On the Developmental Relationship between Visual Processing and Visual Attention: Examining Behavior and Functional Brain Connectivity

by

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Chapter 1: General Introduction

Visual selective attention develops over the first decade of human life (Amso & Scerif, 2015; Oakes & Amso, 2018). This selective process allows us to filter out irrelevant information in the service of our goals. As a consequence, It has been shown to be important for the development of object perception (Amso & Johnson, 2006), numerical cognition (Ansari, Lyons, van Eimeren, & Xu, 2007) and executive functions (Colombo & Cheatham, 2006; Fox & Calkins, 2003; Garon, Bryson, & Smith, 2008; Posner, Rothbart, & Rueda, 2014). Attention may be allocated to a specific location and/or visual feature, such as orientation, color and motion. In this way, attention binds an object's constituent visual features to its location in space and enhances visual perceptual processing at the attended location (Carrasco, 2011). Neurally, both visuo-spatial and feature-based attention influence cortical visual processing (Ling & Carrasco, 2006; Ling, Liu, & Carrasco, 2009) through feedback connections from higher-order brain regions (i.e., frontoparietal & high-level visual regions) (Bichot, Heard, DeGennaro, & Desimone, 2015; Chelazzi, Miller, Duncan, & Desimone, 2001). It follows that the integrity of visual processing may thus shape attentional allocation. Child development thus provides a unique window to examine this notion because visual processing, like visual attention, improves across childhood, both behaviorally and within the visual cortex (Gomez et al., 2019; Gomez, Natu, Jeska, Barnett, & Grill-Spector, 2018; Knoblauch, Vital-Durand, & Barbur, 2001; Leat, Yadav, & Irving, 2009). There has been little consideration for how developmental change in visual processing impacts the development and function of visual attention. Here, I examine visual attention development through the lens of visual processing. The hypothesis driving this work is that visual attention development maybe be driven by visual processing development across the first decade of life (Amso & Scerif, 2015; Kim & Kastner, 2019).

Visual features are processed in parallel across the visual field and visual attention binds these features to a specific location to support object perception (Treisman & Gelade, 1980). Parallel visual feature processing is demonstrated in ‘pop-out’ feature search where a search target defined by one feature value (e.g., red) is presented among homogenous distractors of a different feature value on the same dimension (e.g., green). In this case, the red target is processed preattentively and recognized quickly. However, attention is required in conjunction search where a search target, defined by two or more feature values (e.g., a red T), is presented among heterogeneous distractors of different feature value conjunctions from the same feature dimensions (e.g., red Ls and green Ts). Here, participants must integrate multiple visual features as they search amongst targets and distractors. During conjunction search, search times for the target increases with increases in distractor number and target recognition therefore takes time, suggesting stimuli are serially processed using feature integration.

Broadly, visual features are processed in relatively distinct, parallel cortical visual processing streams (Felleman & Van Essen, 1991; Ungerleider & Haxby, 1994; S. M. Zeki, 1978a). Whereas some visual features are processed in relatively distinct pathways, others are processed within the same pathway. Two of these, the dorsal and ventral visual pathways, support visuospatial and motion processing, and color and object processing, respectively. Both color and motion information are processed separately within striate visual cortex (V1) and are then routed to separate higher-level extrastriate cortical areas human visual region 4 (hV4) and human middle temporal area (hMT), respectively

(Gegenfurtner, 2003; Seymour, Clifford, Logothetis, & Bartels, 2009; Shipp & Zeki, 1995; Sincich & Horton, 2005). However, luminance information proceeds, with motion information, from striate cortex to hMT. Thus, feature integration may occur across separate visual pathways (e.g., color and motion) or within the same visual pathway (e.g., luminance and motion).

After an initial feedforward sweep, feedback connections from fronto-parietal and high-level visual processing regions combine signals from distinct visual processing streams (Rockland & Knutson, 2000; Rockland & Virga, 1989; S. Zeki & Shipp, 1988) and are thought to mediate the influence of top-down attention on visual processing (Chelazzi et al., 2001; McAdams & Maunsell, 2000; Motter, 1994). Adult non-human primate work shows that allocating attention to an object modulates feature-specific processing in hMT, hV4, and V1 (McAdams & Maunsell, 1999, 2000; Treue & Maunsell, 1996; Treue & Trujillo, 1999), and connectivity between striate and extrastriate regions, including between V1 and V4 (Bosman et al., 2012), between V1 and MT (Saproo & Serences, 2014), to support processing of an object's constituent visual features. This suggests that attention to different combinations of features may modulate connectivity between distinct regions that code distinct visual features (e.g., color, motion). One might predict that attention therefore modulates connectivity between the dorsal and ventral visual pathways (e.g., hV4, hMT). However, connectivity between these visual regions changes with age across childhood. While functional connectivity across the striate and extrastriate cortices is overall weaker in children relative to adults (Jolles, Van Buchem, Crone, & Rombouts, 2011), recent work suggest connectivity strength increases across childhood (Kipping, Tuan, Fortier, & Qiu, 2017). Non-human primate work suggests that *within* visual pathway functional connectivity changes across early development in a hierarchical, caudal-to-rostral manner (Kovacs-Blaint et al., 2018). Yet, it remains unclear whether functional connectivity *between* the dorsal and ventral visual pathways changes across childhood.

In the first study, I examined the development of dorsal and ventral visual pathway integration across middle childhood using a network-level approach to resting-state fMRI. Specifically, I tested whether connectivity between visual pathways changes across childhood (4 – 12 years old). I predicted that between pathway integration would develop differently than within pathway integration. I show that between pathway integration followed a non-linear developmental trajectory across childhood.

Behaviorally, children's visual search abilities resemble adult-like patterns of behavior, increases in RT with additional distractors for conjunction search, but not such increase with 'pop-out' feature search. Across childhood, overall processing speed improves and children become less influenced by increasing distractor number with age (decrease in RT slope) (Donnelly et al., 2007; Gerhardstein & Rovee-Collier, 2002; Lobaugh, Cole, & Rovet, 1998; Trick & Enns, 1998). This improvement occurs across middle childhood (7 to 10 years) for color and orientation conjunctions (e.g., oriented color bar; Donnelly et al., 2007) and luminance and shape (e.g., black circle; Merrill & Lookadoo, 2004). However, these studies examine conjunctions of visual features *within* the ventral visual pathway. One could then predict that integrating visual feature between the dorsal and ventral pathways might develop differently than within pathway integration.

In the second study, I examined the development of visual attention (4 – 10 years old) for feature combinations that may require integration between or within dorsal and

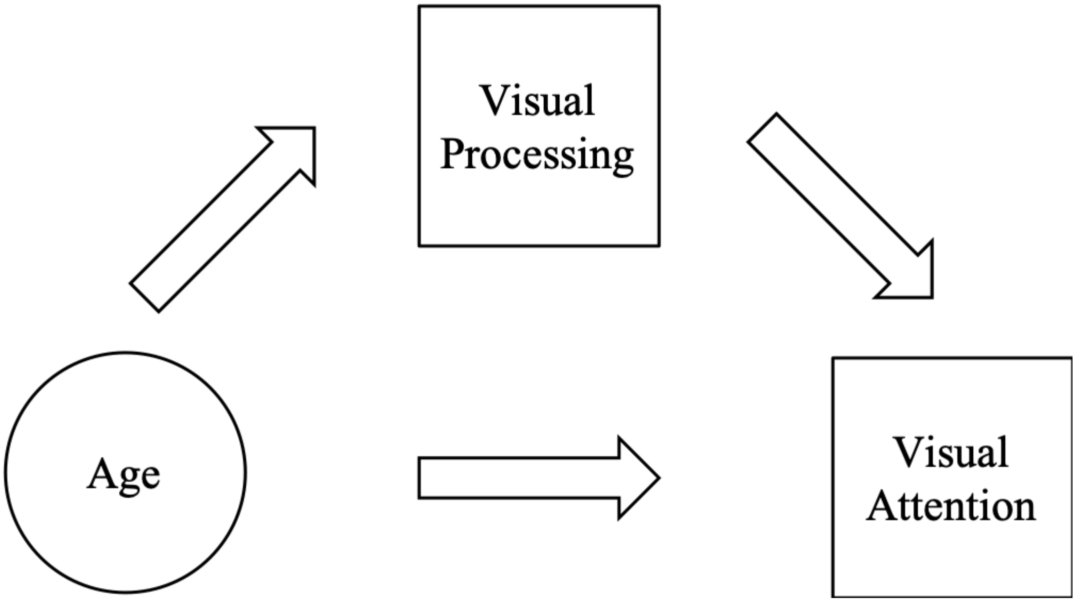

Figure 1. Developmental model of Visual Processing and Attention.

ventral pathways. Specifically, using a conjunction search task, I tested children's ability to search for color-motion and luminance-motion defined targets presented among varying number of distractors. I predicted that attention to targets whose features are coded in distinct visual pathways should develop differently relative to targets with feature coded within the same visual pathway. I show that feature integration and conjunction search for feature coded across the dorsal and ventral visual pathways may develop differently than for feature coded within the dorsal pathway.

Yet, it remains unclear whether improvements in visual feature processing, per se, underlie changes in visual attention across child development. Visual feature processing occurs at multiple levels of analysis across both the dorsal and ventral visual pathways. At a specific location within the visual field, stimulus-driven deviations in visual feature contrast (e.g., color, luminance) are coded within V1 and measured behaviorally as contrast sensitivity (Albrecht & Hamilton, 1982). Visual feature are coded at multiple scales across the visual field as receptive fields increase along the visual pathway (e.g., Albrecht &

Hamilton, 1982; Movshon, Thompson, & Tolhurst, 1978). During childhood, both chromatic and luminance contrast sensitivity improve with age (Almoqbel, Irving, & Leat, 2017; Knoblauch et al., 2001; for review see, Leat et al., 2009). Children also become faster with age to detect a pop-out search target defined by color, orientation, and size. (Donnelly et al., 2007; Gerhardstein & Rovee-Collier, 2002; Trick & Enns, 1998).

<u>In study three,</u> I examined the relationship between these improvements in visual feature processing and visual selective attention abilities across childhood (4 – 9 years old) for feature combinations that may require integration between or within dorsal and ventral pathways. For both color and luminance features I measured children's 1) contrast sensitivity, 2) pop-out feature search performance, and 3) conjunction search performance where children searched for color-motion or luminance-motion defined targets.

I first tested whether children's contrast sensitivity and 'pop-out' search performance improves with age and whether this developmental change depends on visual feature. Similar to Study 2, I then tested whether children's conjunction search abilities depend on visual feature combinations. Throughout visual search tasks I tested whether children's ability to integration motion with either color or luminance depended on the task goal (i.e., search for red target vs. search for moving red target). Lastly, I tested whether contrast sensitivity and feature integration predict conjunction search performance. I predicted that contrast sensitivity and pop-out search performance for both visual features would improve across childhood. Moreover, I predicted that contrast sensitivity and top-down feature integration abilities would influence conjunction search performance across childhood specifically for the color-motion condition, whose feature are presumable coded in distinct visual pathways.

Chapter 2

2. Characterizing developmental trajectories of dorsal-ventral visual pathway integration across childhood

2.1 Abstract

Functional brain networks change across the first decade of life. I aimed to characterize developmental changes in human cortical functional connectivity across childhood both *within and between* the dorsal and ventral visual pathways. I identified 6 visual networks including the dorsal and ventral visual pathways, as well as early visual regions, that reflected the underlying topographical and hierarchical organization of striate and extrastriate cortices. I found that only right dorsal network integration changed across childhood, with decreases from early to middle childhood and increases from middle to late childhood. This right dorsal network integration was driven by a change across childhood in the number of connections with the right ventral pathway as well as in the number of connections with early visual regions. This work has value for understanding developmental change in feature integration across dorsal and ventral visual pathways, and accordingly developmental improvements in visual attention.

2.2 Introduction

Visual attention improves and functional brain networks change across the first decade of life (Fransson, Åden, Blennow, & Lagercrantz, 2011; Gao et al., 2011; Hwang, Hallquist, & Luna, 2013; Marek, Hwang, Foran, Hallquist, & Luna, 2015; Oakes & Amso, 2018). A principle argument of the prominent Feature Integration Theory (FIT) is that an object's constituent visual features (e.g., shape, color, motion direction) are first processed separately but in parallel, and only integrated for the object's identification during subsequent attentive processing (Humphreys, 2016; Treisman & Gelade, 1980; Wolfe, 2014). Neurally, visual feature processing can be localized within distinct visual cortical pathways (e.g., ventral pathway for color, dorsal pathway for motion) (Felleman & Van Essen, 1991; Ungerleider & Haxby, 1994; S. M. Zeki, 1978a). Computationally, across a visual scene, visual salience models process constituent visual features within individual feature channels, which are subsequently integrated (e.g., Itti & Koch, 2001). Behaviorally, for both children (Lynn, Festa, Heindel, & Amso, 2020) and older adults (Festa et al., 2005), integration of visual features processed across the dorsal and ventral visual pathways is poorer than integration of visual features processed within a pathway. Moreover, recent works shows that patients with Alzheimer's Disease, which is characterized disrupted corticocortical connectivity, show greater behavioral disruption in binding feature across the dorsal and ventral pathways. Together, these data raise the possibility that functional connectivity *between* the dorsal and ventral visual pathways and *within* each pathway may follow different developmental trajectories. Here, I examine the development of functional integration of the dorsal and ventral visual pathways across childhood.

Adult human and non-human primate work shows that visual information is processed across a distributed set of hierarchically organized, parallel cortical pathways (e.g., Felleman & Van Essen, 1991; Ungerleider & Haxby, 1994; S. M. Zeki, 1978a). The dorsal and ventral pathways are thought to represent visuospatial and object processing, respectively (Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982). Small receptive fields represent simple, local visual features across striate cortex (V1) and increasingly larger receptive fields represent increasingly complex, global visual features across increasingly higher levels of the extrastriate cortex (e.g., V4, V5/MT+) (Hubel & Wiesel, 1974; A. T. Smith, 2001; S. M. Zeki, 1978b). Further, the strength of functional connectivity follows a topographic organization, such that striate regions are more strongly connected to extrastriate regions in a way that maintains visual field topography (Vincent et al., 2007; Wang, Mruczek, Arcaro, & Kastner, 2015). While the structural architecture of the visual cortex is established early in development (e.g., Baldwin, Kaskan, Zhang, Chino, & Kaas, 2012), cellular development across childhood is protracted (e.g., Huttenlocher & de Courten, 1987; Huttenlocher, de Courten, Garey, & Van der Loos, 1982). Characterizing developmental changes in functional connectivity throughout childhood may provide insight into how information in integrated across the striate and extrastriate cortex.

The connectomics literature often parcels whole brain functionally connectivity into networks thought to support self-referential thought (i.e., default mode network, DMN), cognitive control (i.e., frontoparietal network, FPN), motor control (i.e., sensorimotor network SMN), and attention (i.e., dorsal and ventral attention networks, DAN/VAN), as well as visual processing (i.e., visual network, VIS) (Power et al., 2011; Thomas Yeo et al., 2011). Functional network 'hubs', which underlie cortical information flow, shift from primary sensory cortex (i.e., visual cortex) in infancy to association cortex in childhood, where they remain throughout adolescence and adulthood (Fransson et al., 2011; Gao et al., 2011; Hwang et al., 2013). Across childhood and adolescence, information is transferred within and between functional networks with increasing efficiency (Collin & Van Den Heuvel, 2013; Supekar, Musen, & Menon, 2009). This is likely supported by decreases in network segregation and increases in network integration (Fair et al., 2007, 2009; Supekar et al., 2009; Vogel, Power, Petersen, & Schlaggar, 2010), potentially through changes in connectivity strength (Collin & Van Den Heuvel, 2013). Indeed, while functional networks show adult-like organization by late childhood, *within*-network connectivity decreases across childhood and adolescence, and *between*-network connectivity first decreases from childhood into adolescence and then increases from adolescence into adulthood (Hwang et al., 2013; Marek et al., 2015). However, this whole-brain network focus overlooks the development of functional connectivity across the dorsal and ventral visual pathways.

Functional connectivity across the striate and extrastriate cortices is weaker in children relative to adults (Jolles et al., 2011), but increases across childhood (Kipping et al., 2017). However, it is unclear whether these findings reflect changes between the dorsal and ventral visual pathways or within each pathway. Indeed, non-human primate work suggests that visual pathway functional connectivity changes across early development in a hierarchical, caudal-to-rostral manner (Kovacs-Blaint et al., 2018). Here, researchers longitudinally examined the development of the dorsal and ventral visual pathways from birth to 3 months in rhesus macaques. Within a given visual pathway, they found evidence of strong functional connectivity in caudal visual regions and poorer functional connectivity in rostral regions.

In the present study, I use graph theory to characterize developmental changes in human visual functional connectivity across childhood, both *within and between* the dorsal and ventral visual pathways. I first verified that the underlying functional connectivity mirrors the known structural and topological organization of cortical regions (e.g., Wang et al., 2015). I then tested whether between pathway functional integration would develops more slowly relative to within pathway integration.

2.3 Methods

2.3.1 Participants

Seventy-eight 4- to 12-year-old children (*M* = 7.17, *SD* = 2.37, 37 female) completed a neuroimaging battery including T1-weighted anatomical and resting-state scans. Data used in this study were drawn from the ongoing Brown University Assessment of Myelination and Behavioral development Across Maturation (BAMBAM) study of neurotypical brain and cognitive development. From the BAMBAM cohort, 78 children between 4 and 12 years of age were selected for inclusion in this study. Only children with known major risk factors for developmental abnormalities at enrollment were excluded. These included: *in utero* alcohol, cigarette or illicit substance exposure; Preterm (<37wks gestation) birth; small for gestational age or less than 1500g; fetal ultrasound abnormalities; preeclampsia, high blood pressure, or gestational diabetes; 5-minute APGAR scores <8; NICU admission; neurological disorder (e.g., seizure disorder); and psychiatric or learning disorder, parents or siblings (including maternal depression requiring medication in the year prior to pregnancy).

