of their expression until 17, which likely impacts education and the diagnosis of visual and cognitive clinical pathologies.

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 (Carrasco, 2011). Our brains must instead use attention to bring important information into focus, while filtering out irrelevant information (Driver, 2001). Attention mechanisms are understood to involve the interaction of specific neural systems that allow for the control of information processing and action (Hopf et al., 2012). Within the visual domain, attention mechanisms operate on different visual representations, such as spatial or location-, feature-, and object-based representations (Hopf et al., 2012). Regardless of the visual representations upon which it is operating, however, the functional consequence of attention mechanisms is believed to be the optimization of the visual system (Carrasco, 2011; Tsotsos, 2011).

But how does attention optimize the visual system or optimize the processing of visual information? Within the spatial domain, previous animal studies have revealed direct evidence that the focus of spatial attention impacts activity in early and intermediate visual areas of the brain, thereby facilitating the processing of relevant visual information (Sundberg, Mitchell, & Reynolds, 2009; Zhang et al., 2014). But, perplexingly, greater levels of suppression are also found for stimuli immediately surrounding the focus of

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attention than for stimuli that are further away (Sundberg et al., 2009). This phenomenon of suppression surrounding the focus of attention is in fact a prediction of the selective tuning (ST) model of attention (Tsotsos, 1995).

According to the ST model, top-down attentional selection prunes and suppresses forward-projecting units or neurons not representing relevant input, leading to enhanced processing of the attended input, but as a consequence also gives rise to spatial suppression surrounding the focus of attention (Tsotsos, 2002). The ST model views the visual processing architecture as a hierarchical and layered pyramid in which units or neurons within the network receive both feedforward (bottom-up) and feedback (top-down) connections. A winner-take-all[1] process initially localizes the neurons with the largest response at the top layer. All of the connections of the 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 or the spotlight of attentional focus, while the pruned connections form the suppressive surround. 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 (Sylvester, Jack, Corbetta, & Shulman, 2008), superior frontal and angular gyri (Ruff & Driver, 2006), and precuneus (Payne & Allen, 2011).

Several studies have provided psychophysical (e.g., Cutzu & Tsotsos, 2003) and neural evidence of surrounding spatial suppression in adult humans (e.g., Boehler, Tsotsos, Schoenfeld, Heinze, & Hopf, 2009). For instance, Cutzu and Tsotsos (2003) had participants discriminate between two target letters and spatial attention was cued to one of the targets. Participants' accuracy at discriminating between the two targets increased as a function of intertarget separation distance, suggesting that a surround suppressive ring accompanied the processing advantage allocated by the spatial cue. In a magnetoencephalography (MEG) study by Hopf and colleagues (2006), it was found that the MEG response was significantly reduced when a target appeared at a position next to where attention was allocated, suggesting that in the immediate surround of the focus of attention, is a region of suppression or neural attenuation. Though these studies demonstrate that attentional surround suppression is observed in human adults, it is not fully known whether this phenomenon is exhibited in development. Notably, typically developing adolescents have recently been found to psychophysically exhibit suppression surrounding the focus of attention (Ronconi et al., 2018), suggesting that the effect can be observed developmentally. For instance, Ronconi and colleagues (2018) found that typically developing adolescents (mean age of 14) exhibit suppression surrounding their focus of attention on a psychophysical task. However, whether younger children also psychophysically exhibit suppression surrounding the focus of attention and whether there are differences in the manifestation of the effect throughout development in comparison to young adulthood, is currently not fully known. The goal of the current study was to examine whether spatial suppression surrounding the focus of visual attention is exhibited in younger age groups and, if so, to determine its developmental course. By examining when in development attentional suppression is observed, we also intended to examine the effectiveness of top-down attentional modulation across development.

Studies focusing on the development of top-down (feedback, intentional or goal-driven) or bottom-up (feedforward, reflexive) attentional processes have revealed differences in the maturation timeline of these processes. Visual search studies, for instance, have shown that bottom-up attentional processes are mature quite early in development, but that top-down processes are still developing in childhood. In difficult cases where the target shares features with the distractors, as in a conjunction search, children up to about 6 to 7 years of age are significantly slower at searching for the target (Donnelly et al., 2007; Trick & Enns, 1998; Woods et al., 2013). Under conditions where the target is more salient, however, and obviously different from distractors, young infants (Adler & Orprecio, 2006) and children (Donnelly et al., 2007; Merrill & Conners, 2013; Taylor, Chevalier, & Lobaugh 2003; Trick & Enns, 1998; Woods et al., 2013) can accurately search and locate a target much like adults. Studies using different tasks have also revealed findings that confirm the interpretation of late developing top-down attentional processes. For example, children have been found to be more vulnerable to capture by irrelevant stimuli than adults, presumably because their top-down attentional processes are still developing (Gaspelin, Margett-Jordan, & Ruthruff, 2015).

Such differential development is incorporated into models and frameworks of attentional development, which propose that early in development visual feedforward and low-level orienting processes are more dominant and as development progresses top-down feedback processes are strengthened (Atkinson, 2002; Amso & Scerif, 2015; Johnson, 1990). Studies on brain development have also pointed to differences in the maturation timeline of low-level feedforward (bottom-up) and feedback (top-down) processes. For instance, in a recent study, Farrant and Uddin (2015) used

