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Attention along the cortical hierarchy: Development matters

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Abstract

We build on the existing biased competition view to argue that attention is an *emergent* property of neural computations within and across hierarchically embedded and structurally connected cortical pathways. Critically then, one must ask, *what is attention emergent from?* Within this framework, developmental changes in the quality of sensory input and feedforward-feedback information flow shape the emergence and efficiency of attention. Several gradients of developing structural and functional cortical architecture across the caudal-to-rostral axis provide the substrate for attention to emerge. Neural activity within visual areas depends on neuronal density, receptive field size, tuning properties of neurons, and the location of and competition between features and objects in the visual field. These visual cortical properties highlight the information processing bottleneck attention needs to resolve. Recurrent feedforward and feedback connections convey sensory information through a series of steps at each level of the cortical hierarchy, integrating sensory information across the entire extent of the cortical hierarchy and linking sensory processing to higher-order brain regions. Higher-order regions concurrently provide input conveying behavioral context and goals. Thus, attention reflects the output of a series of complex biased competition neural computations that occur within and across hierarchically embedded cortical regions. Cortical development proceeds along the caudal-to-rostral axis, mirroring the flow in sensory information from caudal to rostral regions, and visual processing continues to develop into childhood. Examining both typical and atypical development will offer critical mechanistic insight not otherwise available in the adult stable state.

This article is categorized under:

Psychology > Attention

KEYWORDS

attention, biased competition, development, neural computation, neuroscience, psychology

1 | INTRODUCTION

The cognitive revolution of the mid-20th century began a prolific several decades of research dedicated to understanding the indefinable “attention.” Scientists initially conceptualized attention as a limited capacity cognitive process whereby

relevant information is selected for further processing and irrelevant information is filtered (Broadbent, 1958; James, 1890; Treisman, 1964). The selected information benefits from an attentional spotlight while irrelevant information fades into the background. Building on this, Anne Treisman's influential "Feature Integration Theory" (Treisman & Gelade, 1980) proposed that attention binds visual features (e.g., color, motion) together into a coherent whole. At the same time, Michael Posner proposed a model of spatial attention (Posner, 1980) that inspired decades of research and helped to delineate a set of underlying neurobiological systems (Petersen & Posner, 2012). A parallel line of neuroscience research at the turn of the 21st century provides evidence that attention is the outcome of biasing competition among features, objects, or locations (Desimone & Duncan, 1995; Kastner & Ungerleider, 2001). Recent psychophysical work has revealed that attention allows relevant information to be processed more deeply than competing information by tuning neural processing at the visual cortical level (Ling et al., 2015), allowing for an enhanced perceptual experience (Carrasco, 2011).

Building on the shoulders of these giants, with a focus on the visual domain, we make the case that attention is an emergent property of neural computations within and across hierarchically embedded and structurally connected cortical pathways, the behavioral result of which is the selection of a target in the presence of competing distraction. This selection occurs across the cortical hierarchy at multiple levels of abstraction, from caudal sensory representations to rostral hierarchical rule structure representations. Within this framework, developmental changes in, or disruptions to, the quality of sensory input and feedforward-feedback information flow shape the emergence and efficiency of attentional selection.

We first describe how the structural architecture and functional properties of the cerebral cortex provide the foundation for a neural computation that is similar across cortical neurons, with inputs that vary by sensory modality and neuronal density (Felleman & Van Essen, 1991; Markov et al., 2014). We then describe attention through the lens of cortical computations with support from neuroscience and computational research, and then offer insight into how attention may emerge across the cortical hierarchy. Most importantly, we ground our perspective in the developmental literature and highlight its potential for understanding the mechanisms underlying typical and atypical attention.

2 | THE ARCHITECTURE OF THE CEREBRAL CORTEX

The structural architecture and functional properties of the cerebral cortex provide the substrate for the neural computations that determine the excitatory and inhibitory activity supporting the experience we call "attention." There are myriad computational models that fit algorithms to explain how neural activity within and across cortical pathways gives rise to attentional phenomena (see Rothenstein & Tsotsos, 2014). Attention computations are supported by several gradients of cortical architecture across the caudal-to-rostral axis. We begin with a discussion of *within cortical area* architecture, showing that neuronal density and columnar architecture are valuable data points for determining how cortical neurons interact. We then extend this to computations *across hierarchically embedded* cortical areas.