2.3.2 Data Acquisition and Preprocessing

Neuroimaging data were acquired on a 3T Siemens Trio scanner with a 12-channel head RF array. T_1-weighted magnetization-prepared rapid acquisition gradient echo anatomical data were acquired with an isotropic voxel volume of $1.2x1.2x1.2mm^3$, resampled to $0.9 \text{ x } 0.9 \text{ x } 0.9mm^3$ Sequence specific parameters were: TE=6.9ms;

TR=16ms; inversion preparation time=950ms; flip angle=15 degrees; BW=450Hz/Pixel. The acquisition matrix and field of view were varied according to child head size in order to maintain a constant voxel volume and spatial resolution across all ages (Dean et al., 2014).

Resting-state functional MRI (rsFMRI) data were acquired with eyes open and the following parameters: TE=34ms, TR=2.5s, flip angle=80 degrees, field of view=24x24cm^2, imaging matrix=80x80, and 32 interleaved 3.6mm slices (for a voxel resolution: 3x3x3.6mm^3). BW=751Hz/pixel, and GRAPPA acceleration factor of 2. I acquired approximately 164 volumes for a total acquisition time of about 7 minutes.

T_1-weighted magnetization-prepared rapid acquisition gradient echo anatomical data were acquired with an isotropic voxel volume of 1.2x1.2x1.2mm^3, resampled to 0.9 x 0,9 x 0.9mm^3 Sequence specific parameters were: TE=6.9ms; TR=16ms; inversion preparation time=950ms; flip angle=15 degrees; BW=450Hz/Pixel. The acquisition matrix and field of view were varied according to child head size in order to maintain a constant voxel volume and spatial resolution across all ages (Dean et al., 2014). Using a multistep registration procedure (O'Muircheartaigh et al., 2014), a series of study- and age-specific anatomical T_1-weighted templates were created corresponding to 48, 60, 72, 84, 96, 108 month ages. At least 10 boys and 10 girls were included in each template. An overall study template was then created from these age templates, which was aligned to the MNI152 template (Lancaster et al., 2007). Each child's anatomical T_1-weighted image was transformed into MNI space by first aligning to their age-appropriate template and then applying the pre-computed transformation to MNI space, with the calculated individual forward and reverse transformations saved and used for the volumetric analysis described below. All template creation and image alignment was performed using a 3D nonlinear approach (ANTS; Avants et al., 2014) with cross-correlation and mutual information cost functions. rsFMRI data were first registered to individuals T1 anatomical images using FSL FLIRT (S. M. Smith et al., 2004) and ANTS (Avants et al., 2014).

2.3.2.1 Nuisance regression and motion censoring. I used the CONN-fMRI toolbox for SPM 12 (Whitfield-Gabrieli & Nieto-Castanon, 2012) in MATLAB to denoise rsFMRI data. Using the implemented CompCor strategy (Behzadi, Restom, Liau, & Liu, 2007), the effect of nuisance covariates including BOLD signal fluctuations from CSF, white matter and their derivatives. Following previously established methods (Satterthwaite et al., 2013; Yan et al., 2013), I include 24-movement parameters derived from individual subject realignment (i.e., x, y, z, roll, pitch, yaw, derivatives, quadradic expansion). I also included global signal regression, including the derivative, and simultaneous band-pass filtering ($0.008<f<0.09$HZ). Finally, I censored ("scrubbed") volumes if there was significant motion during data acquisition (i.e., DVARS > 5 or FD were > .5) (Power et al., 2014).

2.3.3 Resting-State Functional Connectivity Processing

For each child, using CONN-fMRI toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012), I calculated Fisher-transformed bivariate correlation matrices for pairwise correlations of spontaneous BOLD activity between each region of interest (see below). When reported, individual matrices were thresholded at multiple network densities (1% - 25%, 1% steps) using the Brain Connectivity Toolbox (Rubinov & Sporns, 2010).

2.3.3.1 Visual network parcellation (Regions of Interest, ROI). I chose an adult-derived probabilistic atlas of topography (Wang et al., 2015). This adult atlas was first transformed to our child atlas using FSL FLIRT and FNIRT (S. M. Smith et al., 2004). I included right (R) and left (L) lateralized regions separately. I included bilateral dorsal-lateral and ventral-temporal regions only. Throughout I refer to TO1 as human middle-temporal complex (hMT) (Amano, Wandell, & Dumoulin, 2009) . Unfortunately, due to the initially small size of region temporal-occipital 2 (TO2), I decided against including this region because of interpolation restraints. This resulted in a total of 32 ROIs. These include 8 dorsal-lateral regions, bilaterally: V1 dorsal (V1d), V2d, V3d, V3a, V3b, lateral-occipital 1 (LO1), LO2, and hMT; and ventral-temporal regions, bilaterally: V1 ventral (V1v), V2v, V3v, human V4 (hV4), ventral-occipital 1 (VO1), VO2, parahippocampal cortex 1 (PHC1), PHC2.

2.3.3.2 Graph theory metrics. I used the Brain Connectivity Toolbox (BCT) to derive network metrics. I choose metrics to support our goals of describing the visual network functional architecture (i.e., modularity) across childhood and examining network integration (i.e., participation coefficient).

2.3.3.2.1 Network partitioning and modularity. I used Newman's Q-algorithm (Newman, 2006) in the BCT to determine visual network structure and modularity of the mean connectivity across all children (group-mean connectivity). I used a representative 10% network density thresholded graph in order to maintain graph connectedness while examining only the strongest connections between ROIs. The Q-algorithm algorithm takes a thresholded network connectivity matrix and assigns each node (i.e., ROIs) to a subnetwork with the goal of maximizing the number of Within-Network connections and minimized the number of Between-Network connections. This results in a modularity metric (Q), which represents the degree to which the network can be divided into clearly defined subnetworks. I use this group-mean derived network structure as our representative functional architecture for network integration analyses. Throughout I refer to these subnetworks as visual networks.

2.3.3.2.2 Participation coefficient. A node's Participation Coefficient (PC) represents the degree to which it is connected to regions in other networks. PC ranges from 0 – representing only Within-network connections, to 1 – representing a wide distribution of connections with Between-networks (Guimerà & Amaral, 2005). As described below, I examine the mean PC collapsed across nodes within each network to understand the development of visual network integration.

2.3.3.2.3 Network degree. A node's Degree (D) is simply the number of edges it shares with other nodes. I distinguish between the of Within-Network and Between-Network Degree (number of connections) for each network. The network-level Within- and Between-Network Degree is the mean Degree across all nodes within a given network.

2.4 Results

2.4.1 Network Architecture

I characterized network architecture using the mean functional connectivity matrix across all children. I divided the visual striate and extrastriate cortex into networks of densely connected nodes across a range of network densities (1% to 25%, 1% steps) using Newman's Q-algorithm (Newman, 2006) in the Brain Connectivity Toolbox (Rubinov & Sporns, 2010). To delineate a representative network, I chose a network density of 10% to maintain a connected network.

I detected six networks with an overall visual cortical modularity of $Q = .5546$. The first sub-network, which I labeled 'Early Visual,' comprised bilateral dorsal and ventral subdivisions of area V1 (i.e., R V1d, L V1d, R V1v, L V1v). The second sub-network, labeled 'R Dorsal,' comprised right lateralized dorsal visual pathway regions (i.e., R V2d, R V3d, R V3A, R V3B, R LO1, R LO2, R hMT). Similarly, the third network, labeled 'L Dorsal,' comprised left lateralized dorsal pathway regions (i.e., L V2d, L V3d, L V3A, L V3B, L LO1, L LO2, L hMT). The fourth network, labeled 'R Ventral,' comprised right lateralized ventral pathway regions (i.e., R V2V, R V3v, R hV4, R VO1, R VO2, R PHC1, R PHC2). The fifth network, labeled 'L Ventral,' comprised left lateralized ventral pathway regions (i.e., L V2V, L V3v, L hV4, L VO1, L VO2, L PHC1, L PHC2).

Figure 1 shows functional connectivity between each network node. Here, I plot the group mean connectivity matrix across all children for the representative network (10%

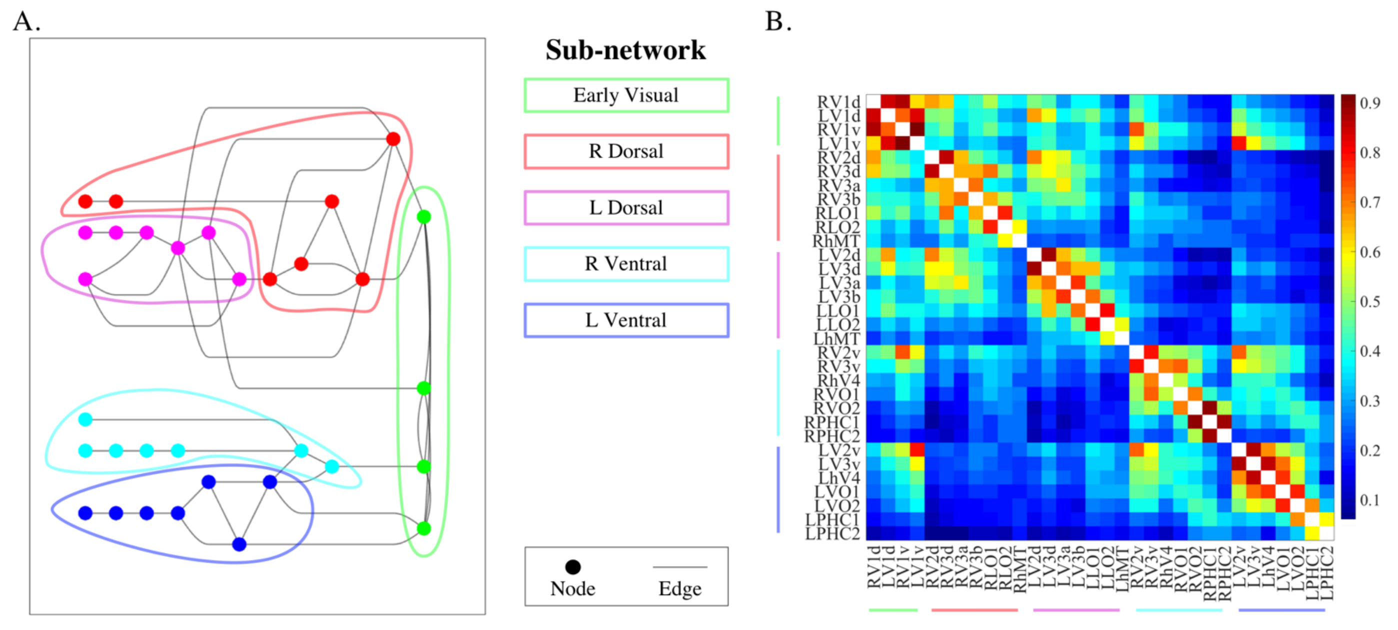

Figure 1. Graphical depictions of representative visual network architecture. A) Group mean graph (10% density). Nodes and edges are plotted in a hierarchical manner, with Early Visual regions confined to the source layer of this hierarchy. The hierarchy then proceeds leftward. Each node color represents a different network, which are then highlighted by matching colored shapes. B) Group mean functional connectivity. Values are Fisher transformed correlation coefficients averaged across all children.

network density), with Early Visual regions confined to the first (‘Source’) layer (e.g., Gansner, Koutsofios, North, & Vo, 1993). Layered graphs reveal the inherent hierarchical nature of the nodes within the graph. Edge lengths were drawn to minimize ‘edge crossing’ and aid visualization. From this depiction it becomes clear that, during childhood, both dorsal and ventral pathway regions are nested within Early Visual regions. This hierarchical relationship of the functional architecture reflects the known hierarchical structural relationship of the visual cortical system (Van Essen & Maunsell, 1983; Wang et al., 2015).

2.4.2 Network Integration

I next examined whether and how these visual networks are integrated with one another across childhood. I use the graph theory metric Participation Coefficient (PC) which measures how connections (i.e., edges) for a given node are distributed across networks. PC ranges from 0 – representing only Within-network connections, to 1 – representing a wide distribution of connections Between-networks (Guimerà & Amaral, 2005). To reduce bias introduced by selecting a network density (and therefore connectivity strength) I calculated the mean PC for each brain region across multiple network densities (1% - 25%, 1% steps). I then averaged across brain regions within each network to obtain a mean PC for each visual network as previously determined from the mean connectivity matrix across all children. Additionally, in each analysis I control for subject-level motion using individual’s mean Framewise Displacement (mean FD).

To characterize the developmental trajectories of network integration, I fit linear, inverse, and quadratic Age models using a curve estimation approach to linear regression on the mean PC for each network. For each model I included children’s mean FD as a covariate. The quadratic model included both linear Age and quadradic Age terms. I determined the best model fit by choosing the model with the lowest AIC. For the Early Visual, L Dorsal, and R Ventral Networks all models were non-significant (*all p's* > .08). For the L Ventral network, the best model was the Age$_{\text{inverse}}$ model (R^2 = .08, p = .051). However, when controlling for FD, the Age$_{\text{inverse}}$ effect was not significant, $t_{(75)}$ = -1.32, p

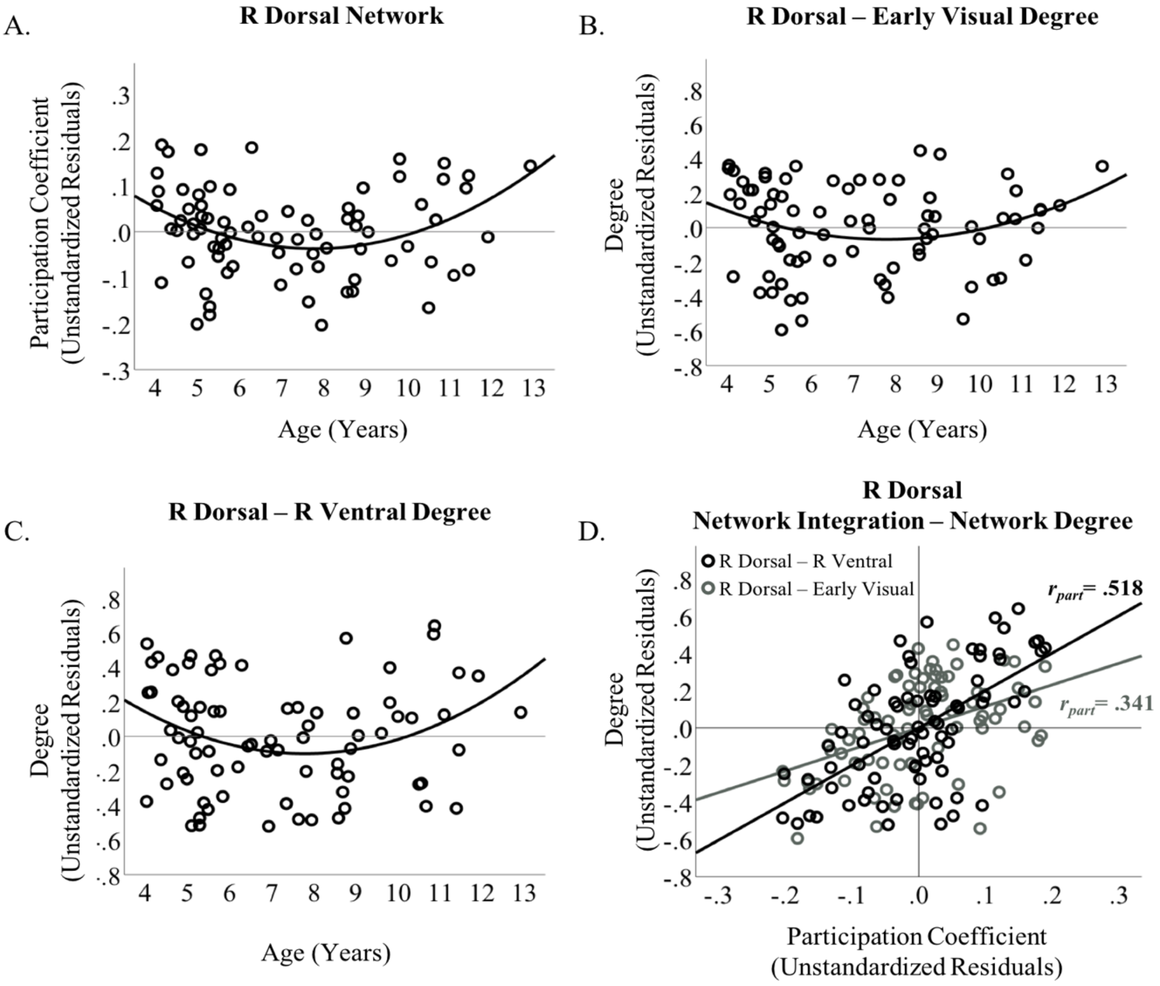

Figure 2. R Dorsal network integration changes across childhood. A) R Dorsal network Participant Coefficient changes quadratically across childhood. B) R Dorsal – Early Visual Degree changes quadratically across childhood. C) R Doral – R Ventral Degree changes quadratically across childhood. D) The mean R Doral – R Ventral Degree and the mean R Dorsal – Early Visual Degree are positively correlated with R Dorsal network Participation Coefficient. Unstandardized Residuals represent the given dependent measure when controlling for subject motion.

= .189. These data indicate that there is not significant developmental change in Early Visual, Ventral and L Dorsal function network integration across childhood.

For the R Dorsal network, the best model was the Age$_{quadratic}$ model (R^2 = .13, p = .017). There was no effect of mean FD per subject, $t_{(76)}$ = -1.39, p = .17. When controlling for subject motion, I found that both the Age$_{linear}$ $t_{(75)}$ = -3.04, p = .003, and the Age$_{quadratic}$ term, $t_{(75)}$ = 3.08, p = .003, were significant. Figure 2A shows that R Dorsal network integration decreases from early to middle childhood and then increases into late childhood.

These findings demonstrate that R Dorsal Network integration with other networks changes across childhood. However, it remains unclear whether these developmental changes in network integration reflect integration between the R Dorsal network and 1) the Ventral pathways as I hypothesized, 2) the contralateral Dorsal network, or 3) the Early Visual network.

2.4.3 Network Degree

Recall that PC reflects the distribution of Between-Network connections. From a graph theory perspective, Degree represents the number of edges connected to a given node. I further characterize the developmental trajectories of R Dorsal network integration by examining mean Degree across multiple network densities (1% to 25%, 1% steps) for Within-Network and Between-Network interactions. Here I focus on age-related changes in network degree between both the R Dorsal and every other network. Network Degree was non-normally distributed for some network interactions, so I added a constant of 1 (to allow a log transformation of zero) to all Degree measures and then log transformed this measure.