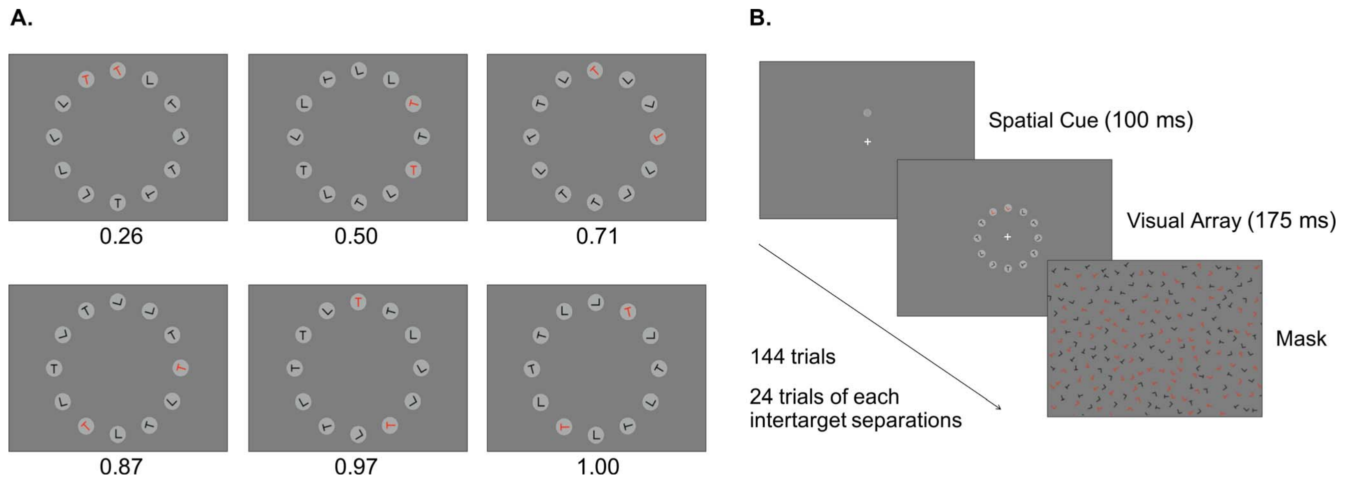

Figure 1. (A) Intertarget separations included in the experiment. At the largest intertarget separation distance, the distance was considered as 1.00. The smaller intertarget distances were considered as a fraction of the largest intertarget distance that it represents. (B) Temporal sequence of Experiment 1.

resting state fMRI to examine the development of two partially segregated attention networks, the dorsal attention network (DAN) and ventral attention network (VAN; Corbetta & Shulman, 2002), in children aged between 7 and 12 years. Each network includes different brain areas that are believed to play a different role in attention. The DAN exhibits activation when attention is focused, and is believed to be responsible for goal-driven top-down processing (Corbetta & Shulman, 2002). The VAN, in contrast, is generally activated in cases where bottom-up processing is active, such as when an unexpected event occurs and breaks an observer's attention from a given task (Corbetta & Shulman, 2002).

Farrant and Uddin (2015) found that for the DAN, children exhibited greater within-network connectivity (short-range functional connectivity) in comparison with 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 the VAN, children showed greater functional connectivity than adults (Farrant & Uddin, 2015). The authors suggested that this overconnectivity in the VAN provides evidence that bottom-up processes may be overrepresented in the children's brain and speculated that it can perhaps explain why children are susceptible to interruption by environmental stimuli and are less able to maintain activities requiring top-down attentional control (Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Gaspelin et al., 2015).

Of relevance, the frontoparietal regions in the DAN are believed to be the sources of attention biases onto the sensory cortex (i.e., visual cortex; Corbetta & Shulman, 2002; Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004), and therefore likely play an important role in the presentation of suppression surrounding the focus of attention. We therefore hypothesized that only young adults, adolescents, and perhaps pre-adolescents would exhibit attentional surround suppression. To test this hypothesis, we examined whether the separation distance between a spatially attended target and a second target affected visual discrimination across development. To this end, Cutzu and Tsotsos's (2003) psychophysical task with young adults was used in Experiment 1 with participants between the ages of 8 years to young adulthood (18+ years). Accuracy was expected to increase as a function of the separation distance between the targets for age groups exhibiting attentional surround suppression (see Figure 1 for the six intertarget separation distances included in Experiment 1 and the temporal sequence of a trial). In our control experiment, Experiment 2, an independent group of participants was tested with a central cue to assure that our findings in Experiment 1 were in fact related to spatial attention. In Experiment 3, we tested an independent group of children with slower task parameters to afford them with a more feasible task and to examine whether their top-down processes need more time to tune their visual system.

Materials and methods

Participants

For Experiments 1, 2, and 3, participants were recruited and tested at the Ontario Science Centre, which provided access to a large and diverse developmental population. For our young adult groups, Undergraduate Research Participant Pool students at

Age groups	Participants	Mean age	Gender
Experiment 1 ($n = 180$)			
Young adults	28	19.75 (18.00–27.34)	Female = 17, Male = 11
Older adolescents	31	16.95 (16.05–17.84)	Female = 21, Male = 10
Younger adolescents	25	14.75 (14.10–15.89)	Female = 7, Male = 18
Pre-adolescents	36	12.80 (12.05–13.89)	Female = 15, Male = 21
Older children	29	10.76 (10.03–11.88)	Female = 6, Male = 23
Younger children	31	8.81 (8.01–9.90)	Female = 16, Male = 15
Experiment 2 ($n = 164$)			
Young adults	19	23.31 (18.01–23.31)	Female = 10, Male = 9
Older adolescents	24	16.95 (16.17–17.96)	Female = 11, Male = 13
Younger adolescents	28	14.68 (14.05–15.93)	Female = 16, Male = 12
Pre-adolescents	31	12.85 (12.01–13.95)	Female = 16, Male = 11
Older children	37	10.61 (10.11–11.87)	Female = 16, Male = 21
Younger children	25	8.73 (8.12–9.99)	Female = 12, Male = 13
Experiment 3 ($n = 57$)			
Older children	30	11.12 (10.08–11.97)	Female = 15, Male = 16
Younger children	27	8.72 (8.03–9.89)	Female = 18, Male = 9

Table 1. General demographics information of participants in Experiments 1, 2, and 3. *Notes*: Participants = number of participants included; Mean age = average age in years.