Neuron density decreases but neuron size increases along the caudal-to-rostral axis (Finlay & Uchiyama, 2015), which results in densely packed smaller neurons in caudal cortex and sparsely packed larger neurons in rostral cortex (Charvet et al., 2015; Collins et al., 2010, 2016). As cell density decreases along the caudal-to-rostral axis, visual information is sampled at increasingly lower resolution (Ricci & Serre, 2020; Smith et al., 2001; Zeki, 1978). This gradient extends into higher-order association areas such as prefrontal cortex where cell density is sparse relative to posterior sensory and anterior motor cortices (Collins et al., 2010, 2016), providing a substrate for higher-order, abstract representations involved in memory, rule-guided behavior, and cognitive control (Badre & D'Esposito, 2009).

Neural activity within caudal visual areas depends on neuronal density, receptive field size, and tuning properties. These visual cortical properties highlight the information processing bottleneck attention needs to resolve. On one hand, objects compete for neural representation in the visual cortex by mutually inhibiting one another (Desimone & Duncan, 1995; Kastner & Ungerleider, 2001). Neural activity is greater for a preferred stimulus (e.g., horizontal bar) within the receptive field relative to a nonpreferred stimulus (e.g., vertical bar), and activity falls between these two rates when both a preferred and nonpreferred stimulus (e.g., horizontal and vertical bar) are present (Moran & Desimone, 1985; Reynolds et al., 1999). On the other hand, adjacent neurons influence each other depending on the stimulus within the receptive field (Gilbert & Li, 2013; Kapadia et al., 2000).

Attention computations across cortical areas are, in turn, influenced by the gradient of within cortical area architecture (e.g., neural density, tuning properties) and activity (e.g., competitive interactions). Feedforward and feedback connections convey visual information through a series of steps at each level of the cortical hierarchy (Felleman & Van Essen, 1991), forming recurrent connections across multiple cortical layers that effectively occur simultaneously

(Markov et al., 2014). Feedback connections indirectly modulate feedforward processing via horizontal connections that link cortical columns and receptive fields (Angelucci & Bressloff, 2006; Liang et al., 2017). Together these gradients support information integration across the cortical hierarchy, while linking sensory processing to higher-order brain regions, which simultaneously send feedback conveying behavioral context and goals.

So far, we have described the underlying structural architecture and functional properties of the cerebral cortex that serve as a substrate to support neural computations giving rise to attention. To reiterate, neuronal density decreases along the caudal-to-rostral cortical axis and is instrumental in determining the resolution and level of abstraction at which cortical areas process information. Recurrent connections carry information along this hierarchy, which influence local neuronal interactions via horizontal connections within the cortical laminae. Next, we discuss the neuroscience and computational research demonstrating that attention is an emergent property of these hierarchically embedded and structurally connected neuronal populations.

3 | EVIDENCE FROM NEUROSCIENCE

Neuroscience research offers further support for the idea that attention emerges from the structural architecture and functional properties of cortical neurons. In a prominent computational model, feedforward connections process visual features (e.g., orientation, color) in parallel to identify salient visual field locations (Itti & Koch, 2001; Koch & Ullman, 1985). First, feature maps code the relative difference between a visual feature value (e.g., vertical bar) and the surrounding feature values (e.g., horizontal bar) within the same feature dimension (i.e., orientation). Then, saliency maps code distinctiveness at each visual field location across all features (e.g., vertical, red) relative to its surroundings (e.g., horizontal, green). The location with the highest saliency value is the “winner-take-all” location and is likely to be attended (Itti, 2005; Itti et al., 1998). Neuroscience studies provide evidence that saliency emerges from local neuronal interactions (Li et al., 2006; Li & Gilbert, 2002) at multiple levels of the cortical hierarchy (see Veale et al., 2017). This feedforward stimulus-driven information (i.e., salience) is then combined with feedback goal-driven information (e.g., behavioral relevant, reward/value) into a priority map (Fecteau & Munoz, 2006).