I first examine developmental changes in R Dorsal Within-Network Degree. Controlling for subject motion (mean FD), I tested for both $\text{Age}_{\text{linear}}$ and $\text{Age}_{\text{quadradic}}$ changes in log R Dorsal Within-Network Degree. I found that R Dorsal Within-Network Degree did not change with age above and beyond individual differences in FD (*all p's* > .8). This finding demonstrates that the average number of connections within the R Dorsal network may remain stable across middle childhood.

I next examined whether R Dorsal Between-Network Degree changes across childhood. For each network, controlling for subject motion (mean FD), I tested for both $\text{Age}_{\text{linear}}$ and $\text{Age}_{\text{quadradic}}$ changes in the log R Dorsal Between-Network Degree. Neither R Dorsal – L Dorsal nor R Dorsal – L Ventral Between-Network Degree changed with age (*all p's* > .3). However, R Dorsal – R Ventral Between-Network Degree also changed quadratically ($r_{(74)} = .275$, $p = .016$), but not linearly ($r_{(74)} = -.197$, $p = .363$) with age (Figure 4B). R Dorsal – Early Visual Between-Network Degree changed quadratically ($r_{(74)} = .232$, $p = .043$), but not linearly ($r_{(74)} = -.055$, $p = .634$) across age (Figure 4B). These findings demonstrate that the number of connections between R Dorsal and R Ventral Network, and between R Dorsal and Early Visual Networks decreases from early to middle childhood, but then increases from middle to late childhood. Figure 4B and 4C show that the number of connections between the R Dorsal, and the R Ventral and Early Visual Networks changes across middle childhood.

Together these findings suggest that developmental changes in R Dorsal network integration (i.e., Participation Coefficient, Figure 4A) may be reflected in changes in R Dorsal Between-Network Degree across middle childhood (Figure 4B and 4C). I therefore regressed both R Dorsal – Early Visual, R Dorsal – R Ventral Degree, $\text{Age}_{\text{linear}}$, $\text{Age}_{\text{quadradic}}$, and mean FD on R Dorsal Network Integration ($R^2 = .724$, $p < .0001$). I found that, when controlling for mean FD and Age-related changes in R Dorsal Network integration, both R Dorsal – Early Visual Network Degree ($r_{part}= .341$, $p < .0001$) and R Dorsal – Ventral Network Degree ($r_{part}= .518$, $p < .0001$) were positively correlated with R Dorsal Network Integration. Figure 4D shows the that the positive relation between R Dorsal Network integration and the number of connections between the R Dorsal Network and the R Ventral and Early Visual Networks.

2.5 Discussion

The current study examined developmental changes in dorsal and ventral visual pathway integration across childhood. I first characterized the functional architecture of striate and extrastriate networks during childhood. Based on the group-mean functional connectivity matrix (10% density), I found 5 networks including early (primary) visual regions as well as the dorsal and ventral visual pathways that were consistent with the known topographical and hierarchical organization of the visual cortex (Wang et al., 2015). I next characterized the developmental trajectories of network integration for each visual network. I found that only R Dorsal network integration changes across childhood, with decreases from early to middle childhood and increases from middle to late childhood (Figure 2). This R Dorsal network integration was driven by a change across childhood in the number of connections with the R Ventral pathway and Early Visual regions.

Our group-level characterization of network functional architecture shows that extrastriate cortex was divided into lateralized dorsal and ventral visual pathway networks (Figure 1). On average, interhemispheric connectivity within each visual pathway is weaker than connectivity within a hemisphere. The earliest visual processing regions (striate cortex, V1) across the dorsal and ventral pathways were functionally integrated across middle childhood, suggesting at the earliest stage of the hierarchy, dorsal and ventral visual pathways are functionally integrated. One could predict that, given our data, from childhood to adolescence, perhaps, V2/V3 would become functionally integrated, possibly integrated into the V1 network. Conversely, one could also predict that from infancy to childhood the earliest levels of the functional hierarchy are functionally segregated. This developmental trend would be in line with Kovacs-Blaint and colleagues whom examined the development of connections between successive hierarchical stages within a visual pathway, and found that functional connectivity changed across early development in a hierarchic, caudal-rostral gradient.

Across childhood, developmental changes in functional connectivity between the dorsal and ventral visual pathways may support integration of visual features coded in these distinct pathways. Our principle hypothesis was that functional integration between the dorsal and ventral visual pathways would change across childhood. I found that R Dorsal network integration first decreased from early- to middle-childhood, but then increased from middle- to late-childhood. This change in network integration was reflected in changes in the number of connections between the R Dorsal and both the R Ventral pathway and Early Visual regions. These data indicate that integration between the dorsal and ventral visual pathways continues to develop throughout childhood.

Feature Integration Theory argues that visual attention to a visual field location binds the visual features of the object at that location. Across childhood, developmental improvement in behavioral color-motion feature integration is protracted relative to luminance-motion feature integration (Lynn et al., 2020). When considering the hierarchical, parallel structure of the striate and extrastriate cortices, it follows that developmental change in functional connectivity between the dorsal and ventral visual pathways (e.g., motion and color) may follow a different developmental trajectory relative to functional connectivity *within* a visual pathway (i.e., ventral). Indeed, adult non-human primate work has shown that, attention modulates neural synchronization between V4 and the V1 (Bosman et al., 2012), as well as motion processing in hMT (Treue & Maunsell, 1996; Treue & Trujillo, 1999). Future work will examine the possibility that the observed developmental changes in dorsal-ventral visual pathway functional integration may support feature integration within these distinct pathways.

Chapter 3

3. What Underlies Visual Selective Attention Development? Evidence that Age-related Improvements in Visual Feature Integration Influence Visual Selective Attention Performance

3.1 Abstract

Visual selective attention (VSA) improves across childhood. Conjunction search tasks require integrating multiple visual features in order to find a target among distractors and are often used to measure VSA. Motivated by the visual system's architecture and developmental changes in neural connectivity, I predicted that feature integration across separate visual pathways (e.g., color and motion) should develop later than feature integration within the same visual pathways (e.g., luminance and motion). Eighty-nine 4- to 10-year-old children completed a visual search task that manipulated whether feature integration was between separate, parallel visual pathways or within the same visual pathway. I first examined whether color-motion integration was associated with a performance cost relative to luminance-motion integration across childhood. I found that color-motion integration was worse than luminance-motion integration in early childhood, but that this difference decreased with age. I also examined whether luminance-motion and color-motion and visual search performance developed differently across childhood. Reaction time (RT) visual search slopes for the luminance-motion condition were both stable across childhood and overall steeper than the color-motion condition. In contrast, RT search slopes for the color-motion condition became steeper across childhood. Finally,

I found that age-related improvements in color-motion integration, relative to luminance-motion integration, was associated with longer color-motion search rates across childhood. These data suggest that age-related improvements in color-motion feature integration may increase competition between color-motion targets and distractors, thereby increasing the amount of time needed to process distractors as non-targets during the selection process.

3.2 Introduction

Visual selective attention (VSA), in which certain visual objects or locations are selected in the presence of competing others (Desimone & Duncan, 1995; Treisman & Gelade, 1980), typically improves during childhood, through adolescence, and peaks in early adulthood (e.g., Hommel, Li, & Li, 2004; Trick & Enns, 1998). VSA has been found to be a critical component of effective learning and memory in both infants (Markant, Ackerman, Nussenbaum, & Amso, 2016; Markant & Amso, 2013) and children (Markant & Amso, 2014). Yet, the mechanisms underlying the development of this key process are not well understood. Here, I ask whether age-related changes in visual feature integration shape VSA.

Visual search tasks, often used to study VSA, require participants to search for a target among competing distractors (e.g., Treisman & Gelade, 1980). Targets and distractors vary along one or more visual feature dimensions (e.g., color, orientation). During a "conjunction search," a target defined by two or more visual features (e.g., a red bar oriented at 60°) is presented among distractors that share one value along one feature dimension, but differ in value along a second feature dimension (e.g., red bars oriented at 90° and green bars oriented at 60°). Thus, participants must *integrate multiple visual features* as they search amongst targets and distractors. Typically, the response time to find conjunction targets increases linearly as distractor number increases (RT slope), reflecting attentional engagement and visual search rate (e.g., Treisman & Gelade, 1980; Wolfe, 1994).

Developmental studies of VSA that employ visual search tasks reveal general improvements in processing speed, but also nuances in VSA as a function of task demands (Lobaugh et al., 1998; Trick & Enns, 1998). Beginning in infancy and toddlerhood, conjunction visual search performance shows patterns consistent with adult patterns in corresponding visual search tasks, but children's search rates (RT slope) become faster across toddlerhood (Gerhardstein & Rovee-Collier, 2002). Similarly, studies have found that, while conjunction search rate for color-defined oriented bars was slower in children relative to adults, search rates became faster from middle (7 years) to late childhood (10 years) (Donnelly et al., 2007). Similarly, conjunction search rate for a luminance-defined shape (e.g., black circle) was slower in middle childhood relative to late childhood which was slower than in adulthood (Merrill & Lookadoo, 2004). However, search rates became adult-like by late childhood when researchers varied the amount of distractor competition by holding one distractor type constant (e.g., black square) while increasing only the second distractor type (e.g., grey circle). Here I asked whether developmental improvements in feature integration are an agent of change in conjunction visual search performance from early, across middle, and into late childhood (4-10 years).

Given that conjunction visual search requires integrating multiple visual features, it is important to consider that visual features are processed in a distributed set of hierarchically organized, parallel neural pathways (e.g., Felleman & Van Essen, 1991; Ungerleider & Haxby, 1994; S. M. Zeki, 1978a). While some visual features are processed in relatively distinct pathways, others are processes within the same pathway. For example, color and motion information are processed in relatively distinct, but overlapping layers in cortical areas V1 and V2 and then routed to separate higher-level extrastriate cortical areas V4 and MT, respectively (Gegenfurtner, 2003; Seymour, Clifford, Logothetis, & Bartels, 2009; Shipp & Zeki, 1995; Sincich & Horton, 2005). However, luminance information proceeds with motion information along the visual hierarchy from V1, through V2, to MT. Thus, feature integration may occur across separate visual pathways (e.g., color and motion) or within the same visual pathway (e.g., luminance and motion). In this example, both across and within pathway feature integration requires motion processing. However, here I ask whether, relative to within pathway integration, across pathway integration may incur additional processing costs because color is processed in the ventral stream, while with motion is processed in the dorsal stream.

Feature integration relies on efficient connectivity between visual processing regions (e.g., Festa et al., 2005). While feature integration within a visual pathway likely relies on short, local connections within each region of the visual hierarchy, feature integration across visual pathways, in addition, likely relies on more distant, distributed connections *between* visual processing regions. Coincidentally, connectivity exhibits dynamic changes, from short- to long-range, across child development (Cao, Huang, & He, 2017; Fair et al., 2007, 2009; Supekar et al., 2009; Uddin, Supekar, & Menon, 2010), providing a unique opportunity to examine distinct feature integration across the visual cortical hierarchy. Together this suggests that, earlier in childhood, integrating features processed in separate pathways (e.g., color and motion) may come with an additional processing cost relative to integrating features processed within the same visual pathway (e.g., luminance and motion). Put another way, the additional processing cost of integrating features across visual pathways may decrease across childhood. Within the same child, an additional cost for color-motion integration, relative to luminance-motion integration, should differentially impact conjunction visual search performance depending on the visual features that define the targets and distractors. This result would strongly suggest that developing visual function is an agent of change in VSA development (Amso & Scerif, 2015). In order to isolate the change in color-motion feature integration relative to global improvements in information processing, I examine color-motion feature integration performance in *relation* to luminance-motion feature integration.

In the current study, 4- to 10-year-old children performed a visual search task. In two conditions, children were asked to search for a moving target that varied by either color or by luminance, placing more or less demand on feature integration across the visual pathways. In both Feature conditions, targets are presented with no distractors, or with 2 or 4 distractors. In the absence of distractors, performance reflects baseline feature integration abilities. In the presence of distractors, performance reflects visual selective attention abilities; specifically, the change in performance with an increase in distractor number (i.e., search slope). I first predicted that color-motion integration would be associated with a performance cost, relative to luminance-motion integration, and that this cost would decrease with age as color-motion integration improves from early to middle childhood. I next predicted that, across early to middle childhood, VSA for color-motion would change more than VSA for luminance-motion. Finally, I predicted that individual differences in developing feature integration may be associated with developmental changes in VSA. Specifically, developmental improvements in feature integration should be associated with steeper visual search slopes, and this should be more evident for the color-motion than luminance-motion visual search conditions. As children become better at integrating color and motion, sensitivity to the conjunction of features that define competing distractors should increase. This would result in a greater amount of time needed to resolve visual competition during target selection.

3.3 Methods

3.3.1 Participants

Eighty-nine 4- to 10-year-old children (Overall: *M* = 7.17, *SD* = 1.82, Range = 4.14 – 10.75, 39 female; Female: *M* = 7.44, *SD* = 1.99, Range = 4.14 – 10.75; Male: *M* = 6.96, *SD* = 1.66, Range = 4.18 – 10.26) comprised the final sample. Children were normally distributed across age (Skewness Z = 0.62). An additional 12 children were tested, but excluded due to non-compliance (n = 4), experimenter or technical error (n = 3), or color blindness (n = 5). I removed 5 children as multivariate outliers and 4 children as univariate outliers, and 10 children that did not contribute data for selective attention trials (e.g., no correct Set Size 3 or 5 trials, see below). Children and their parents were recruited through advertisements and were all local community members. Children provided assent and adults provided consent in accordance with the University IRB. Families were compensated 15 US dollars for their time.

Children's race make-up included 78% White, 7% Multi-racial, 8% Black/African-American, 6% "Other", and 2% declined to answer. Ethnicity make-up included 84% non-Hispanic, 14% Hispanic, and 2% declined to answer. Participants' average IQ, as determined by the Woodcock-Johnson Brief Intelligence Assessment (Woodcock, McGrew, & Mather, 2007), was *M*= 109.53, *SD*= 16.08 points. One child did not complete IQ testing.

3.3.2 Stimuli & Apparatus

Stimuli consisted of red, green, white, and black circles (approximately 1.25° in diameter) that moved either vertically or horizontally in phase synchrony. Circles oscillated approximately 1.25° in either direction around their initial starting point at a speed of approximately $3° s^{-1}$. Using a ColorCal MKII colorimeter (Cambridge Research Systems), I measured the luminance (Y) and Commission Internationale de l'Eclairage (CIE) coordinates (x, y) of the stimuli. Luminance-matched red ($Y = 19$ cd/m^2; $x = 0.60$; $y = 0.34$) and green circles ($Y = 19$ cd/m^2; $x = 0.32$, $y = 0.51$) appeared on a black background ($Y = 0.25$ cd/m^2; $x = 0.26$; $y = 0.26$). Chromaticity-matched black ($Y = 0.25$ cd/m^2; $x = 0.26$; $y = 0.26$) and white circles ($Y = 185$ cd/m^2; $x = 0.33$; $y = 0.32$) appeared on a gray background ($Y = 16.10$ cd/m^2; $x = 0.314$; $y = 0.342$). Circles were presented in one of six concentric locations equidistant from the screen center (approximately 6°), where an orange cartoon clown fish ("Nemo") served as a fixation point. Children were allowed to move their eyes freely throughout the trials. Within a given trial, children saw a search display (Figure 1) for up to 3500ms. If a response was recorded, the search display was removed. Following each search display, a cartoon fish was presented for 1000ms, to direct children's attention to the center of the screen.

3.3.3 Procedure

Children were first screened for color blindness using the Ishihara tests for color-deficiency. All children in the final sample passed these tests and showed no evidence of color blindness. Prior to the trials of interest, children were also asked to point to, or verbally discriminate between, red and green, and black and white circles, as well as vertical (or ‘jumping’) and horizontal (or ‘sideways’) motion. Children were instructed to “press the button as quickly as you can”, once they found the target on target-present trials, and were instructed to “not press the button” on target-absent trials. Next, children completed two practice trials to ensure they understood the instructions. This procedure was repeated if children failed to correctly indicate a color or motion direction, or if they incorrectly responded to either practice trial. Children were then asked to verbally indicate the target stimulus identity (“a jumping red/black circle”) to the experimenter. Children then searched for a vertically moving target circle among distractor circles. Across two Feature conditions, I manipulated which visual feature required integration with motion. In the luminance-motion Feature condition, the target was a vertically moving black circle, and distractors were vertically moving white circles and horizontally moving black circles. In the color-motion Feature condition, the target was a vertically moving red circle, and distractors were vertically moving green circles and horizontally moving red circles. Thus, children were required to integrate motion with either luminance or color information. I also manipulated the number of stimuli presented within each Feature condition. Across three Set Size conditions, stimuli were presented in sets of 1, 3 or 5. Target circles were present in 50% of trials and absent in 50% of trials. Target locations was randomly selected. Feature conditions (luminance-motion and color-motion) were blocked and counterbalanced. Set Size conditions (1, 3, 5) were pseudorandomly ordered. In total, children completed 96 trials, 48 for each Feature condition (luminance-motion and color-motion) and 16 (8 target-present, 8 target-absent) for each Set Size within each Feature

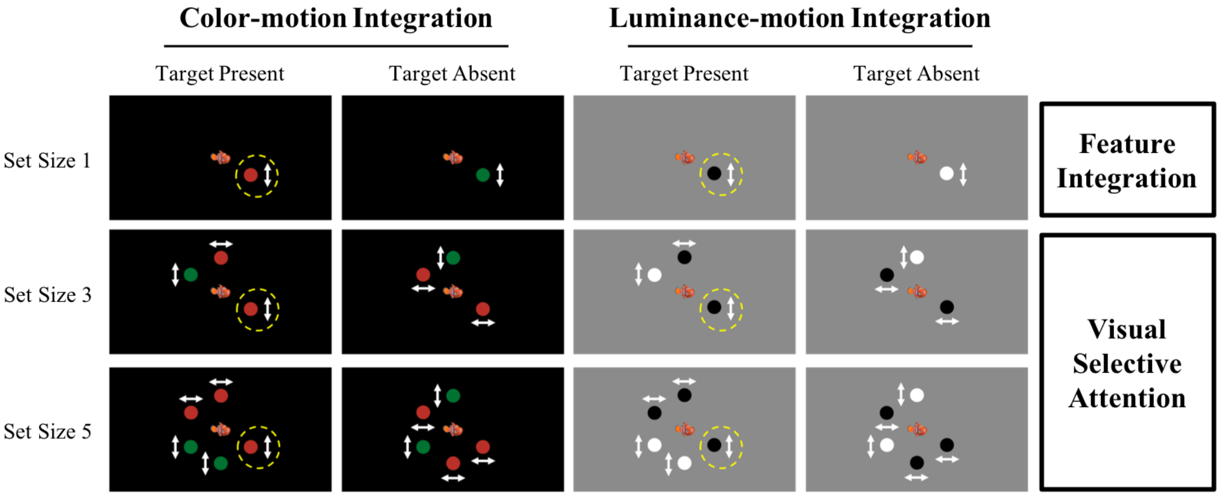

Figure 1. Illustrations of search displays for Feature and Set Size conditions for both Target-Present and Target-Absent trials. The left-most columns depict target-present and target-absent color-motion integration trials. The right-most columns depict target-present and target-absent luminance-motion integration trials. Rows depict Set Size trials, within an increase in distractors from top to bottom. The top row depicts Feature Integration trials. The bottom two rows depict Visual Selective Attention trials. Target stimuli are highlighted by a dotted yellow circle. White arrows were not presented to participants, but instead represent motion direction. Distractors could differ from the target in either color or luminance, but share vertical motion. Or, distractors could differ in motion direction, but share either color or luminance value. Each display was presented until the child responded (up to 3500 ms) and was followed by a fixation display (1000 ms).

condition. Each child was offered a short break every 24 trials. Figure 1 illustrates sample search displays for each Feature, Set Size and Trial Type (target-present, target-absent).