York University were also recruited to participate in the study. Written consent was obtained from all young adults who participated in the study. Verbal assent was provided by the younger participants (legal minors) and written consent was obtained from their parents or legal guardian. The study was approved by the Office of Research Ethics at York University. The general demographic information of all age groups in all three experiments is presented in Table 1.

Experiment 1: Visual discrimination as a function of distance from the focus of attention

This experiment assessed whether a ring of suppression surrounding an attended item is observed in young adults and younger age groups. We replicated the first experiment of Cutzu and Tsotsos's (2003) psychophysical study, but with both young adults and developmental age groups. Participants aged between 8 and 27 years ($n = 180$) were required to detect two red letter character targets (Target 1 and Target 2) from among black letter distractors and report whether the targets were identical (L-L and T-T) or different (L-T or T-L).

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. Participants were instructed to register their decision whether Target 1 and Target 2 were identical (L-L or T-T) or different (T-L or L-T), irrespective of their orientation, by pressing one of two keys on the keyboard connected to the mounted laptop. A two-alternative forced-choice (2AFC) method was used, in which participants were told that they had to make the choice between identical or different for each trial.

Throughout the entire task there was a white cross, the size of 0.6° in visual angle, at the center of the screen. Participants were instructed to maintain fixation on the cross while they completed the task. The participants' spatial attention was cued to one of the two letter targets (Target 1). 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. Visual discrimination was therefore expected to improve as a function of intertarget separation—that is, the distance between Target 1 and Target 2, as a consequence of a lessening of spatial surround suppression as the distance from the attended location increased. All participants were told about the spatial cue and its benefits during the instruction and practice.

The experimental sequence began with the cue, a light gray disk, which was briefly displayed and anticipated the location of the first target. The cue was presented for a duration of 100 ms and was valid on all trials. Following the cue, the visual array was displayed and consisted of six randomly oriented Ls and six 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 4° and the character size was 0.6° 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 color to the cue disk. Two of the letter characters were red, one of which was the cued target, Target 1, while the remainder of the characters were black. The distances between the two target letters varied among six values of intertarget separation distances. The intertarget separation distances varied from where targets were neighbors, to where two targets were diametrically opposite, with five distractor characters between them. The intertarget distances were measured as a line segment between Target 1 and Target 2. At the largest intertarget separation distance, the distance was considered 1.00. The smaller intertarget distances were considered as a fraction of the largest intertarget distance that it represents. The orientation of the line segment connecting Target 1 and Target 2 was random across all trials. Figure 1A and B depicts examples of the six intertarget separation distances included in this experiment and the temporal sequence of a trial, respectively.

Participants were given three blocks of practice trials. For the first block, the visual array was on for 500 ms, for the second, 250 ms, and finally for the third, 175 ms. The decreasing duration of the visual array presentation during practice was found in pilot testing to greatly help younger age groups understand the task. During the instruction and practice phase, it was assured that all participants were able to identify the difference in the L stimuli and T stimuli. This was specifically important for the children participating in the study. To this end, prior to the start of the practice trials, all participants were shown examples of the targets in varying orientations and were told which combinations are considered identical and different. Participants were subsequently presented with another small set of example targets and were asked whether they should be considered as identical or different. Only if the participants understood the goal of the task, as evidenced by their correct judgments of whether the targets were identical (L-L or T-T, irrespective of their orientation) or different (T-L or L-T, irrespective of their orientation), would the session proceed. 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 intertarget separations were presented a total of 24 times, with 12 of those times being in the identical targets condition (L-L or T-T, six times each) and 12 times in the different targets condition (L-T or T-L, six times each). Trials were divided into four blocks. This provided the participants a short break in between each block and assured that all the participants remained focused on the task throughout the entire experiment. During the pilot phase of this study, a group of 6- to 7-year-olds were tested ($n = 18$), but they were unable to properly complete the task (e.g., could not complete all blocks, could not maintain focus, etc.) and were therefore excluded from the final study.

The participants' discrimination accuracy, defined as the proportion of correct responses (number of correct trials / total number of trials), were computed for all six intertarget separation values for analysis.

Experiment 2: Control experiment

In this experiment, an independent group of participants aged between 8 and 23 years ($n = 164$) were tested on a similar paradigm as in Experiment 1, with the exception of a central cue being presented instead of a spatial cue. This experiment was included to verify whether the results of Experiment 1 were in fact a consequence of spatial attention.

Experiment 3: Slower task parameters for children (8–11 years)

In Experiment 3, yet another independent group of 8- to 11-year-olds ($n = 57$) were tested on a modified version of the Experiment 1 paradigm, where the cue presentation time was doubled. All other task parameters remained the same as the Experiment 1 task. Experiment 3 allowed us to examine whether top-down feedback processes in 8- to 11-year-olds require more time in order to optimize the visual processing of attended stimuli and suppress the processing of surrounding stimuli.

Results

Experiment 1: Visual discrimination as a Function of Distance from The Focus of Attention

A 6 × 6 mixed-effects analysis of variance (ANOVA) was conducted with age group (8–9, 10–11, 12–13, 14–15, 16–17 and 18+ years) and intertarget separation distance between the spatially cued target and the second target (0.26, 0.50, 0.71, 0.87, 0.97, 1.00) as factors, and accuracy as the dependent variable. Analyses were conducted in R statistical software (R Core Team, 2013). The main effect of age group on accuracy was not significant, $F(5, 174) = 2.23$, $p > 0.05$. The main effect of intertarget separation was significant, $F(5, 870) = 7.26$, $p < 0.0001$. The interaction of age group and intertarget separation was also significant, $F(25, 870) = 1.73$, $p < 0.05$.