3.3.4 Dependent Measures

For each Feature and Set Size condition, I recorded RTs on target-present trials and calculated target detection sensitivity (*d'*) across target-present and target-absent trials. Initial data inspections revealed that accuracy was at ceiling in many cases, across many conditions. Thus, I applied a log-linear correction to the calculation of *d'* (Hautus, 1995; Stanislaw & Todorov, 1999). Briefly, .5 was added to both Hit Rates and False Alarm Rates and 1 was added to both the number of target present and target absent trials. I then calculated *d'* by subtracting the normalized False Alarm Rate from the normalized Hit Rate.

3.3.4.1 Feature Integration Performance. I define feature integration as the detection sensitivity for a target defined by multiple visual features (e.g., Treisman, 1998), *without spatially competing distractors*. Children were instructed to press a button when they found the target stimulus. Targets were either present (e.g., vertically moving red circle) or absent (e.g., horizontally moving red circle or vertically moving green circle). I generated a target detection sensitivity (*d'*) value for each Feature condition, when targets were presented without distractors (Set Size 1).

I also created a Feature Integration Index to measure the added cost of integrating color and motion features relative to luminance and motion features. To do this, I subtracted each participant's luminance-motion from color-motion integration performance value. A larger negative Feature Integration Index reflects greater performance cost for color-motion relative to luminance-motion feature integration, while a positive reflects greater performance cost for luminance-motion relative to color-motion feature integration. A value of zero thus reflects no performance cost for either color-motion and luminance-motion feature integration. Since this index was significantly skewed ($Z = -2.95$), I rank this measure to reduce skewness ($Z = -0.65$).

3.3.4.2 Visual Selective Attention Performance. I measure visual selective attention (VSA) performance as the change in children's performance as a function of distractor number (i.e., search slope). I thus calculated the performance slope for both reaction time (RT) and target detection sensitivity (*d'*) as the ratio of change in performance across Set Size over the change in Set Size. I then control for age-related differences in manual dexterity across our wide age range by dividing this performance slope value by performance on Set Size 1 trials. This estimates the visual search rate (e.g., RT slope) proportional to each individual child's baseline performance. Thus, *larger* RT search slope values reflect *slower* visual search rates, while *smaller* RT search slope values reflect *faster* visual search rates. In contrast, *smaller d'* search slope values reflect *greater* influence of distractors on accuracy, while *larger d'* search slope values reflect *smaller* influence of distractors on accuracy.

3.4 Results

3.4.1 Feature Integration Performance

Following the removal of outliers, additional outliers were revealed and Feature Integration measures remained skewed (color-motion *d'*: $Z = -7.79$, luminance-motion *d'*: $Z = -8.69$, color-motion RT: $Z = 3.90$, luminance-motion RT: $Z = 5.55$). To reduce the potential influence of outliers and skewness I first collapsed across Feature conditions and then rank-transformed each Feature Integration measure, resulting in less skewed distributions (color-motion *d'*: $Z = -2.39$, luminance-motion *d'*: $Z = -3.54$, color-motion RT: $Z = -0.11$, luminance-motion RT: $Z = 0.10$).

I predicted that color-motion Feature Integration would be associated with a performance cost, relative to luminance-motion integration, and that this cost would decrease with age as color-motion integration improves from early to middle childhood. To test this prediction, I submitted both Feature Integration performance measures (Set Size 1 ranked RT for correct target-present trials only and Set Size 1 ranked target detection sensitivity) to separate repeated measures ANCOVAs with Feature condition (color-motion, luminance-motion) as a within-subjects variable and Age (in years) as a continuous variable. See Table 1 for dependent variable descriptive statistics, collapsed across age.

For correct target-present RTs, I only found a main effect of Age, $F(1,87)=57.073$, $p < .001$, partial eta = .396, all other *p's* > .865. I thus submitted the unranked (raw) mean RTs, collapsed across Feature conditions, to Spearman's ranked correlations and found that that RTs decreased with age $r_s(89) = -.608$, $p < .001$. This indicates that children become faster to correctly detect a target across childhood.

For *d'*, there was a main effect of Feature condition, $F(1,87) = 9.454$, $p = .003$, partial eta = .098, where color-motion integration was worse than luminance-motion integration (Table 1). There was also a main effect of Age, $F(1,87) = 27.112$, $p < .000$, partial eta = .238, where overall target detection sensitivity improved across early to middle childhood, $r_s(89) = .564$, $p < .001$. As predicted, there was additionally an Age by Feature condition interaction, $F(1,87) = 6.362$, $p = .013$, partial eta = .068. To understand the interaction, I submitted raw (unranked) *d'* measures to Spearman's ranked correlations and found that, while both Feature conditions show age-related improvement, Age was correlated with color-motion integration, $r_s(89) = .529$, $p < .001$, to a greater extent than luminance-motion integration, $r_s(89) = .255$, $p = .016$.

Table 1
Summary of Behavioral Performance Measures

	Color-motion				Luminance-motion			
	Feature Integration		Visual Selective Attention		Feature Integration		Visual Selective Attention	
	d'	RT	*d'*	RT	*d'*	RT	*d'*	RT
N	89	89	87	89	89	89	89	89
Mean	2.70	1141.90	-0.04	0.11	2.95	1152.75	-0.05	0.12
Median	3.19	1080.13	0.00	0.10	3.19	1084.00	-0.06	0.10
Standard Deviation	0.79	279.14	0.15	0.13	0.45	311.21	0.11	0.13
Minimum	-0.31	692.75	-0.50	-0.25	1.00	722.00	-0.43	-0.21
Maximum	3.19	2123.83	0.36	0.46	3.19	2475.00	0.16	0.46

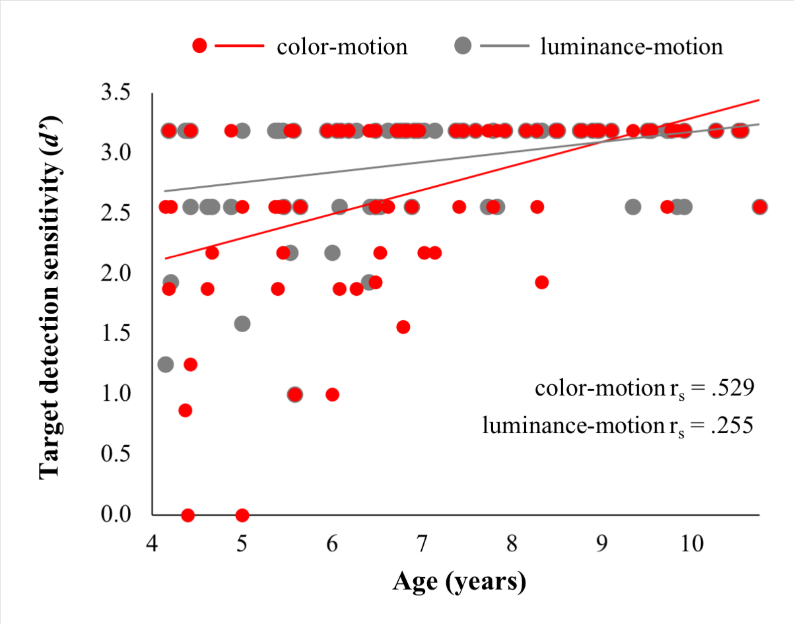

Figure 2. Age-related changes in Feature Integration accuracy, as measured by target detection sensitivity (*d'*) for Set Size 1 trials. Color-motion target detection sensitivity increased with Age to a greater extent than luminance-motion target detection sensitivity.

Figure 2 shows that color-motion integration is worse than luminance-motion integration in early childhood, but feature integration becomes equivalent by middle childhood. This finding is consistent with our prediction that color-motion feature integration would be associated with a performance cost relative to luminance-motion integration. However, the added cost of binding color and motion across visual pathways decreases across childhood. In other words, color-motion integration, relative to luminace-motion integraiton improves across childhood.

3.4.2 Visual Selective Attention Performance

3.4.2.1 Age-related changes. I predicted that, across childhood, visual search performance for color-motion targets would change more than search for luminance-motion target. To test this prediction, I submitted baseline-corrected search slopes for each dependent variable (RT and *d'*) in separate repeated measures ANCOVAs with Feature condition (luminance-motion, color-motion) as a within subject variable and Age (in years) as a continuous variable. I found no effects for the baseline-corrected *d'* search slopes, all *p's* > .06.

For baseline-corrected RT search slopes, I found a main effect of Feature condition, *F*(1,87) = 5.236, *p* = .025, partial eta = .057, where search rates were slower for luminance-motion relative to color-motion conditions. There was also a main effect of Age, *F*(1,87) = 13.315, *p* < .001, partial eta = .133. Pearson correlations showed that, an increase in distractor number was associated with *greater* slowing for search with Age, *r*(89) = .364, *p* < .001. Critically, there was also an Age by Feature condition interaction, *F*(1,87) = 4.917, *p* = .029, partial eta = .053, suggesting luminance-motion and color-motion visual search change with Age differently across childhood. Figure 3A shows that color-motion, *r*(89) = .432, *p* < .001, but not luminance-motion, *r*(89) = .125, *p* = .242, visual search performance changed across early to middle childhood. These data suggest, as predicted, that luminance-motion visual search is stable earlier than color-motion. Moreover, the pattern of results shows that children have steeper color-motion RT slopes with Age, indicating that they become more sensitive to additional distractors with Age in the color-motion search condition only.

3.4.2.2 Individual differences in Feature Integration. I predicted that individual differences in Feature Integration may influence VSA across childhood. In particular, stronger visual feature integration should strengthen both target and distractor processing and therefore increase competition with increasing distractor number. This would result in slower visual search as distractor number increases.

To test this prediction, I submitted baseline-corrected search slopes for each dependent variable (RT and *d'*) to separate repeated measures ANCOVAs with Feature condition (luminance-motion, color-motion) as a within subject variable and the ranked Feature Integration Index (i.e., difference score between Set Size 1 *d'* color-motion – luminance-motion) as a continuous variable. See Table 1 for descriptive statistics for each condition. For baseline-corrected *d'* search slopes, I found no significant effects, all *p's* > .169.

For RTs, I found a main effect of Feature condition, $F(1, 87) = 5.779$, $p = .018$, partial eta = .062, with slower search rates for the luminance-motion condition relative to the color-motion condition. There was no main effect of Feature Integration Index, $p = .294$. However, there was a Feature condition by Feature Integration Index interaction, $F(1, 87) = 5.800$, $p = .018$, partial eta = .062. Figure 3B shows that when luminance-motion Feature Integration is better than the color-motion, luminance-motion RT visual search slopes are steeper. Within the same child, as color-motion Feature Integration performance approached luminance-motion performance, this difference in visual search RT slope values decreased. Thus, as color-motion Feature Integration performance approached luminance-motion performance, visual search RT slopes increased for the color-motion, $r_s(89) = .243$, $p = .022$, but not for luminance-motion condition, $r_s(89) = -.067$, $p = .533$ (Figure 3B). Thus, improvements in color-motion Feature Integration, relative to luminance-motion, resulted in greater slowing for color-motion search.

So far, I have shown that (1) Feature Integration performance for color-motion targets improves with Age (Figure 2), (2) VSA performance on color-motion trials reflects increased sensitivity to distractors with Age (Figure 3A), and (3) improvement in color-motion, relative to luminance-motion, Feature Integration is associated with greater sensitivity to color-motion distractors during visual search (Figure 3B). These findings indicate that the relationship between Age, Feature Integration, and VSA in our age-range is specific to the color-motion visual search condition. To directly test this claim, I submitted baseline-corrected RT search slopes to a repeated measures ANCOVA with Feature condition (luminance-motion, color-motion) as a within subject factor and the Age by Feature Integration Index interaction as a covariate (or continuous variable). As before, I found a main effect of Feature condition, $F(1,86) = 7.882$, $p = .006$, partial eta = .083, where search rates were slower for luminance-motion search relative to color-motion search. I also found a Feature condition by Age by Feature Integration interaction, $F(1,86)$

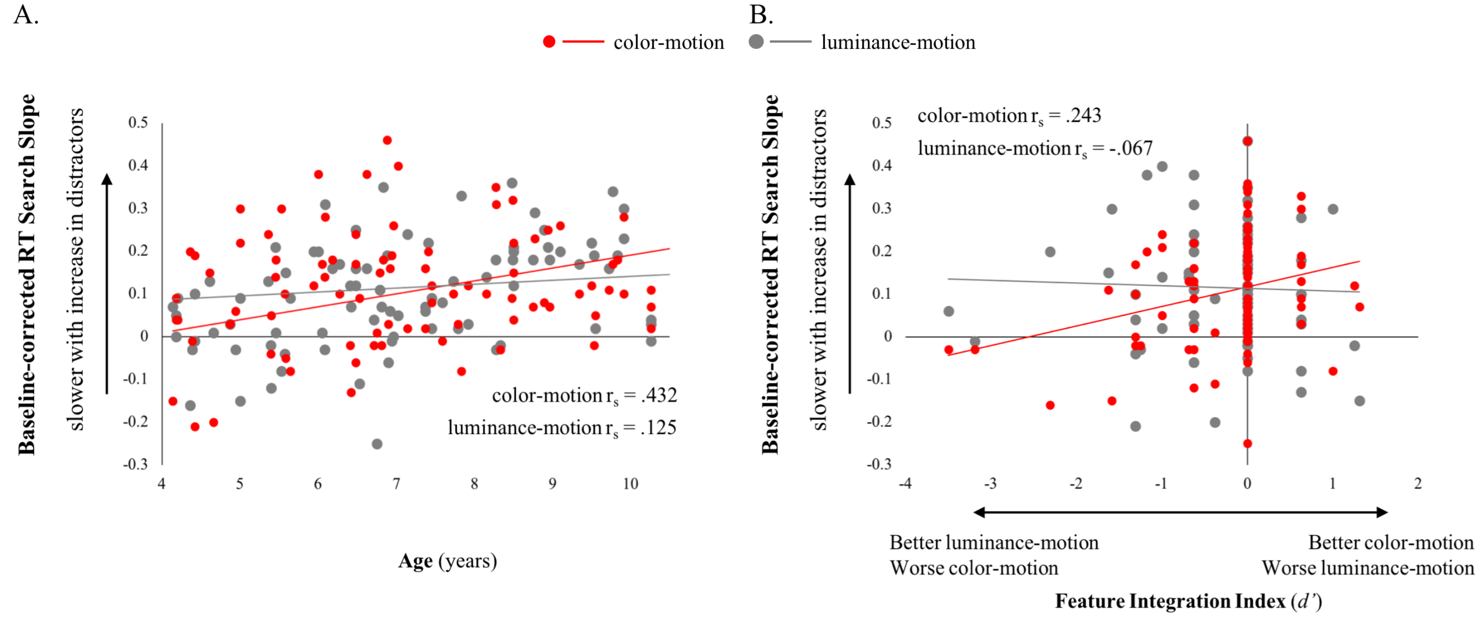

Figure 3. A) Age-related changes in Visual Selective Attention Performance. Color-motion visual search rates slowed across childhood, but this effect is not evidence in luminance-motion visual search. B) Individual differences in Feature Integration predict Color-motion Visual Selective Attention Performance. Worse color-motion integration, relative to luminance-motion integration, is associated with slower color-motion visual search rates. Raw Feature Binding Index is plotted for easier interpretation.

= 8.475, *p* = .005, partial eta = .089. These results suggest that, regardless of a child's age, when luminance-motion integration is better than color motion integration, luminance-motion search rates are slower overall. In contrast, as color-motion feature integration comes to approximate luminance-motion feature integration with age, color-motion search rates become slower. When feature integration is equal, however, both search rates are similar and color-motion search rates slow with age. Thus, age-related changes in color-motion integration may increase children's sensitivity to color-motion distractors, as revealed by steeper visual search RT slopes.

3.5 Discussion

I examined whether children's feature integration and visual selective attention abilities for objects in motion change with age. First, I found that, while feature integration improved with age, this effect was larger for color-motion integration relative to luminance-motion integration. This suggests that while color-motion integration was worse than luminance-motion integration in early childhood, the two become equivalent by middle childhood. Second, while RT search slopes were, on average, steeper for the luminance-motion condition, slopes increased with age for the color-motion condition. This result revealed that while luminance-motion search performance was robust across childhood, older children were more influenced by additional color-motion distractors. Third, when luminance-motion integration was better than color-motion integration, luminance-motion RT search slopes were steeper, indicating that children were more sensitive to the addition of luminance-motion distractors that competed with the to-be selected target. In contrast, age-related improvements in color-motion feature integration were associated with steeper RT search slopes.

Our results add to the visual search developmental literature in two important ways. First, I demonstrate that, in the absence of distractors, younger children are worse at integrating multiple visual features relative to older children. This pattern was especially evident for color-motion integration relative to luminance-motion integration. Prior work found that, in the absence of distractors, both children and adults were slower at detecting a target defined by two features compared to a target defined by one feature (Trick & Enns, 1998). Our results are consistent with the interpretation that younger children, relative to older children, are slower to integrate feature information during conjunction visual search. I add that integrating feature information across parallel visual streams may be costlier early in childhood relative to integrating feature information within a visual stream.

Second, the present study examined how differences in feature integration impact visual selective attention. To our knowledge, ours is the first study to examine, conjunction visual search performance as a function of variable feature integration demands across or within visual pathways within the children. Previous work in adults has shown that visual search performance varies by visual sensitivity (Hunter, Godde, & Olk, 2018; Li, Sampson, & Vidyasagar, 2007). Previous work in children has shown that distractor number (Donnelly et al., 2007; Gerhardstein & Rovee-Collier, 2002) and top-down cues (Lookadoo, Yang, & Merrill, 2017; Merrill & Lookadoo, 2004) impact developmental visual search trajectories. Still other work has shown that basic oculomotor information processing and improvement in visuospatial abilities impact visual search development across adolescence (Burggraaf, van der Geest, Hooge, & Frens, 2019). Our work is also consistent with recent work showing that the ability to track a moving target among distractors improves across late childhood (Wolf et al., 2018). I found that, relative to the color-motion visual search, children were slowed by increasing distractor set size more when searching for luminance-motion targets, but this effect was constant across the 4-10-year-old age-range. In contrast, color-motion visual search became slower with additional distractors with age, and this slowing was associated with age-related improvements in color-motion feature integration. Visual search performance, thus, depends on many factors, which may differentially influence this ability at different times in development. Moreover, together these findings show that there is no single visual search developmental trajectory, but multiple developmental trajectories that likely interact across development. Future work will consider whether feature integration across and within visual pathways is stable by adolescence, and if so whether visual search slopes would then show a decline with age, perhaps reflecting general information processing mechanisms.

These data suggest that the development of the attentional mechanisms that support learning and memory (Markant & Amso, 2014; Markant, Worden, & Amso, 2015; Werchan, Lynn, & Kirkham, 2019) may be impacted by the changes in robustness of visual processing across childhood (Amso & Scerif, 2015). The present study provides evidence that, across early to middle childhood, as the ability to integrate color and motion visual features improves, competition between targets and distractors may increase, thereby increasing the time needed to resolve this competition by processing additional distractors during the target selection process. Thus, developmental changes in visual feature integration abilities may be important for developmental changes in VSA. These findings have important implications for developmental work showing that learning and memory for features processed in separate visual pathways may follow distinct developmental trajectories (Lange-Küttner & Küttner, 2015), which may be related to visual processing development (see, Braddick & Atkinson, 2011). Indeed, visual acuity, luminance and chromatic contrast sensitivity (e.g., Bradley, Arthur and Freeman, 1982; Ellemberg, Lewis, Hong Liu, & Maurer, 1999; Knoblauch et al., 2001), and global motion direction sensitivity (e.g., Ellemberg, Lewis, Maurer, Brar, & Brent, 2002; Hadad, Maurer, & Lewis, 2011) all improve across childhood. Moreover, some suggest that luminance thresholds necessary for form perception improve from middle to late childhood (Bertone, Hanck, Guy, & Cornish, 2010). Future work will examine the impact of visual feature processing development on feature integration abilities across early to middle childhood.

Our findings also mirror those from patients with Alzheimer's disease (AD), whose cortical connectivity is disrupted (see, Delbeuck, Linden, & Collette, 2003). AD patients exhibit greater age-related slowing for conjunction visual search when compared to healthy elderly adults (Foster, Behrmann, & Stuss, 1999). AD patients are better at detecting global motion that requires feature integration *within* one visual pathway relative to feature integration *between* distinct, parallel visual pathways (Festa et al., 2005). Thus, greater improvement in color-motion feature integration across childhood, relative to luminance-motion feature integration, may suggest that integration across relatively distinct visual pathways may develop later in childhood than integration features processed within a single visual pathway. This age-related improvement in pathway integration is in line with developmental patterns of network connectivity (Cao et al., 2017; Fair et al., 2007, 2009; Hagmann et al., 2010; Supekar et al., 2009; Uddin et al., 2010) and increasing coherence across visual cortices during childhood (Kipping et al., 2017). Future work will also examine whether feature integration reflects underlying functional connectivity within and between visual pathways.

Chapter 4

4. Examining the Relationship between Visual Feature Processing, Feature Integration, and Visual Selective Attention

4.1 Introduction

In Study 2 I examined the influence of visual feature combination on the development of visual attention (4 – 10 years old). Specifically, using a conjunction search task, I tested children's ability to search for color-motion and luminance-motion defined targets presented among a varying number of distractors. I predicted that attention to targets whose features are coded in distinct visual pathways should develop differently relative to targets with features coded within the same visual pathway. Study 2 showed that integrating motion with luminance may develop earlier than with color, and thus differentially impacts target-distractor similarity during the visual selective attention process across childhood. As color-motion integration improved across childhood, selective attention slowed with increasing distractor number, suggesting competition between color-motion defined targets and distractors increased. Mechanistically, as color-motion feature integration improves across the visual scene, increases in distractor number may results in more locations competing for selection.

Thus, there is value in understanding how different visual feature combinations, the building blocks of the visual scene, may impact visual attention and its development. This also suggests that differences in visual feature processing (e.g., color, luminance, motion) may impact visual attention development. Therefore, I created a battery of psychophysical and visual search tests to measure visual feature processing and integration, and visual selective attention within each child (4 – 9 years old). For both color and luminance, children completed a contrast sensitivity task, pop-out search task and a conjunction search task. I also manipulated motion information across visual search tasks to examine feature integration development.

Study 3 was designed to better parse the precise mechanisms underlying differences in the development trajectories of feature integration and visual attention depending on visual feature combinations (Lynn et al., 2020). I included a ‘pop-out’ search task where target and distractors varied by a single feature rather than a combination of features (i.e., Treisman & Gelade, 1980). Within a pop-out search task, I measure baseline feature integration performance during trials without concurrent distractors (Set Size 1). I further manipulated stimulus motion across two Motion Present conditions (static, moving) where motion information was irrelevant to finding the target. When children searched for a color- or luminance-defined target during the moving condition, motion information was not relevant and may be *incidentally* integrated with either color or luminance to support target selection. Critically, visual information during moving pop-out search trials without concurrent distractors (Set Size 1) matched visual information during conjunction search without distractors. The only difference between these conditions was the instruction to search for a target defined by one feature (pop-out search) or for a target defined by two features (conjunction search). But, motion information was relevant during conjunction search and may be *deliberately* integrated with either color or motion to support target selection. By parsing the feature integration process in this way allowed us to capture the influence of visual feature combinations on incidental and deliberate feature integration across childhood.

Our goal was to better understand the relationship between visual feature processing, feature integration, and visual selective attention across childhood. Here, I examined the development of visual feature processing (i.e., contrast sensitivity and pop-out search) for color and luminance feature channels across childhood. I also examined whether two types of feature integration change with age. More specifically I tested whether incidental integration develops differently than deliberate integration depending on whether motion is integrated with either color or luminance. Similar to Study 2, I also examined whether visual selective attention develop differently depending on these visual feature combinations. Finally, I examine our critical hypothesis that visual feature processing and integration may influence visual selective attention across childhood. And, that this relationship may differ as a between feature combinations (e.g., color-motion, luminance-motion).

I predicted that 1) both contrast sensitivity and pop-out search performance would improve with age similarly for both color and luminance 2) overall feature integration would improve with age, but 3), color-motion feature integration would improve more with age relative to luminance-motion feature integration, but this would be specific to incidental motion integration, 4) conjunction search performance will change with age for the color-motion but not luminance-motion condition, and 5) contrast sensitivity and feature integration abilities would be related to children's color-motion conjunction search abilities, potentially accounting for developmental improvements.

4.2 Methods

4.2.1 Participants

Ninety-two 4- to 9-year-old children (53 female) comprise the final sample. Each child completed a contrast sensitivity task, a feature search task, and a conjunction search task. I remove 2 children who did not contribute a full set of contrast sensitivity data and 9 children who were univariate or multivariate conjunction search outliers. Preliminary data conjunction search data exploration revealed 9 children with outliers in one or more cell mean (e.g., color-motion, Set Size 5). I therefore remove these children from subsequent

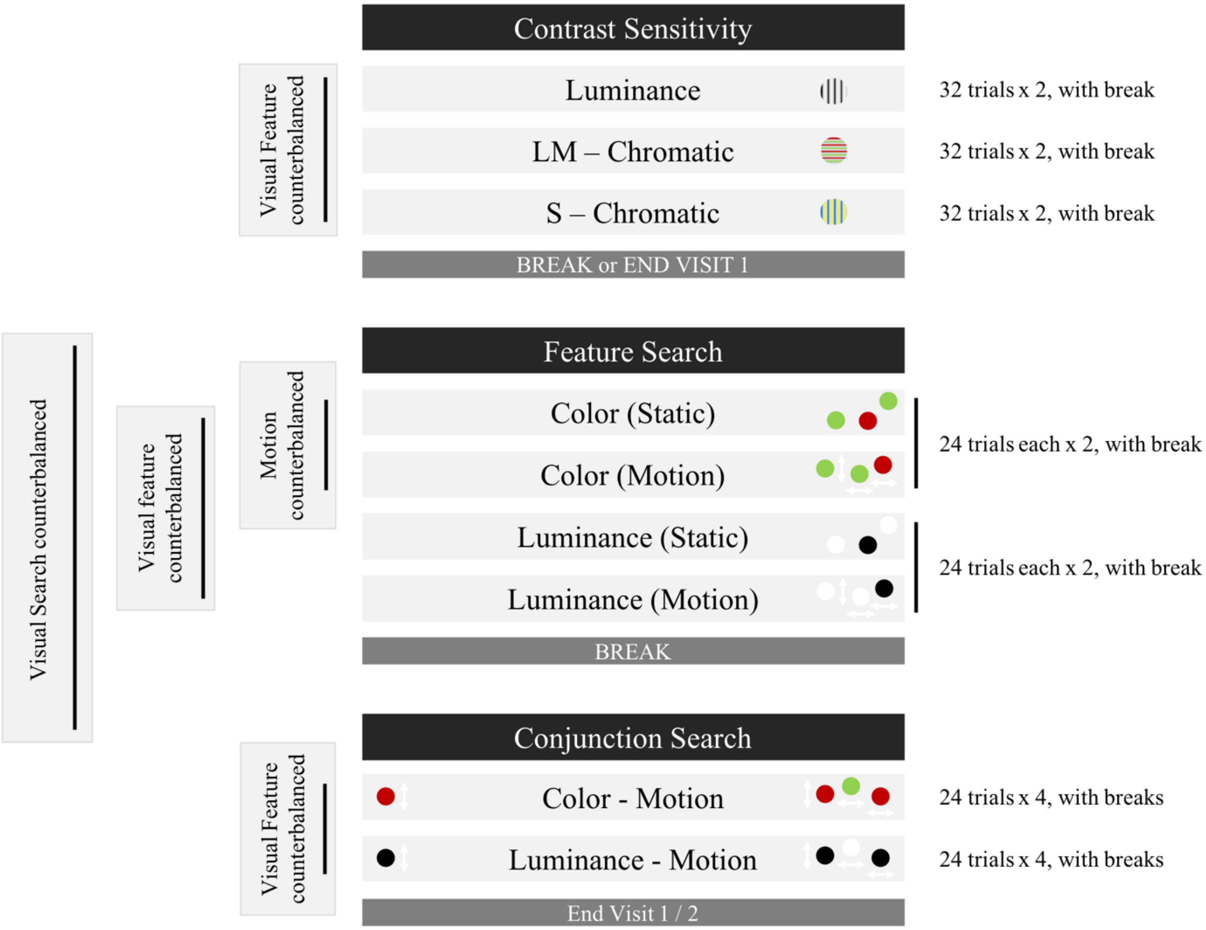

Figure 1. Example of Study Flow.

analyses. Children's race make-up included 83.7% White, 3.3% Black/African-American, 3.3% Asian or Pacific Islander, 4.3% Multi-racial, 4.3% Other, and 1% declined to answer. Ethnicity make-up included 87% non-Hispanic, 12% Hispanic, and 1% declined to answer. Children and their parents were recruited through advertisements and were all local community members. Children provided assent and adults provided consent in accordance with the University IRB. Families were compensated 15 US dollars for their time.

4.2.3 Equipment & Calibration

I used a NVIDIA Quadro FX1800 and EIZO CG2420 ColorEdge monitor to obtain 10-bits-per-channel color resolution. This allowed for presentation of much finer-grain color differences than would be possible under standard 8-bit rendering and therefore greater precision in the psychophysical measurements. To precisely control color and luminance feature information I created a look-up table (LUT) to then be used in stimulus generation. Briefly, I first measured the chromaticities and gamma functions of the red, green and blue monitor primaries using a ColorCal MkII and Minolta CS200. Chromaticities for each color primaries were converted tristimulus values. I then created a 5000-step tristimulus-RGB conversion matrix - a 3x3 matrix which when matrix-multiplied by a tristimulus triplet returns an RGB triplet. Since this conversion assumes a linear relationship between the primary (RGB) value and the output (luminance, Y, in cd/m^2), I then applied a gamma-correction. The resulting 5000-step LUT allowed conversion from MacLeod-Boynton color space to RGB for use in stimulus generation.

4.2.4 Contrast Sensitivity Task

Children completed a contrast sensitivity task presented using PsychToolbox and MATLAB. Children were asked to rest their head on a chin rest in an effort to reduced head motion during the task. During breaks children were reminded to hold still if they frequently moved their head during testing. Children completed the procedure outlined below three times, once for each feature (i.e., color-LM, color-S, luminance). Children were asked to indicate the orientation of contrast modulated Gabor patches Spatial frequency (2cpd) and phase were held constant across all Gabor patches. See Figure1 for a schematic representation of the order of tasks and counterbalance.

***4.2.4.1 Stimuli**.* Stimuli were either color- or luminance-contrast modulated Gabor patches. Color-contrast modulated Gabor patches varied along either the LM or S axis. To isolate color information, color-contrast modulated Gabor patches (both LM and S

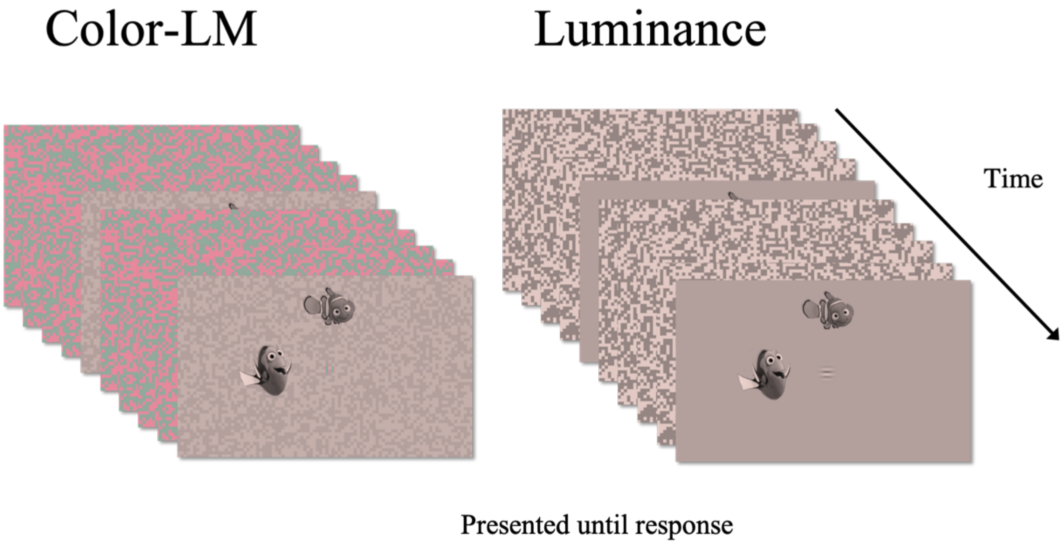

Figure 2. Illustration contrast sensitivity trials. Color-LM probe trial presented with luminance noise. Luminance probe trials presented without noise. Temporal noise masks were presented between each probe to disrupt respective feature channel. Color-S trials not shown. Children completed 64 trials for each visual feature condition.

channels) were embedded in luminance noise (Figure 2; 10 pixel squares, 45cd/m2 and 55cd/m2). The mean luminance of each stimulus was about 50cd/m2. I used the QUEST+ adaptive psychometric procedure to modulate Gabor patch contrast at the trial level (Watson, 2017). QUEST+ was initiated this algorithm as follows: contrast ranged from -40 to 0 dB; slope ranged from 2 to 5, guess rate was held constant at 0.5, and attentional lapse rate ranged from 0 to 0.04. On each trial, the algorithm was updated with children's previous trial accuracy to determine the contrast-level to be presented on the following trial. Generally, a higher contrast Gabor patch was more likely to be presented following error, and a lower contrast patch was more likely to be presented following a correct response. This procedure proceeded in a way that optimized the contrast-level on a given trial to maximize the ability to determine the psychometric function.

4.2.4.2 Procedure. Children first completed the instruction phase in which a schematic representation of a Gabor patch was oriented to one of two cartoon fish reference images (Figure 2). During the instruction phase, the experimenter explained that vertical lines were "going up-and-down" and horizontal lines were "going side-to-side" to ensure children understood the direction of vertical and horizontal lines. Following this instruction, children viewed a series of vertical and horizontal schematic Gabor patches and were asked to verbally indicate whether the lines were "going up-and-down" or "going size-to-side." Next, children saw a series of vertical and horizontal schematic Gabor patches. This time, to facilitate their understanding of the task, I provided luminance-normalized cartoon fish reference images (e.g., "Nemo" and "Dory"). Children were asked to indicate which cartoon image the "lines are pointing to" by press the corresponding button (i.e., vertical or horizontal orientation). I provided children with two blue buttons (xKeys Orby Switch, ~6.3cm,). Buttons were attached to a response pad with the cartoon reference images presented directly below the corresponding button. This response pad was simply to serve as a reminder for children.