Bonferroni corrected post hoc analyses demonstrated that collapsed across age group, participants' accuracy at 0.26 ($M = 0.57$, $SD = 0.11$) was significantly lower than at 0.87 ($M = 0.59$, $SD = 0.13$), 0.97 ($M = 0.64$, $SD = 0.14$), and 1.00 ($M = 0.65$, $SD = 0.13$; $p < 0.01$). Participants' accuracy at 0.50 ($M = 0.56$, $SD = 0.12$) was also significantly lower than at 0.87 ($M = 0.59$, $SD = 0.13$), 0.97 ($M = 0.64$, $SD = 0.14$), and 1.00 ($M = 0.65$, $SD = 0.13$; $p < 0.01$).

The breakdown of the significant interaction of age group and intertarget separation was examined in separate repeated-measures ANOVAs for each age group. The analyses were conducted using the linear mixed-effects function. Intertarget separation was set as a fixed variable and subject as a random variable. This interaction breakdown was important to determine whether any of the specific age groups exhibited spatial suppression surrounding the focus of attention, a question that could not be answered with the omnibus ANOVA. To further examine the hypothesis that accuracy is affected, and in fact improves as a function of intertarget separation, a linear regression analysis of the dependence of accuracy on intertarget separation was also performed. The specific results are reported below.

Visual discrimination accuracy increased as a function of intertarget separation only in the 12- to 22-year-olds but not in 8- to 11-year-olds, suggesting that spatial suppression surrounding the focus of attention is only observed in the older developmental age groups. However, unlike in young adults where accuracy gradually increased as a function of intertarget 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. This finding is surprising given that it suggests that the suppressive surround may encompass a larger area in 12- to 17-year-olds. The 8- to 11-year-olds did not exhibit any differences in accuracy across intertarget separation. Figure 2A depicts each age group's mean visual discrimination accuracy across intertarget separation for Experiment 1.

Young adults (18–22 years)

Accuracy improved with increasing intertarget separation in the young adults, increasing from approximately 60% when the targets were immediately adjacent to about 72% when diametrically opposite. Notably, the accuracy values and shape of the accuracy curve across intertarget separation of the adults in the current study (Figure 2A) were similar to what was reported in the Cutzu and Tsotsos (2003) study.

The repeated-measures ANOVA revealed a significant main effect of intertarget separation on accuracy, $F(5, 135) = 11.33$, $p < 0.0001$. Bonferroni-corrected post hoc tests revealed that young adults' accuracy was significantly lower at the minimum intertarget separation of 0.26 ($M = 0.60$, $SD = 0.07$) compared with separations of 0.71 ($M = 0.67$, $SD = 0.10$), 0.87 ($M = 0.70$, $SD = 0.11$), 0.97 ($M = 0.71$, $SD = 0.11$), and 1.00 ($M = 0.72$, $SD = 0.11$; $p < 0.001$ for 0.26 compared with 0.71 and $p < 0.0001$ for all other comparisons). Accuracy was also lower at the intertarget separation 0.50 ($M = 0.62$, $SD = 0.11$) compared with 0.87 ($M = 0.70$, $SD = 0.11$), 0.97 ($M = 0.71$, $SD = 0.11$), and 1.00 ($M = 0.72$, $SD = 0.11$; $p < 0.01$).

The linear regression model was significant, $F(5, 162) = 6.20$, $p < 0.0001$, indicating that the null hypothesis of all the slope coefficients being equal to 0 can be rejected. In young adults, accuracy therefore increased as a function of intertarget separation. The R^2 statistic of the linear regression model was $R^2 = 0.16$, which as an index of effect size represents a medium effect (Cohen, 1988).

Older adolescents (16–17 years)

Accuracy in 16- to 17-year-olds improved with increasing intertarget separation, increasing from approximately 58% when the targets were immediately adjacent to 70% when diametrically opposite. The repeated-measures ANOVA revealed a significant main effect of intertarget separation on accuracy, $F(5, 150) = 9.50$, $p < 0.0001$. Bonferroni-corrected post hoc tests revealed that the 16- to 17-year-olds' accuracy was significantly lower at the minimum intertarget separation of 0.26 ($M = 0.58$, $SD = 0.12$) compared with separations of 0.97 ($M = 0.69$, $SD = 0.13$) and 1.00 ($M = 0.70$, $SD = 0.12$; $p < 0.0001$). Accuracy was lower at intertarget separation 0.50 ($M = 0.59$, $SD = 0.11$) compared with 0.97 ($M = 0.69$, $SD = 0.13$) and 1.00 ($M = 0.70$, $SD = 0.12$; $p < 0.001$). Accuracy was also lower at 0.71 ($M = 0.59$, $SD = 0.13$) compared with 0.97 ($M = 0.69$, $SD = 0.13$) and 1.00 ($M = 0.70$, $SD = 0.12$; all p values < 0.001).

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. In 15- to 16-year-olds, accuracy therefore increased as a function of intertarget separation. The R^2 statistic of the linear regression model was $R^2 = 0.15$, which as an index of effect size represents a medium effect (Cohen, 1988).