Following the instruction phase, children then completed 6 randomly ordered practice trials. Practice trials were presented at 25%, 50% and 100% contrast in order to demonstrate to children that the contrast would vary. Following practice trials, children completed 64 experimental trials. Each trial began with a fixation cross embedded in a full-screen 5Hz temporal noise mask matching the target feature (e.g., color-LM, color-S, luminance) to disrupt the feature processing and reduced possible after-image effects. For example, on color-LM trials, four masks of red and green checks were presented across the 800ms ITI. Following the temporal noise mask, children viewed a contrast-modulated Gabor patch and then pressed one of two buttons corresponding to horizontal or vertical orientation. Both color-LM and color-S contrast-modulated Gabor patches were embedded in luminance noise across the entire screen (10-pixel squares, approx.) that approximated the same spatial frequency (2cpd) of the Gabor patch.

4.2.4.3 Dependent Measures. By using the QUEST+ adaptive psychometric procedure, I was able to estimate the threshold and slope of the contrast sensitivity function. I primarily focus our analyses on differences in contrast sensitivity thresholds between the three Feature Channel conditions across our age range. I also briefly examine the slope and proportion of attentional lapses.

4.2.5 Visual Search Task

Children completed two visual search tasks, a pop-out feature search and a conjunction search. In the pop-out search, the target was defined by one visual feature (e.g., color) and in the conjunction search the target was defined by a combination of visual features (e.g., motion and color). Children were instructed to “press the button as fast as you can when see” a target and “don’t press the button if you don’t see” a target. Targets were present (required button press) on half of all trials or absent (no button press, wait for trial to time out) on half of all trials. Across both visual search tasks, target location was randomly selected among 12 possible locations. Distractors were pseudorandomly assigned to the remaining locations, with the requirement that one distractor be adjacent to the target. Children were allowed to move their eyes freely throughout trials.

For both types of search, I manipulated Visual Feature and Set Size. In the color condition targets and distractors were red and green. In the luminance condition targets and distractors were black and white. I defined the background for each color and luminance condition in a way that equated color or luminance contrast between stimuli and the background. Stimuli were presented in varying Set Sizes (1, 3, 5, 7, 9, and 11). On target present trials, only one target was presented. For Set Size 1, either a target or a distracter was presented (no concurrent distractors). Pop-out search displays were presented for a maximum of 2s and conjunction search displays for a maximum of 3s. On each trial, if a response was recorded the search terminated. The remaining trial duration time was then added to the ITI (min 1.5s). Following each search display, a cartoon fish was presented for 1000ms to direct children’s attention to the center of the screen.

4.2.5.1 Pop-out Search. Children completed a pop-out feature search task in which they search for red or black target circle presented among distractors across two Visual Feature conditions (color and luminance, respectively). The search display was presented for up to 2000ms. Across all blocks, stimuli were presented in Set Sizes 1,3,5,7,9, and 11

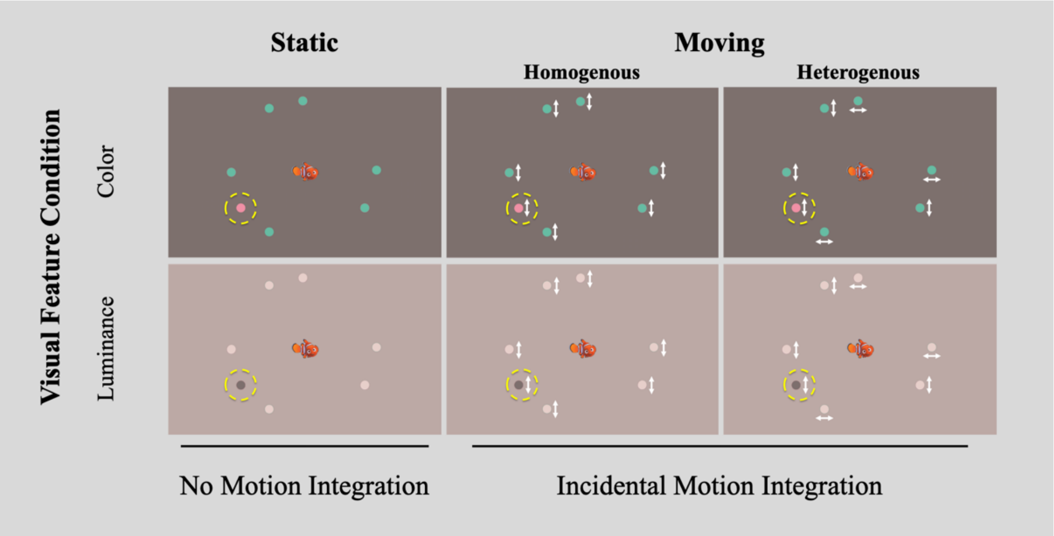

Figure 3. Illustration of pop-out search Conditions. Only Set Size 7 trials are depicted. Yellow dashed circles highlight the target. White arrows represented motion direction. Only target present trials are presented. Target absent trials were the same except the target is replaced with a distractor.

and were randomly ordered, with the constraint that no more than three of the same Set Size conditions were presented consecutively. Set Size trials were distributed equally across all conditions. Visual Feature conditions were presented in blocks of 96 trials and counterbalanced. See Figure 3 for an illustration of pop-out search conditions and trial types.

Within each Visual Feature condition, I manipulated motion information in two Motion Present conditions (static, moving). Static and moving conditions were presented in blocks and counterbalanced. For each Visual Feature condition, children completed 48 static and 48 moving trials across two blocks. Within the moving condition only, I also manipulated stimuli Motion Type (heterogeneous, homogeneous). In the homogeneous condition, stimuli were moving in phase synchrony in the same direction. In the heterogeneous condition, about half the stimuli moved vertically while the other half moved horizontally. Homogeneous and heterogeneous trials were randomly ordered within moving condition blocks. Children were offered a break between each block of trials. Critically, motion information was not required detect the color- or luminance-defined target.

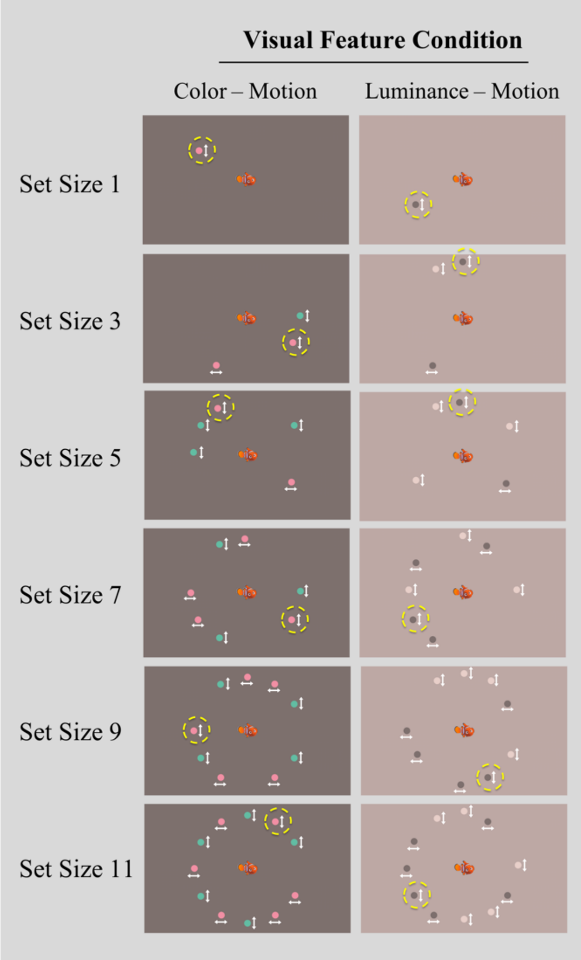

Figure 4. Illustration of Conjunction Search Conditions. Yellow dashed circles highlight the target. White arrows represented motion direction. Only target present trials are presented. Target absent trials were the same except the target is replaced with a distractor.

4.2.5.2 Conjunction Search Task. Across two Visual Feature conditions (color-motion, luminance-motion), children completed a conjunction search task in which they search for a *vertically moving* color- *or* luminance-defined target presented among vertically and horizontally moving color- *or* luminance-defined distractors. The search display was presented for up to 3000ms. Across all blocks, stimuli were presented in Set Sizes 1,3,5,7,9, and 11 and were randomly ordered. Visual Feature conditions were counterbalanced. For each Visual Feature condition, children completed 4 blocks of 24 trials. Children were offered a break between each block of trials. Critically, motion information was required to be integrated with either color or luminance information for target selection. The adjacent distractor type (e.g., vertically moving green circle, horizontally moving red circle) was counterbalanced across all trials. See Figure 4 for an illustration of conjunction search conditions and trial types.

4.2.5.3 Stimuli. Stimuli consisted of red, green, white, and black circles (approximately .5° in diameter). Circles were either static (static Motion Present condition) or oscillated approximately .5° in either direction around their initial starting point at a speed of approximately $1^\circ * s^{-1}$ (moving Motion Present condition, conjunction search). Red and green colors were matched for luminance. Black and white colors were matched for chromaticity. Circles were presented in one of 12 concentric locations equidistant from the screen center (approximately 8°), where an orange cartoon clown fish (‘‘Nemo”) served as a fixation point.

Stimulus color values were extracted from the LUT I created during monitor calibration. I equated the luminance contrast between the background and the stimuli for each Feature Condition (i.e., red & green circles, black & white circles) independently. For example, the absolute value of the contrast between background luminance and black and white circles was equal to the contrast between the background luminance and red and green circles.

4.2.5.4 Dependent Measures. I measured children’s performance using the inverse efficiency score for correct responses only. To calculate IES I divided children’s RT by their hit rate for each condition. This measure represents efficient processing speed. I then took the log of this measure because IES distributions were skewed. A higher logIES score is interpreted as overall *worse* performance (i.e., slower).

4.3 Results

4.3.1 Visual Feature Processing

I first examined whether contrast sensitivity improved with age across childhood. During a contrast sensitivity task, children saw a vertically or horizontally oriented centrally-presented 2cpd Gabor patch across three Visual Feature conditions (color-LM, color-S, luminance). I used the QUEST+ function to systematically manipulate stimulus contrast and to estimate contrast sensitivity (threshold), slope, and attentional lapses for each Visual Feature condition. I converted children's contrast threshold (dB) to Michelson contrast, then calculated contrast sensitivity (1/contrast threshold) for each child. I predicted that both color and luminance contrast sensitivity would improve with age, but that color sensitivity would be lower than luminance sensitivity across childhood.

4.3.1.1 Does Contrast Sensitivity Improve Across Childhood? I submitted contrast sensitivity values (1/contrast threshold) to a repeated measures MANCOVA with Visual Feature condition as a within-subjects factor, and Age as a continuous variable. I found a main effect of Age, $F_{(1,90)} = 39.001$, $p < .0001$, *partial eta-squared* = .302, suggesting contrast sensitivity improves with Age. I also found a Visual Feature by Age interaction, $F_{(2,89)} = 16.928$, $p < .0001$, *partial eta-squared* = .276, suggesting contrast sensitivity changes with Age differently between Visual Feature conditions (Figure 5). However, I did not find a main effect of Visual Feature, $F_{(1,89)} = 1.359$, $p = .262$, *partial eta-squared* = .030.

A Helmert contrast revealed that this interaction was driven by the difference across age between luminance and the aggregate of color Visual Feature conditions (color-LM and color-S), $F_{(1,90)} = 34.218$, $p < .0001$, *partial eta-squared* = .275, and not by the

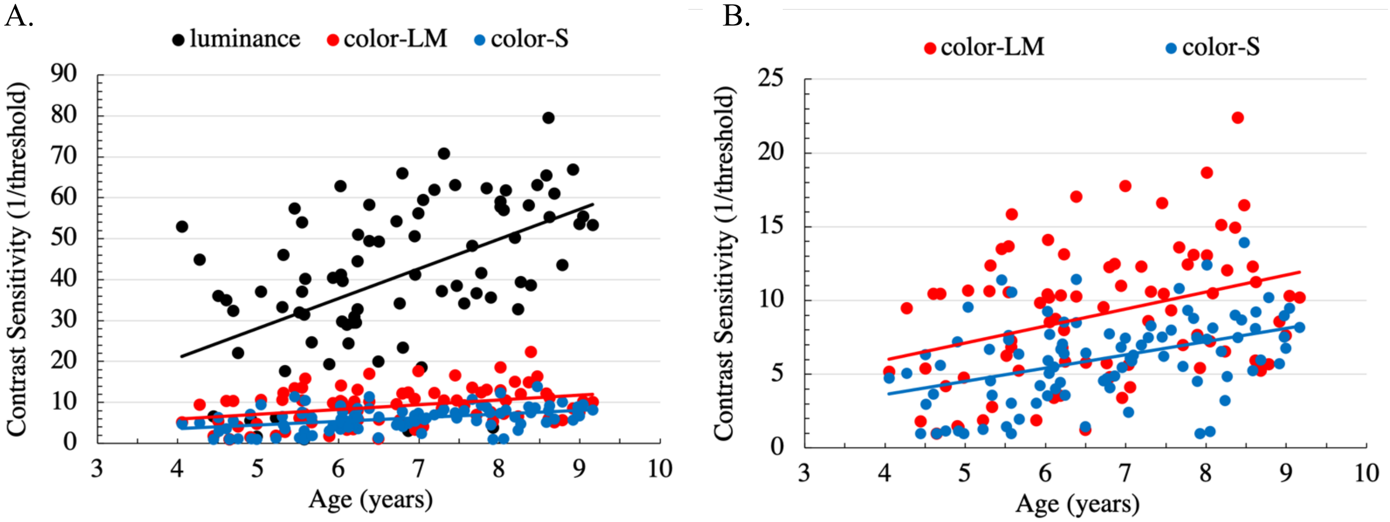

Figure 5. Developmental Improvement in Contrast Sensitivity across Luminance and Color Feature Channels. A) Luminance contrast improves with age at a greater rate with age relative to color-LM and color-S contrast sensitivity. B) Color-LM and color-S conditions improved similarly with age. Color conditions are depicted in both panels A and B for easier comparisons with the luminance condition and with each other. Overall contrast sensitivity improves with age for all visual feature conditions. Black = luminance; Red = color-LM, Blue = color-S.

difference between each color Visual Feature condition, $F_{(1,89)} = .408$, $p = .525$, *partial eta-squared* = .005. This suggests that luminance and color contrast sensitivity improve at difference rates across childhood. Post-hoc tests showed that luminance contrast sensitivity more with age, $r_{(103)} = .545$, $p < .0001$, relative to both color-LM, $r_{(103)} = .329$, $p = .001$, and color-S contrast sensitivity, $r_{(103)} = .426$, $p < .0001$.

These findings show that while both luminance and color contrast sensitivity improve across middle childhood, luminance contrast sensitivity improves more with age relative to color contrast sensitivity.

4.3.1.2 Does Incidental Motion Information Impact Pop-Out Search Performance Across Childhood? Recall that during a pop-out search task, children searched for a color- or luminance-defined target across two Visual Feature conditions. Within each of these conditions, targets and distractors were presented across multiple Set

Size conditions (3,5,7,9,11). Children saw either a target presented among distractors (target present) or an array of distractors (target absent) and were instructed to press a button when they had found a target.

I further manipulated stimulus motion across two Motion Present conditions (static, motion) to examine the influence of integrating motion with either color or luminance during salience processing. During static pop-out search no motion was present, but targets and distractors differed by color or luminance. During motion feature search, circles were in motion, but this motion information was irrelevant to children's search goal. Thus, any change in performance between Motion Present conditions reflects incidentally integrating motion with either color or luminance, either between or within respective visual processing pathway. Across these conditions, I measured children's performance using logIES (correct responses only), which incorporates RT and hit rate into one measure of efficient processing speed. A higher logIES score is interpreted as overall *worse* performance (i.e., slower).

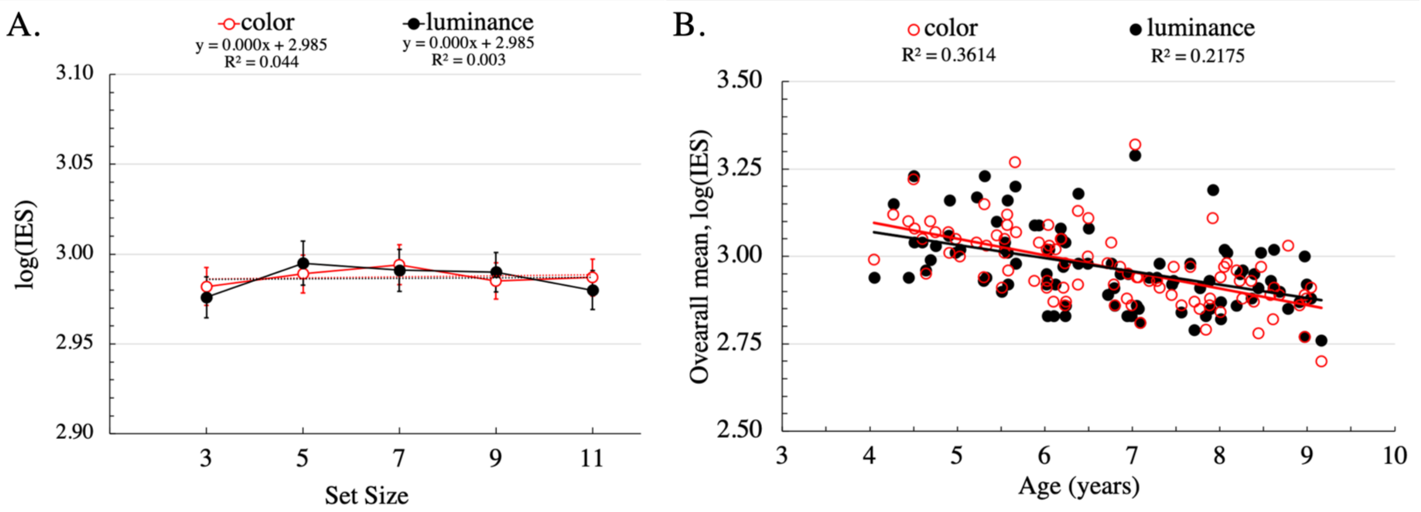

Figure 6. Color and Luminance Pop-out Search Performance. A) Pop-out search performance did not differ depending on the number of distractors. B) While overall pop-out search performance improved with age, color pop-out performance improved slightly faster with age. LogIES = log(RT/HitRate).

I predicted that integrating motion information with either color would change with age differently than integrating motion with luminance, reflecting differences in between and within pathway visual processing. I lastly predicted that better contrast sensitivity would support better pop-out search performance across childhood for both color and luminance.

I submitted pop-out search logIES values to an omnibus repeated measures MANCOVA with Visual Feature, Motion Present, and Set Size (3 – 11) conditions as within-subject factors, and Age as a continuous variable. I specifically tested for a linear Set Size effect and interactions. I found a main effect of Age, $F_{(1,90)} = 40.952$, $p < .0001$, *partial eta squared* = .313, suggesting that overall pop-out search performance improved with Age (Figure 6B). However, I did not find any other effects or interaction (all p's > .07) (Figure 6A). Together these findings suggest that both color and luminance pop-out search performance improve across childhood, but does not appear to be influenced by incidental motion information or number of distractors.

4.3.1.3 Does Contrast Sensitivity Predict Pop-out Search Performance Across Childhood? Using a linear regression approach, I tested whether contrast sensitivity and/or Age predict children's pop-out search performance for each Visual Feature condition separately (overall performance mean, collapsed across Set Size condition). For the color condition, I found that together Age and color-LM contrast sensitivity accounted for a significant portion of individual differences in color pop-out search performance, $R^2 = .368$, $F_{(2,91)} = 25.874$, $p < .00001$. While age predicted mean color pop-out search performance, $b = -.572$, $t = -6.413$, $p < .0001$, color-LM contrast sensitivity did not, $b = -.087$, $t = -.972$, $p = .334$. For the luminance condition, I also found that together Age and luminance contrast sensitivity accounted for a significant portion of individual differences in luminance pop-out search performance, R^2= .242, $F_{(2,91)}$ = 14.223, p < .0001. While Age significantly predicted mean luminance pop-out search performance, b = -.364, t = -3.213, p = .001, luminance contrast sensitivity did not, b = -.187, t = -1.701, p = .092. Together, these findings suggest that contrast sensitivity, our metric of visual feature processing, and pop-out search performance were independent across childhood. That is, better contrast sensitivity did not translate to better performance on the pop-out search task above and beyond age.

4.3.1.4 Summary. Together these findings suggest that both contrast sensitivity and pop-out search performance improve across childhood, for both color and luminance features. Luminance contrast sensitivity improves at a greater rate, relative to color contrast sensitivity across childhood. Improvements in contrast sensitivity and visual salience remain independent across this age range.

4.3.2 Feature Integration

I measured feature integration in two ways, using Set Size 1 trials (no concurrent distractors). In pop-out search Set Size 1 trials, children searched for a color or luminance-defined target across two Motion Present conditions (static, moving). During static pop-out search no motion was present. During moving pop-out search, circles were in motion, but this motion information was *irrelevant* to finding the target. Thus, any change in performance between Motion Present conditions reflects integrating motion with either color or luminance incidentally. In contrast, in conjunction search Set Size 1, children were instructed to search for a color-motion or luminance-motion target. Critically, visual information between conjunction search and motion present pop-out search conditions remained the same, except whether motion was relevant for finding the target. In a sense, this manipulation allowed us to distinguish between incidental feature integration at the visual processing level and deliberate feature integration based on task instructions. I examined these two feature integration measures for both color and luminance Visual Feature conditions. I predicted that color-motion integration would be worse than luminance-motion integration, but this difference would decrease with age, reflecting developmental changes in between relative to within-pathway integration (Lynn et al., 2020).

4.3.2.1 Does Feature Combination Differentially Impact Incidental Motion Integration Across Childhood? I submitted logIES values to a repeated measures ANCOVA with Visual Feature (color, luminance) and Motion Present (static, motion) conditions as within-subject factors, and Age as a continuous variable. I predicted that a Motion Present effect would be present in the color but not luminance condition. I found a main effect of Age, $F_{(1,90)} = 51.266$, $p < .0001$, *partial eta squared* = .363, suggesting that overall logIES improved with age. I did not find a main effect of Visual Feature, $F_{(1,90)} = .282$, $p = .597$, *partial eta squared* = .003, or a Visual Feature by Age interaction, $F_{(1,90)} = .269$, $p = .605$, *partial eta squared* = .003.

However, I found a main effect of Motion Present, $F_{(1,90)} = 6.563$, $p = .012$, *partial eta squared* = .068, suggesting performance was *worse* in the motion condition relative to the static condition. I also found a Motion by Age interaction, $F_{(1,90)} = 4.426$, $p = .038$, *partial eta squared* = .047, a Visual Feature by Motion interaction, $F_{(1,90)} = 4.705$, $p = .033$, *partial eta squared* = .050, and a marginal Visual Feature by Motion by Age interaction,

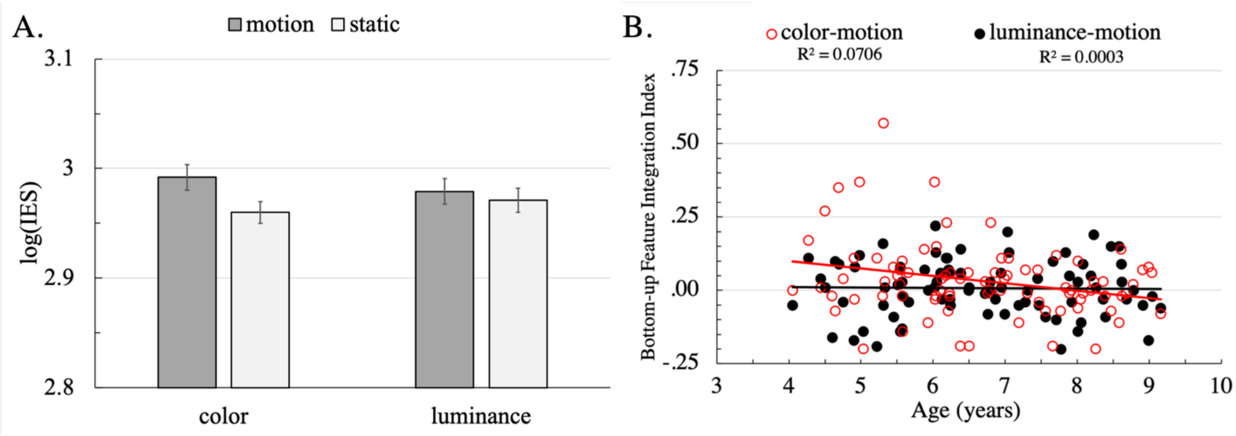

Figure 7. Bottom-up Feature Integration A) Bottom-up feature integration effects for color-motion but not luminance-motion stimuli. B) Color-motion bottom-up feature integration improves with age, but luminance-motion integration is stable. LogIES = log(RT/HitRate). Bottom-up feature integration index is calculated as static pop-out performance minus irrelevant motion pop-out performance (Set Size 1 trials only).

$F_{(1,90)} = 3.599$, $p = .061$, *partial eta squared* = .038. This suggests that motion integration differs between color and luminance and this difference may change with age.

To further understand this interaction, followed up by examining the Motion Present effect in each Visual Feature condition separately, with Age as a continuous variable. In the color condition, I found a main effect of Motion, $F_{(1,90)} = 8.889$, $p = .004$, *partial eta squared* = .090, and a Motion by Age interaction, $F_{(1,90)} = 6.359$, $p = .013$, *partial eta squared* = .066. But, in the luminance condition, neither the main effect of Motion, $F_{(1,90)} = .093$, $p = .761$, *partial eta squared* = .001, nor Motion by Age interaction, $F_{(1,90)} = .024$, $p = .877$, *partial eta squared* = .000, were significant. Figure 7A shows a motion effect in the color condition, but not the luminance condition. Together, these findings suggest that overall incidental motion integration with either color or luminance, changes with age, but that this change may be specific to integrating motion with color.

I had reasoned that any change in performance between Motion Present conditions must then be due to integrating motion with the respective visual feature. However, the data indicate that rather than incidentally *integrate* motion with color/luminance, motion may have been more distracting to young children in the color condition. To visualize this effect, I then calculated an incidental feature integration index by subtracting static from moving pop-out search Set Size 1 performance for each Visual Feature condition separately. Thus, a larger positive incidental feature integration index reflects a larger performance *slowing* when irrelevant motion is present relative to when it is not present. Figure 7B shows that color-motion target detection improves with age, but luminance-motion does not. Here, younger children were slower for color-motion relative to luminance-motion detection, but this performance difference is negligible by late childhood.

4.3.2.2 Does Feature Combination Differentially Impact Deliberate Motion Integration Across Childhood? Next, I submitted Set Size 1 mean logIES values to a repeated measures ANCOVA, with Visual Feature (color, luminance) and Condition (moving pop-out search, conjunction search) as within-subject factors and Age as a continuous variable. I predicted a condition effect would be present in the color condition, but not the luminance condition because the former requires between-pathway integration. I found a main effect of Age, $F_{(1,90)} = 55.463$, $p < .0001$, *partial eta squared* = .363, suggesting that overall logIES improved with age. I also found a marginal Condition by Age interaction, $F_{(1,90)} = 3.643$, $p = .06$, *partial eta squared* = .039, suggesting that overall deliberate feature integration performance may change with age. I did not find any other effects of or interactions (all p's > .13).

To visualize this effect, I then calculated a deliberate feature integration index by subtracting moving pop-out search performance from conjunction search performance. For

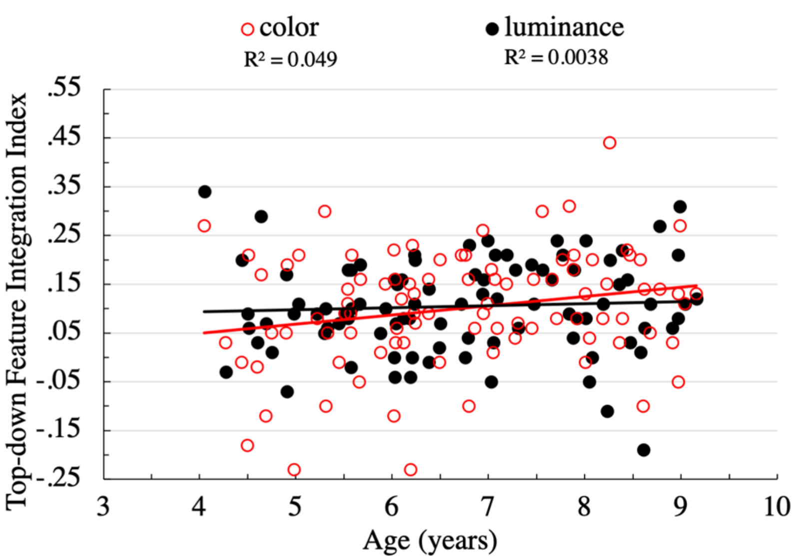

Figure 8. Top-Down Feature Integration. Overall top-down feature integration improves with age. Here, color-motion top-down integration is costlier with increasing age, but luminance-motion integration is stable. Top-down feature integration index is calculated as irrelevant motion pop-out performance minus conjunction search performance (Set Size 1 trials only).

consistency I plot Visual Feature conditions separately. Thus, a larger positive deliberate feature integration index reflects slower performance when motion was relevant relative to when it is incidental to target detection. Figure 8 shows that top-down color-motion feature integration worsens with age, but luminance-motion integration does not. Here, older children are slowed by deliberate feature integration for target detection requiring a conjunction of features, relative to when motion is incidental to target detection. This graph also suggests that the data are underpowered to detect the Visual Feature by Search by Age interaction. While overall performance improves for Set Size 1 trials, the difference between motion present pop-out and conjunction search performance shows that top-down feature integration between motion color worsens with age. However, these effects are small and therefore suggest that overall both color-motion and luminance-motion top-down integration similarly change across middle childhood.

4.3.2.3 Does Feature Combination Differentially Impact Conjunction Search Feature Integration Trial Performance Across Childhood? Next, I submitted Set Size 1 mean logIES values for conjunction search only to a repeated measures ANCOVA, with Visual Feature (color-motion, luminance-motion) as within-subject factors and Age as a continuous variable. I predicted an Age effect would be present in the color-motion condition, but not the luminance-motion condition because the former requires between-pathway integration. I found a main effect of Age, $F_{(1,90)} = 40.587$, $p < .0001$, *partial eta squared* = .311, suggesting that overall logIES improved with age. But, I did not find any other effects of or interactions (all p's > .9).

Similar to our previous study (Lynn et al., 2020), I also submitted rank-transformed d'prime values to a repeated measures ANCOVA, with Visual Feature (color-motion, luminance-motion) as within-subject factors and Age as a continuous variable. Again, I found a main effect of Age, $F_{(1,90)} = 40.587$, $p < .0001$, *partial eta squared* = .193, suggesting that overall d'prime improved with age. But, I did not find any other effects of or interactions (all p's > .5). Thus, in contrast to Study 2, I found no evidence that color-motion feature integration develops differently than luminance-motion integration.

4.3.2.4 Summary. These findings show that incidental feature integration improves across childhood for color-motion relative to luminance-motion feature combinations. Younger children were overall slower for color moving pop-out search relative to color static-pop out search, but this difference is not evident by late childhood. Moreover, deliberate feature integration may change with age similarly for between and within pathway features coded. Interestingly, this I found that color-motion deliberate feature integration worsens with age. However, when examining conjunction search Set Size 1 trials separately from moving pop-out search trials, I found that both color-motion and luminance-motion integration changed with age similarly. Together these findings suggest that our observed differences in color-motion deliberate feature integration maybe driven by changes in incidental motion integration with color across childhood. Indeed, within the color condition, incidental and deliberate feature integration values were highly correlated, $r_{(92)} = -.707$, $p < .0001$.

4.3.3 Visual Selective Attention

Here I first examined whether feature combinations differentially impact visual selective attention development. I then examined whether visual processing and feature integration explain age-related developmental change in visual selective attention across childhood. In a conjunction search task, children searched for a vertically moving color- or luminance-defined target across two Visual Feature conditions. Within each of these conditions targets and distractors were presented across multiple Set Sizes (3,5,7,9) conditions. Preliminary results revealed that performance did not change linearly, but quadratically, with Set Size. Figure 8 shows that Set Size 11 seems to be responsible for this quadradic effect. Indeed, Set Size 11 hit rates for both color-motion and luminance motion conditions were below 65%. Since our hypotheses are specific to a linear effect of Set Size, I exclude Set Size 11 from our selective attention analysis, examining a linear effect of Set Size for sets 3 through 9. Across these conditions, I measured children's performance using logIES (correct responses only), which incorporates RT and hit rate into one measure of efficient processing speed. A higher logIES score is interpreted as overall *slower* performance. To measure selective attention, I fit each child's logIES to a linear model to extract the slope across Set Size 3 through 9. Steeper slopes reflect greater slowing with increasing distractor number.

Based on previous work (Donnelly et al., 2007; Merrill & Lookadoo, 2004; Trick & Enns, 1998) I predicted that visual selective attention would improve with age (decrease in slopes). However, based on Study 2 findings, I predicted that target detection would be slower in the color-motion relative to the luminance-motion condition and that color-motion search slopes would increase with age. Lastly, I predicted that together contrast sensitivity and feature integration would predict conjunction search slopes, but that feature integration would be a stronger predictor of selective attention performance.

4.3.3.1 Does Conjunction Search Performance Improve across childhood? I submitted logIES values to an omnibus repeated measures MANCOVA, with Visual Feature and Set Size conditions as within-subject factors, and Age as a continuous variable. I specifically tested a linear contrast for Set Size effects and interactions. I found a main effect of Age, $F_{(1,92)} = 49.088$, $p < .0001$, *partial eta squared* = .348, suggesting that overall conjunction search performance improved with age. I found a main effect of Visual Feature, $F_{(1,92)} = 18.549$, $p = .0004$, *partial eta squared* = .168, and a Visual Feature by Age interaction, $F_{(1,92)} = 13.873$, $p = .0003$, *partial eta squared* = .131, suggesting that, as in Study 2, conjunction search performance changed with age differentially between color-motion and luminance-motion conditions.

I also found a linear effect of Set Size, $F_{(1,90)} = 16.754$, $p < .0001$, *partial eta squared* = .157, a Visual Feature by Set Size linear interaction, $F_{(1,90)} = 6.917$, $p = .01$, *partial eta squared* = .071, and a Visual Feature by Set Size linear by Age interaction, $F_{(1,90)} = 4.844$, $p = .03$, *partial eta squared* = .051. Figure 9A shows that linear Set Size

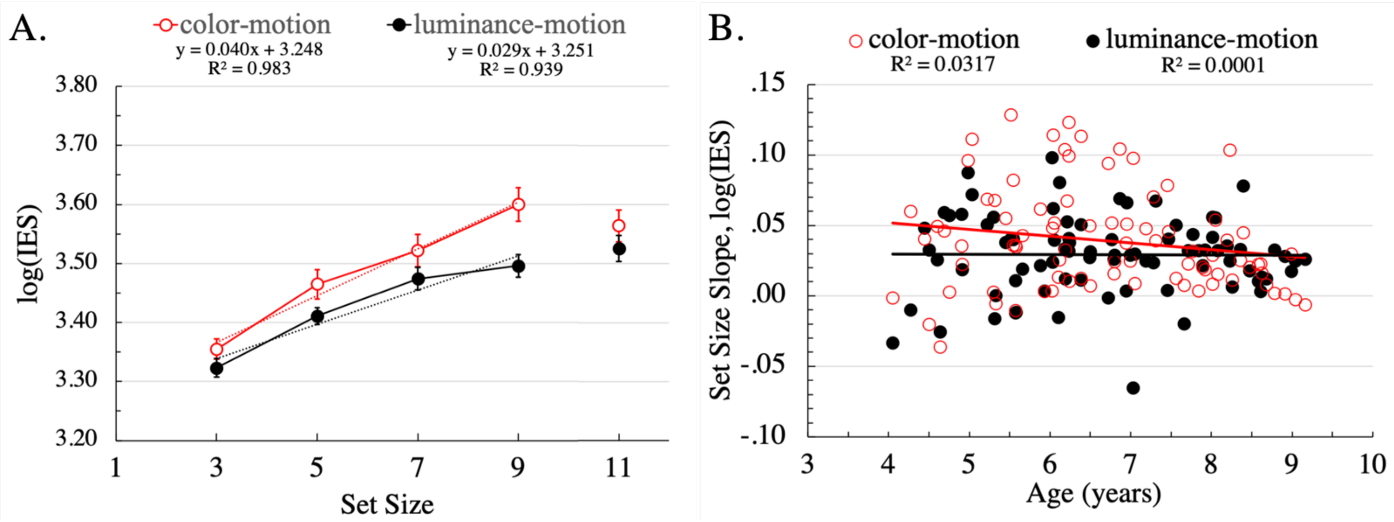

Figure 9. Conjunction search performance. A) Performance as a function of Set Size. Color-motion was slower than luminance-motion search and is effect increased with distractor number. B) Search performance slopes as a function of age. Color-motion selective attention improves across childhood. LogIES = log(RT/HitRate).

effect is larger in the color-motion condition relative to the luminance-motion condition. I then correlated children's slope for each Visual Feature condition with their age. I found that color-motion slopes decreased with age ($r_{(92)}$ = -.245, p = .018), but luminance-motion slopes did not change ($r_{(92)}$ = -.035, p = .740). Figure 9B shows that color-motion performance slopes decrease with age, but luminance-motion slopes are stable.