Younger adolescents (14–15 years)

Accuracy in 14- to 15-year-olds improved with increasing intertarget separation, increasing from 60%

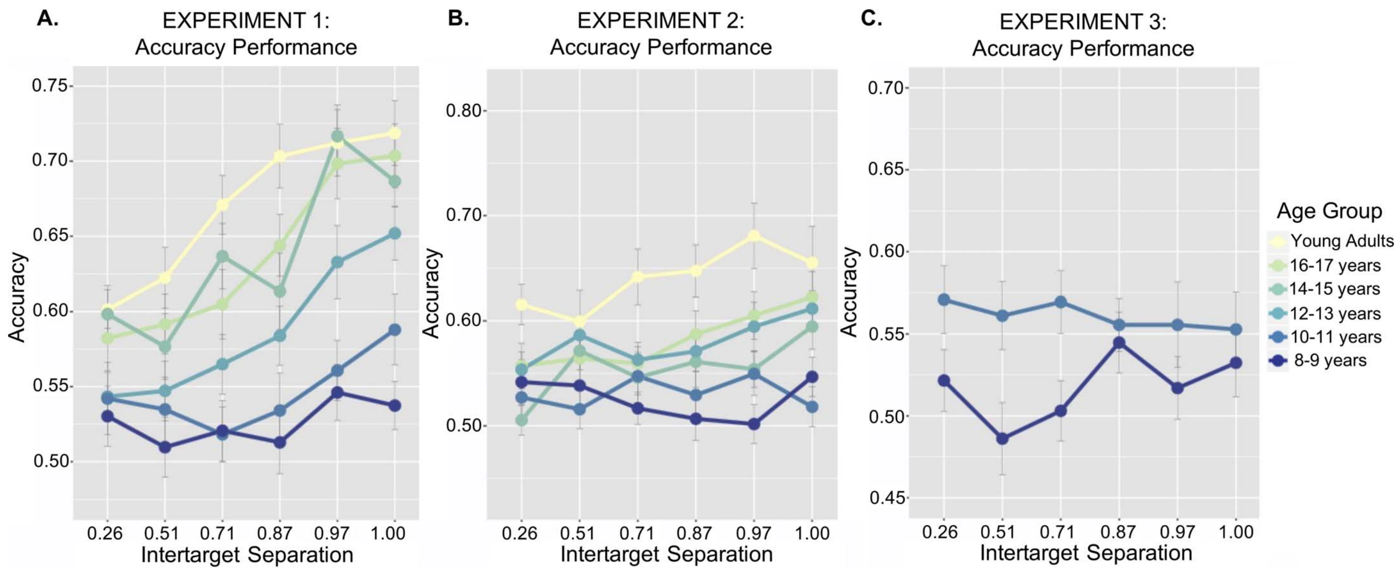

Figure 2. (A) Visual discrimination accuracy of all ages in Experiment 1. Mean visual discrimination accuracies for each intertarget separation are depicted by age group (total $n = 180$). Visual discrimination accuracy significantly increased as a function of intertarget separation in the 12- to 17-year-olds and the young adults. However, in the 12- to 17-year-olds accuracy improvements were mainly observed when the targets were largely separated such as for the intertarget separations of 0.97 and 1.00. Intertarget separation did not affect accuracy in the 8- to 11-year-olds. The error bars indicate standard errors. (B) Visual discrimination accuracy of all ages in Experiment 2. Mean visual discrimination accuracies for each intertarget separation are depicted by age group (total $n = 160$). Unlike in Experiment 1, visual discrimination accuracy did not increase as a function of intertarget separation. The error bars indicate standard errors. (C) Visual discrimination accuracy of the 8- to 11-year-olds in Experiment 3. Mean visual discrimination accuracies for each intertarget separation are depicted by age group (total $n = 57$). Visual discrimination accuracy was not affected by intertarget separation. The error bars indicate standard errors.

when the targets were immediate neighbors to about 69% when diametrically opposite. The repeated-measures ANOVA revealed a significant main effect of intertarget separation on accuracy, $F(5, 120) = 9.32$, $p < 0.0001$. Bonferroni-corrected post hoc tests revealed that participants' accuracy was significantly lower at the minimum intertarget separation of 0.26 ($M = 0.59$, $SD = 0.09$) compared with separations of 0.97 ($M = 0.72$, $SD = 0.10$) and 1.00 ($M = 0.69$, $SD = 0.09$; $p < .001$). Accuracy was lower at intertarget separation 0.50 ($M = 0.57$, $SD = 0.10$) compared with accuracy at 0.97 ($M = 0.72$, $SD = 0.10$) and 1.00 ($M = 0.69$, $SD = 0.09$; $p < 0.05$). Accuracy was lower at 0.71 ($M = 0.64$, $SD = 0.11$) compared with 0.97 ($M = 0.71$, $SD = 0.10$). Accuracy was also lower at 0.87 ($M = 0.61$, $SD = 0.13$) compared with 0.97 ($M = 0.72$, $SD = 0.10$) and 1.00 ($M = 0.69$, $SD = 0.09$; $p < 0.05$).

The linear regression model was significant, $F(5, 120) = 7.85$, $p < 0.0001$, indicating that the null hypothesis of all the slope coefficients being equal to 0 can be rejected. In 14- to 15-year-olds, accuracy therefore increases as a function of intertarget separation. The R^2 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).

Pre-adolescents (12–13 years)

Accuracy in 12- to 13-year-olds improved with increasing intertarget separation, increasing from 54% when the targets were immediate neighbors to about 65% when diametrically opposite. The repeated-measures ANOVA revealed a significant main effect of intertarget separation on accuracy, $F(5, 175) = 7.26$, $p < 0.0001$. Bonferroni-corrected post hoc tests revealed that the 12- to 13-year-olds' accuracy was significantly lower at the minimum intertarget separation of 0.26 ($M = 0.54$, $SD = 0.10$) compared with separations of 0.97 ($M = 0.63$, $SD = 0.14$) and 1.00 ($M = 0.65$, $SD = 0.11$; $p < 0.001$ for both comparisons). Accuracy was lower at intertarget separation 0.50 ($M = 0.56$, $SD = 0.10$) compared with of 0.97 ($M = 0.63$, $SD = 0.14$) and 1.00 ($M = 0.65$, $SD = 0.11$; both at $p < 0.001$). Accuracy was also lower at 0.71 ($M = 0.57$, $SD = 0.11$) compared with 1.00 ($M = 0.65$, $SD = 0.11$; $p < 0.01$).

The linear regression model was significant, $F(5, 210) = 5.27$, $p < 0.001$, indicating that the null hypothesis of all the slope coefficients being equal to 0 can be rejected. In 12- to 13-year-olds, accuracy therefore increased as a function of intertarget separation. The R^2 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).

Older children (10–11 years)

Accuracy in 10- to 11-year-olds remained at around 55% (range = 52%–59%) and did not improve with increasing intertarget separation.[2] The repeated-measures ANOVA showed no significant main effect of intertarget separation on accuracy, $F(5, 140) = 1.81$, $p > 0.05$. The linear regression model was not significant, $F(5, 168) = 1.23$, $p > 0.05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 could not be rejected. The R^2 statistic of the linear regression model was $R^2 = 0.04$.

Younger children (8–9 years)

Accuracy in 8- to 9-year-olds remained at around 53% (range = 51%–55%) and did not improve with increasing intertarget separation.[3] The repeated-measures ANOVA showed no significant main effect of intertarget separation on accuracy, $F(5, 150) = 0.58$, $p > 0.05$. The linear regression model was not significant, $F(5, 150) = 1.80$, $p > 0.05$, indicating that the null hypothesis of all the slope coefficients being equal to 0 cannot be rejected. The R^2 statistic of the linear regression model was $R^2 = 0.01$.

Experiment 2: Control experiment

In Experiment 2, when the cue was presented centrally and no longer directed attention to the location of one of the targets, accuracy was not affected by intertarget separation. This strongly suggests that the spatial suppression exhibited by participants in Experiment 1 was related to the focus of attention. Figure 2B depicts each age group's mean visual discrimination accuracy across intertarget separation in Experiment 2.

A 6 × 6 mixed-effects ANOVA was conducted with age group (8–9, 10–11, 12–13, 14–15, 16–17, and 18+ years) and intertarget 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, $F(5, 158) = 2.57$, $p < 0.05$. The main effect of intertarget separation was not significant, $F(5, 790) = 1.61$, $p > 0.05$. The interaction of age group and intertarget separation was also not significant, $F(25, 790) = 1.73$, $p > 0.05$.

Bonferroni-corrected post hoc analyses demonstrated that collapsed across intertarget separation, the young adults ($M = 0.64$, $SD = 0.12$) performed significantly greater than the 14- to 15-year-olds ($M = 0.56$, $SD = 0.11$; $p < 0.05$). No other age group comparison was significant. Therefore, we believe that the significant difference in accuracy between young adults and 14- to 15-year-olds is likely not developmental in nature and instead sampling error.

Experiment 3: Slower task parameters for children (8–11 years)

Doubling the cue presentation time did not lead to the exhibition of spatial suppression surrounding the focus of attention in 8- to 11-year-olds, suggesting that the lack of surround suppression at these ages in Experiment 1 was not due to insufficient time for attentional feedback processes to have an impact. Figure 2C depicts each age group's mean visual discrimination accuracy across intertarget separation.

A 2 × 6 mixed-effects ANOVA was conducted with age group (8–9 and 10–11 years) and intertarget separation (0.26, 0.50, 0.71, 0.87, 0.97, 1.00) as factors, and accuracy as the dependent variable. Neither the main effect of age group, $F(1, 55) = 2.88$, $p > 0.05$, nor intertarget separation, $F(5, 275) = 0.19$, $p > 0.05$, were significant. The interaction of age group and intertarget separation was also not significant, $F(25, 275) = 0.95$, $p > 0.05$.

Discussion

In adulthood, that attentional feedback processes impact visual processing by modulating activity in the visual cortex has been well established (Hopf et al., 2012). Visual cortex activity modulation occurs due to top-down attentional selection pruning forward-projecting units or neurons not representing relevant input, which as a consequence gives rise to suppression surrounding the focus of attention (Tsotsos, 2002). In development, these attentional mechanisms are even more critical because it is a time period during which an immense amount of learning and psychological change is taking place. Understanding the development of attention and more specifically the development of top-down attentional projections is therefore important to better understand how the typically developing brain processes visual information. Indeed, if the role of attention is to bring important information into focus while filtering out irrelevant information (Driver, 2001), then considering how an immature or a less-than-fully developed version of this process impacts visual processing and subsequently learning, is of relevance to any theory of development. The current study examined whether attentional surround suppression, a predicted by-product of top-down attentional modulation, is observed across a wide developmental age range. The current findings show that spatial attention similarly influences visual processing in young adulthood and older developmental age groups. Spatial suppression surrounding the focus of attention was observed in young adults, adolescents, and pre-adolescents, as predicted by studies of top-down attentional development.

According to the ST model (Tsotsos, 1995), selective attention is viewed as a top-down, hierarchical, competitive process realized using a winner-take-all process, 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. As a result, the selected stimulus in the input layer—for instance, the spatial location of the cued target for Experiment 1—repropagates through the network and is processed by neurons without the distracting effects of surrounding stimuli. The eliminated or pruned projections of the neurons not representing the selected target stimulus form the suppressive surround. In adulthood, ST provides a solution for the signal interference problem in the visual system caused by receptive fields that 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 and 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, 1993), specifically ameliorating this interference problem with the recurrent surround suppression mechanism. In the current study, ST's explanation can likely be applied to preadolescents and adolescents, who also exhibited attention-modulated surround suppression. In the current study, not only did ST provide a framework for an examination of top-down attentional development, it could also be used to correctly predict that preadolescents to young adults, whose top-down attentional mechanisms are nearly mature or mature, would exhibit suppression surrounding the focus of attention.