These findings suggest that conjunction search performance slows with increases in distractor number more for color-motion relative to luminance-motion search, and this feature-specific distractor effect decreases across childhood. These findings show that 1) conjunction search performance improves overall with age, 2) color-motion selective attention is slower than luminance-motion selective attention, but 3) this feature combination difference decreases with age.

4.3.3.2 Does Contrast Sensitivity and/or Feature Integration Support Color-Motion Conjunction Search Across Childhood? I calculated conjunction visual search performance as the logIES slope across Set Size 3 through 9. Since I found developmental improvements in conjunction search performance for the color-motion but not luminance-motion condition, I aim to predict the developmental change in color-motion selective attention relative to luminance-motion selective attention. Our variable is therefore the individuals' difference between color-motion relative to luminance-motion Set Size slope.

Using a linear regression approach, I tested whether color contrast sensitivity and our two measures of feature integration on Set Size 1 trials (incidental, deliberate) had predictive value for changing visual search slopes. For feature integration I submitted individuals' difference between color-motion relative to luminance-motion feature integration scores as predictor variable. This therefore reflects the degree to which each feature integration type was influenced by feature integration within each child. Together with age, color contrast sensitivity, and incidental and deliberate feature integration account for a significant portion of individual differences in color-motion conjunction search slopes, $R^2 = .188$, $F_{(5,91)} = 3.991$, $p = .003$. Neither color contrast sensitivity nor incidental feature integration predicted pathway-specific color-motion conjunction search slopes. But, Age and deliberate color-motion feature integration relative to luminance-motion integration predicted pathway-specific color-motion conjunction search slopes. See Table X for results. These findings show that robust, deliberate color-motion feature integration is associated with steeper color-motion conjunction search slopes.

Table 2. Correlations between Predictor Variables

Variable	n	M	SD	1	2	3	4
1 Age	92	6.72	1.37	--			
2 Color-LM Contrast Sensivitiy	92	9.00	4.46	.329**	--		
3 Incidental Feature Integration Index (color-motion - luminance-motion)	92	0.025	0.156	-0.196#	-0.175#	--	
4 Deliberate Feature Integration Index (color-motion - luminance-motion)	92	-0.004	0.140	0.15	0.086	-.675**	--

# p < .10. ** p < .01.

Table 3. Predictors of color-motion relative to luminace-motion conjunction search slope

Variable	B *(SE)*	t
Constant	.000 *(.098)*	0.00
Age	-0.305 *(0.106)*	-2.89 **
Color-LM Contrast Sensivitiy	.080 *(.105)*	0.76
Incidental Feature Integration Index (color-motion - luminance-motion)	-.072 *(.136)*	-.53
Deliberate Feature Integration Index (color-motion - luminance-motion)	.259 *(.134)*	1.93#

$p = .057$. ** $p < .01$

As a control, I also tested whether age, color contrast sensitivity, and incidental and deliberate color-motion feature integration relative to luminance-motion integration predict color pop-out search performance, which improves with age. Together these variables accounted for a significant proportion of individual differences in color pop-out search performance $R^2 = .369$, $F_{(4,91)} = 12.707$, $p < .0001$. However, only Age predicted pop-out search performance, $b = -5.68$, $t = -6.227$, $p < .0001$. All other predictors were not significant (*all p's* > .3). This suggests that neither contrast sensitivity nor feature integration support pop-out search performance across childhood.

4.3.3.3 Summary. These findings show that 1) while conjunction search performance improves overall with age, color-motion search is slower than luminance-motion search, but 2) this feature combination difference decreases with age, suggesting color-motion and luminance-motion conjunction search performance is similar by late childhood. Or, put another way, while luminance-motion search performance remains stable, color-motion search performance continues to improve across middle childhood. Moreover, I show that stronger deliberate color-motion feature integration is associated with less efficient (i.e., steeper performance slopes) indicating more performance cost as the number of color-motion distractors increases.

4.4 Discussion

In the present study I found that both contrast sensitivity and pop-out feature search performance improve with age. I also found distinct developmental changes across two types of feature integration, specifically for color-motion integration. While color-motion incidental feature integration improves across childhood, color-motion deliberate feature integration may become slower with age. Similarly, color-motion conjunction search is slower with more distractors than luminance-motion conjunction search. Moreover, color-motion conjunction search becomes less influenced by increasing distractor number with age, but luminance-motion search remains similarly influenced by distractors across childhood. Interestingly, better deliberate color-motion feature integration is associated with *less efficient* color-motion conjunction search, relative to luminance-motion search. This suggests that, above and beyond age, feature combinations may differentially impact feature integration and selective attention, and feature integration influences selective attention across childhood.

4.4.1 Visual Processing

Developmental psychophysical studies show that luminance contrast sensitivity improves across early childhood and may reach adult-like levels as early as 7 years old (Ellemberg et al., 1999) or as late as 12 years old, depending on spatial frequency, method of measurement (e.g., staircase, ssVEP, etc), and stimulus orientation (e.g., vertical vs diagonal) (Almoqbel et al., 2017; Beazley, Illingworth, Jahn, & Greer, 1980; Mayer, 1977). However, while color vision improves across infancy (e.g., Brown, 1990), it is less clear how chromatic sensitivity changes across childhood. Knoblauch and colleagues (Knoblauch et al., 2001) tested infants, children and adults on a forced-choice preferential looking or pointed (depending on age) task. They found that across multiple color axes, chromatic sensitivity improved until about 16 years old. In the present study, within each child, I utilized an adaptive algorithm validated for use in children (Farahbakhsh, Dekker, & Jones, 2019) to estimate contrast sensitivity across both luminance and chromatic channels, controlling for task demands and spatial frequency. Consistent with the reviewed literature, I found that luminance sensitivity developed at a greater rate across childhood, relative to chromatic sensitivity. Moreover, I show that contrast sensitivity for both the LM and S color pathways improve similarly across childhood. And, as expected, color-S sensitivity was overall lower than both color-LM and luminance sensitivity.

Pop-out search performance also improves across childhood for orientation, color, shape, and size (Donnelly et al., 2007; Grubert, Indino, & Krummenacher, 2014; Sun et al., 2018). Donnelly and colleagues (2007) show that 6 and 7 year-old children find color targets faster than orientation targets, but 9 and 10 year-old children and adults find color and orientation targets equally fast. Since children were instructed to find the 'odd-one-out' during pop-out search and the pop-out feature changed (e.g., color, orientation) from trial to trial (Donnelly et al., 2007; Grubert et al., 2014), younger children may not readily adopt a strategy to detect a deviant location independent of the visual feature, thought this tendency develops around mid- to late-childhood (Grubert et al., 2014). In line with this literature I found that pop-out search performance improved with age across childhood, but this improvement did not depend on visual feature. This discrepancy is likely due differences in task design. In the present study, I instructed children to search for a red or black circle and therefore provided a top-down goal during pop-out search. Children may more readily adopt a strategy of detecting a deviant feature signal at a given location and respond accordingly, rather than identify the target feature value prior to responding. Moreover, children completed pop-out search in blocks of visual feature trials which may continuously prime detection of the target on the following trials within the block (Grubert et al., 2014).

4.4.2 Feature Integration

Feature integration performance represents children's ability to bind visual features to a visual field location in the service of target selection (Treisman, 1998; Treisman & Gelade, 1980). I measured feature integration performance while children searched for a target without concurrent distractors (Set Size 1) (Lynn et al., 2020). Our previous work demonstrated that color and motion integration was weaker than luminance and motion integration in younger children, but integration was similar for both feature combination by late childhood. Others have found that, in the absence of distractors, both children and adults are slower to detect a target defined by two feature relative to a target defined by a single feature (Trick & Enns, 1998). This suggests that integration of multiple visual feature to support a goal may be costlier than one feature. I distinguished between incidental and deliberate feature integration to highlight that integration may occur at the visual-processing level or at the cognitive level via a goal provided through task instructions. When holding children's goal constant, but varying the visual information presented I measured incidental feature integration as the change in Set Size 1 pop-out search performance when a target stimulus was moving relative to when it was static. When holding visual information constant, but varying children's goal, I measured deliberate feature integration as the change in performance between conjunction search (two features in mind) and pop-out search (one feature in mind) when stimuli were moving. I found that incidentally integrating motion with color information improved across childhood. This developmental difference was not found for luminance-motion integration. These findings are consistent with our previous work that shows color-motion feature integration develops across childhood, but luminance-motion integration does not (Lynn et al., 2020). Younger children may have found the irrelevant motion more distracting than older children and were therefore slower to detect the moving color target during pop-out search. Relative to conjunction search, the ability to suppress the irrelevant motion information during pop-out search may improve faster across childhood resulting in an apparent change in color-motion deliberate integration. Either way, this unexpected finding suggests that, across childhood, the ability to hold two visual features in mind may depend on whether features are integrated between or within visual pathways. The specificity of developmental differences in incidental feature integration to color-motion may also reflect that integrating feature information across parallel visual streams may be costlier early in childhood relative to integrating feature information within a visual stream, even when the constituent features are not behaviorally relevant.

4.4.3 Selective Attention

Conjunction search is typically slower with increases in distractor number, but this effect typically decreases with age across childhood (Donnelly et al., 2007; Gerhardstein & Rovee-Collier, 2002; Trick & Enns, 1998), indicating more efficient visual search and better selective attention performance. Overall, the extant developmental literature shows improvements across childhood for visual search for targets defined by features mostly coded within the ventral visual stream (i.e., color, orientation, objects) (Donnelly et al., 2007; Gerhardstein & Rovee-Collier, 2002; Merrill & Lookadoo, 2004; Trick & Enns, 1998). I found that children become faster to find conjunction of both color-motion and luminance-motion conjunction targets with age. However, color-motion but not luminance-motion selective attention becomes more efficient with age. Our findings highlight that selective attention may develop differently depending on the visual feature combinations, suggesting that integrating visual feature between visual pathways may be more costly relative to within pathways (Festa et al., 2005; Lynn et al., 2020).

It is important to note the present findings are in contrast to our previous work where I found that color-motion selective attention became *less* efficient with age (Lynn et al., 2020). In both studies' luminance-motion selective attention remained stable across childhood. I suspect that this difference is likely due to more set size conditions and thus a better estimate of selective attention abilities in the present study. Alternatively, these discrepant findings may suggest color-motion selective attention follows a non-linear developmental trajectory across childhood, suggesting there is no single visual search developmental trajectory, but multiple developmental trajectories that likely interact across development. Future work should explore color-motion and luminance-motion selective attention in younger children and adolescence, to determine whether visual search slopes change quadratically with age.

Critically, the current study shows that changes in deliberate feature integration may influence visual selective attention across child development. Specifically, I found that, relative to luminance-motion, better deliberate color-motion feature integration is associated with less efficient color-motion selective attention. Previous work showed that improvements color-motion feature integration was associated with less efficient selective attention, suggesting better integration increased the competition across the visual field (Lynn et al., 2020). In the present study, I show that this feature integration effect may be specific to integrating motion with color information to support a top-down goal. However, because I compare conjunction search trials to pop-out search trials when motion information may be distracting to children, it remains unclear whether this effect is specific to integrating motion with color within working memory or inhibiting irrelevant motion information.

Chapter 5: Conclusions

Motivated by the structural and functional organization of the visual cortex, the primary aim of this dissertation was to test whether visual feature processing and feature combinations differentially impact visual attention development. Rather than examining visual attention development as a finite discernible network of attentional processes with a uniform developmental trajectory (Petersen & Posner, 2012), I view visual attention through the lens of the hierarchical organization of cortical visual pathways and their emerging functionality (Amso & Scerif, 2015). The hypothesis driving this work is that the integrity of visual processing may shape visual attention development across childhood. Attention binds visual features to a location in space to support object perception (Treisman & Gelade, 1980), which in turn enhances visual perceptual processing and cortical visual processing at the attended location (Carrasco, 2011; Ling & Carrasco, 2006; Ling et al., 2009), through feedback connections from higher-order brain regions (Bichot et al., 2015; Chelazzi et al., 2001). In this way, visual attention development may be conceptualized as a biased competition computation (Amso & Scerif, 2015; Desimone & Duncan, 1995; Kim & Kastner, 2019).

In the first study, I examined whether functional integration between the dorsal and ventral visual pathways develops differently than within pathway integration across middle childhood (4 – 12 years old). I utilized a network-level, graph theoretical approach to resting-state fMRI to show that functional integration of the right-lateralized dorsal visual pathway with the rest of the visual cortex changes with age across childhood, with decreases from early to middle childhood and increases from middle to late childhood. This developmental change was driven primarily by the number of functional connections between the right dorsal pathway and the right ventral pathway. This study provides preliminary evidence that, at the neural level, dorsal and ventral visual pathway integration changes across childhood.

In the second study, I examined whether feature combinations that may require integration between or within dorsal and ventral pathways differentially impact the development of visual attention (4 – 10 years old). Using a conjunction search task in which children searched for color-motion and luminance-motion defined targets, I showed that 1) color-motion integration was worse than luminance-motion integration in early childhood, but that this difference decreased with age, 2) while luminance-motion search performance was robust across childhood, older children were more influenced by additional color-motion distractors, and 3) age-related improvements in color-motion feature integration were associated with *steeper* color-motion search slopes. This study suggests that visual attention may depend on visual feature integration, which differentially influences selective attention abilities at different times in development and indicates that there is no single developmental trajectory of visual attention, but multiple developmental trajectories that likely interact.

In study three, I examined whether visual feature processing and visual selective attention abilities changes across childhood (4 – 9 years old) depending on feature combinations, again, that may require integration between or within dorsal and ventral visual pathways. I created a battery of psychophysical and visual search tasks to measure color and luminance feature processing, color-motion and luminance-motion integration and visual selective attention within each child (4 – 9 years old). I found that color and luminance feature processing improved with age. By adding a manipulation to the pop-out search task, I showed that 1) incidentally processing motion information specifically impacts color processing for younger children relative to older children and 2) integrating motion with color to support a top-down goal was slower in older children relative to younger children. I also found that color-motion conjunction search efficiency improved across childhood (relative to luminance-motion search). Critically, better top-down, deliberate color-motion feature integration predicted *less efficient* color-motion conjunction search. This study suggests that visual feature integration, rather than visual feature processing per se, may underlie visual selective attention development across childhood. More specifically, these findings suggest that integrating features to guide visual search goals, rather than incidentally integrating features to support visual perception, may influence visual selective attention efficiency.

Together, these studies provide evidence that the integrity of visual feature integration, which may be influenced by functional connectivity, may shape visual attention development. As the connectivity between and within visual pathways changes across childhood, the output of these feedforward projections may force the need for top-down attentional modulation of these visual pathways. Put another way, as visual feature processing and integration improve, competition between targets and distractors may increase, resulting in more locations competing for selection across the visual scene. After visual competition is resolved though bottom-up mechanisms such as visual salience and grouping, the remaining competition must be resolved through top-down feedback to these visual pathways (Kim & Kastner, 2019). Children with relatively better between visual pathway integration may, therefore, be more sensitive to color-motion distractors relative to luminance-motion distractors. These findings suggest that there is value in conceptualizing visual selective attention development as a biased competition computation (e.g., Desimone & Duncan, 1995) that is carried out within the visual cortex, potentially by a multiple networks underlying different attentional processes (Petersen & Posner, 2012).

Future work is needed to further understand the relationship between visual processing and both top-down and bottom-up attentional mechanisms. In this dissertation I primarily focused on the top-down processes of conjunction search and feature integration. Recent works suggests that older children may spontaneously subset conjunction search arrays to help reduce target-distractor competition, and younger children are able to adopt this strategy when instructed to do so (Lookadoo et al., 2017). The ability for a child to subset a search array to a specific feature may be limited by the integrity of children's visual feature processing for that feature dimension. For example, when searching for a vertically moving red circle among horizontally moving red circles and vertically moving green circles, a child may choose to focus their attention on the subset of red stimuli. When doing so effectively, the search array is reduced to a set of red circles, only one of which is moving vertically. However, this may be limited by the child's ability to discriminate red from green (i.e., chromatic contrast sensitivity) and vertical from horizonal movement. Thus, one goal of future work is to determine how visual feature processing abilities are related to children' ability to deploy top-down goals based on the same feature dimension. This principle also applies to bottom-up attentional mechanisms. Younger children are less likely than older children to perceive illusory contours formed by Pacman shapes (Nayar, John, Adolph, & Kiorpes, 2015). The current model would predict that children's ability to perceive an illusory square among 4 Pacman shapes would be related to children's contrast sensitivity, and that this may depend on the visual feature (e.g., color) that defines the local features responsible for the illusion. That is to say, if luminance contrast sensitivity continues to improve across childhood relative to color contrast sensitivity, within the same child, illusory contours defined by color may be more readily detected relative to those defined by luminance.

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