The lack of an intertarget separation effect on accuracy when a central cue was used (Experiment 2), confirmed that our findings of surround suppression when a spatial cue was used (Experiment 1), were indeed related to spatial attention. In Experiment 2, a centrally presented cue presumably lead to the suppressive surround manifesting around the center of the screen. Therefore, the targets and distractors would be equally partially suppressed, and suppression would thus not vary across intertarget separation. In Experiment 1, 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 intertarget separation 0.26 and the targets are side by side, it falls in the suppressive surround and becomes difficult to visually discriminate.

Neural development and visual attention

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). That in the current study attentional surround suppression was only observed in the young adults and older developmental age groups is consistent with these theoretical frameworks. In adults, long-range functional connectivity between the DAN, a neural network activated when top-down attention is focused, 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 immature top-down feedback projections that are not as strongly connected to further afield cortical regions. Indeed previous research has demonstrated that in children under the age of 12 years, the DAN 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 also shown that the maturity of structural connectivity is protracted, continuing into adulthood. In a longitudinal study, Lebel and Beaulieu (2011) used diffusion tensor imaging 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 20s (Lebel & Beaulieu, 2011). These association tracts connecting the frontal areas to other brain regions support complex cognitive function such as inhibition, executive function, and importantly, attention (Blakemore & Choudhury, 2006; Jung & Haier, 2007; Lebel & Beaulieu, 2011; Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005). In the context of the current study, it can therefore be speculated that these diffusion tensor imaging 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 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, 2002). White matter volume continues to increase with age during childhood and adolescence, 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 are only about 1.37% per year (Sowell et al., 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.

But, for the pre-adolescents and adolescents, why did they exhibit a greater area of spatial suppression surrounding their focus of attention in comparison to adults? In adolescence functional activation is more spatially diffuse between frontal and parietal regions, whereas in adults activation is more focal and fine-tuned within the fronto-parietal network (Durston et al., 2006; Konrad et al., 2005). 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 toward more focal functional activation is believed to be a result of synaptic pruning, which improves the signal-to-noise ratio in the neural system and strengthens relevant connections (Durston et al., 2006). Perhaps in the current study, 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 as 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.

More research is needed to specify the neural mechanisms that contribute to the lack of and reduced attentional surround suppression observed in developmental age groups.

Development of top-down attention

Our findings illustrate a developmental timeline for the expression of attentional surround suppression and converge well with previous research that would implicate a protracted maturation of top-down attention mechanisms as a cause for that development. Visual search studies, for instance, have shown that despite bottom-up attentional mechanisms maturing early in development (Adler & Orprecio, 2005; Donnelly et al., 2007; Merrill & Conners, 2013; Taylor et al., 2003; Trick & Enns, 1998; Woods et al., 2013), top-down mechanisms are still developing in childhood (Donnelly et al., 2007; Trick & Enns, 1998; Woods et al., 2013). The maturation of executive attention, the process of resolving conflict between competing inputs for the purpose of a goal-driven task (Posner & Petersen, 1990), is also slow. Executive attention does not become more adult-like until approximately 14 years of age (Luna, Garver, Urban, Lazar, & Sweeney, 2000). Our findings provide further support for the interpretation of late developing top-down attentional processes, by showing that surround suppression, a predicted by-product of top-down attentional modulation on visual processing, is not present in children under the age of 12 years.

Models of visual attention development have proposed that early in development visual feedforward and low-level orienting mechanisms are more dominant, while top-down feedback processes are strengthened throughout development (Amso & Scerif, 2015; Atkinson, 2000; Johnson, 1990). Consequently, in younger age groups, feedforward mechanisms are believed to be more heavily relied upon (Amso & Scerif, 2015), which can account for why the children in the current study did not exhibit attentional surround suppression, even when their attention mechanisms were given more time to tune their visual system. Importantly, an overreliance on feedforward processes can also explain other development findings. 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). As previously discussed, the VAN, an attention network activated in cases where bottom-up processing is taking place, shows greater functional connectivity in children in comparison to adults (Farrant & Uddin, 2015). One possibility as to why a reliance of feedforward processes in children is beneficial or necessary at younger ages is that it enables the detection of salient stimuli, which phylogenetically was important for survival (Farrant & Uddin, 2015). Throughout development, as top-down feedback processes mature, greater top-down attentional modulation takes place.

Having a better understanding of when and how attentional mechanisms develop and their effects on visual processing in development is not just of theoretical importance, it also has practical relevance as well. 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). Having a better understanding of when top-down attentional processes develop and how immature attentional mechanisms impact visual and cognitive processes can therefore have major pedagogical implications.

From a clinical perspective, pervasive neurodevelopmental disorders such as Autism Spectrum Disorder (ASD) have been found to not only consist of social-communicative and behavioral impairments (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). Indeed, the previously mentioned study by Ronconi and colleagues (2018) found that typically developing adolescents (mean age of 14) exhibit suppression surrounding their focus of attention. In comparison to the typically developing adolescents, however, ASD adolescents exhibited weaker attentional surround suppression. In a second experiment, Ronconi et al. (2018) used dense-array electroencephalography 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 et al., 2009) and time (Ronconi, Pincham, Cristoforetti, Facoetti, & Szűcs, 2016), was suppressed 300 ms after an attentional probe for targets appearing in the surround of the attentional focus. In contrast, the ASD children did not exhibit the N2 effect, highlighting their deficits in inhibiting visual information outside the focus of attention.

The fact that an attentional surround-modulated N2 effect in 11-year-olds was observed 300 ms after an attention probe in the Ronconi and colleagues' (2018) study, raises the question of whether the temporal parameters used in our study made the tasks too difficult for the younger children to complete, admittedly a potential limitation of our current study. Increasing the cue time in Experiment 3 was meant to overcome this limitation by providing the younger participants with more time for feedback processes to be completed, but instead, perhaps increasing the visual array duration is what is necessary to make the task more feasible for them. For instance, keeping the spatial cue duration at 100 ms and increasing the duration of the visual array from 175 to 250 ms 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 ms would allocate close to the 300 ms for the top-down processes to complete before the response mask. After all, the attentional surround-modulated N2 effect in the 11-year-olds of Ronconi et al. (2018) study was observed 300 ms after the attention probe. In a subsequent study, therefore, 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 can 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.

Other considerations for a better delineation of the development of surround suppression would be to examine whether the phenomenon 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 (5–12 years) and adults (Gomez, Natu, Jeska, Barnett, & Grill-Spector, 2018). And, in the current study, the visual array projected onto 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, 1984), and that low level visual abilities such as spatial acuity (Lai, Wang, & Hsu, 2011; Norcia & Tyler, 1985), contrast sensitivity (Almoqbel, Irving, & Leat, 2017), and orientation discrimination (Jeon, Hamid, Maurer, & Lewis, 2010; Lewis, Kingdon, Ellemberg, & Maurer, 2007) are adult-like by the age of 8 years, the youngest age group featured in the current study. However, the possibility exists that larger and more salient stimuli could have made the task more feasible for the younger children. This is especially plausible, 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). However, we expect that potentially reducing crowding would only improve the overall performance of younger age groups and not impact the effect of attentional surround suppression on visual discrimination accuracy for several reasons. First, the distance between each individual letter and circle it is overlaid on in our stimuli was larger (1.26° visual angle) than the documented distance (7.84 arcmin or 0.13° visual angle) where crowding effects have been observed in the youngest age group included in our study. Secondly, attentional surround suppression, as indexed in the current study by discrimination accuracy increasing as a function of the separation distance between an attended target and a second target, is likely distinct from pure crowding effects. In Experiment 1, the distance between the targets and any of the surrounding distractors (black letters) was the same for each intertarget separation, and as a result, the potential level of crowding would not have varied across intertarget separation. Additionally, if crowding was the primary factor impacting the participants' performance in the current study, it would be expected that intertarget separation would also impact discrimination accuracy when attention is not spatially allocated as in Experiment 2, but this was not observed in our findings. Finally, crowding effects have been found to be reduced under condition of spatially focused attention. For instance, when attention is spatially directed to the target location via peripheral cues, visual discrimination performance in crowded displays is improved (Huckauf & Heller, 2002; Yeshurun & Rashal, 2010). Altogether, this suggests that crowding is likely not a primary factor driving the findings of the current study.

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 a more appropriate task for younger age groups may reveal different findings. For example, the orientation discrimination task used in the MEG study by Hopf and colleagues' (2006) may be slightly simpler, since there is only one target. Using this task with younger age groups could also allow for further examination of the attentional profile of attention across development. Further, by using neuro techniques, possible neurophysiological mechanisms underlying the developmental differences in attentional surround suppression could be uncovered. It would be compelling to examine whether MEG results in adolescents, for example, would mimic the current psychophysical findings of greater suppression in this age group.

Conclusions

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

Attention is undoubtedly important 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 information to access conscious perception and explicit memory (Shim, Alvarez & Jiang, 2008). In development, attention is likely even more critical because it is a period of time during which an immense amount of learning and psychological change is taking place. Understanding the development of attention and more specifically the development of top-down attentional 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 function differently in childhood.

Our findings show that younger children may have more difficulty processing visual information surrounded by clutter, which may have potential implications for a wide array of disciplines. For instance from a clinical perspective, further characterization of the typical development of suppression surrounding the focus of attention can be informative of atypical development in clinical populations and can potentially be used as a diagnostic tool for disorders with visual sensory deficits, such as ASD. Finally, the current findings may also have potential implications for machine learning algorithms and the field of artificial intelligence. Deep learning networks have been successful in yielding state-of-the-art image recognition and have done so through a hierarchical organization of feature extraction similar to the cortical layers of the human visual system (Cadieu et al., 2014), lending support to its applicability to understand human vision and its relevance to artificial intelligence. However, natural training and visual experience occurring in human development is very different from the training data fed into current machine learning systems (Smith & Slone, 2017). For instance, unlike machine learning algorithms, human infants experience an egocentric view where not all items in the environment are in view and with many repeated occurrences of a very few items (Smith & Slone, 2017). If machine learning aims to mimic human learning, the current study highlights yet another important factor that should be taken into consideration—that developmental differences in this key mechanism of visual attention, and other perhaps interacting anatomical and physiological mechanisms of vision (Siu & Murphy, 2018), result in ever changing and diverse visual experiences or input across development, but despite this, visual learning and the maturity of the visual system still takes place.

Keywords: vision, attention, surround suppression, development, selective tuning

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Commercial relationships: none.
Corresponding author: Audrey M. B. Wong-Kee-You.
Email: audrey@ski.org.
Address: Smith-Kettlewell Eye Research Institute, San Francisco, CA, USA.

Footnotes

[1] Winner-take-all is a parallel algorithm that localizes the maximum value of a set (Koch & Ullman, 1985)
[2] Preliminary examination showed that more than half of 10- to 11-year-olds (62%) above chance in Experiment 1 (overall accuracy collapsed across intertarget separation above 51%).
[3] More than half 8- to 9-year-olds (58%) performed above chance in Experiment 1 (overall accuracy collapsed across intertarget separation above 51%).

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