Higher-order cognitive regions (e.g., frontal cortex) provide indirect feedback conveying behavioral context and goals onto caudal cortical regions (Gilbert & Li, 2013) in service of resolving competition for neural representation (Baldauf & Desimone, 2014; Bichot et al., 2015; Gregoriou et al., 2014; Serences et al., 2004; Zhou & Desimone, 2011). Visual features and objects compete for neural representation within visual cortex by mutually inhibiting one another (Kastner et al., 2001). Neural activity is greater when attention is directed to a neuron's preferred stimulus and less when directed to its nonpreferred stimulus (Desimone, 1998; Reynolds et al., 1999). This biasing of neural competition is found across the visual hierarchy, including V1, V2, V4, MT, and IT (Chelazzi et al., 2001; Moran & Desimone, 1985; Reynolds et al., 1999), with larger effects in higher-order visual regions which provide feedback onto lower-order visual regions (Buffalo et al., 2010). These feedback connections modulate visual processing by influencing the local horizontal connections that drive receptive field activity (Gilbert & Li, 2013; Liang et al., 2017; Stettler et al., 2002) and differentially impact visual processing by increasing neural activity for the relevant stimulus and decreasing activity for the irrelevant stimulus (Kapadia et al., 2000; Li et al., 2004).

While we focus the majority of this piece on visual attention, we note that frontal cortex receives indirect input from most sensory cortices and codes multiple levels of behavioral goal abstraction via sparsely packed neurons (Badre & D'Esposito, 2009; Finlay & Uchiyama, 2015). Neuroimaging studies show that frontal cortex is organized such that increasingly rostral regions code increasingly abstract action rules that support behavioral flexibility and cognitive control (Badre & D'Esposito, 2007). That is, caudal frontal cortex supports simple stimulus–response rules, while rostral frontal cortex supports context-dependent rules. In concert with the basal ganglia, rostral frontal regions bias processing in caudal frontal regions through several steps until reaching premotor cortex where the appropriate action supporting the higher-order goal is selected (Chatham & Badre, 2015). This cascade proceeds down the action hierarchy from abstract rule contingencies to simple stimulus–response actions. At the same time, frontal cortex also provides indirect feedback onto sensory and association cortices to bias neural processing for the relevant stimuli (Baldauf & Desimone, 2014; Bichot et al., 2015). In this way, attention emerges at multiple levels of the cortical hierarchy simultaneously via biased competition computations, from the information bottlenecks in early sensory cortex to abstract rules governing behavior in frontal cortex.

Together these findings demonstrate how recurrent connections between disparate cortical regions that vary by neuronal density, receptive field size, and sensory input provide the neural substrates across which neural computations

give rise to attention. Across sensory and association cortices, attention emerges from the excitation of neurons coding relevant stimuli (e.g., visual features, objects, locations), and inhibition of neurons coding irrelevant stimuli. Across frontal cortex, attention emerges from excitation of neurons coding a relevant action rule and inhibiting neurons coding the irrelevant action rules. In both cases, the biased competition computation is implemented to reduce the attentional bottleneck and prioritize neural processing for relevant information. Critically, these computations occur simultaneously and influence one another through feedforward-feedback information flow. Thus, attention emerges across the cortical and behavioral hierarchy to support multiple embedded levels of cognitive processing, from visual processing to action selection. Next, we describe how this conceptualization may be especially valuable when paired with studies of both typical and atypical development of attention.

4 | VIEWING ATTENTION DEVELOPMENT THROUGH THE LENS OF BIASED COMPETITION AND VICE VERSA

The notion of biased competition neural computations presupposes a competition among visual features, locations, thoughts, and memories that must be resolved. Allocating neural resources to resolve competition is only valuable when there is *sufficient competition to resolve*. For example, consider an image of a person wearing a red dress. Within the current framework, competition among orientation and intensity maps of the scene would be similar between a 2-month-old and a 5-year-old, but competition among color feature map would be negligible for the 2-month-old with still emerging color processing abilities. Theoretically, the daily life of the 2-month-old requires less exercise of the biased competition computation because there is less distraction as constrained by their visual system. Indeed, orientation sensitivity is evident in the first few postnatal weeks (Braddick et al., 1986), contrast and color sensitivity in the first few months (Atkinson et al., 1977; Brown, 1990), and full motion sensitivity is evident by 6 months (Banton & Bertenthal, 1997). But, sensitivity and discrimination for these visual features continues to improve throughout childhood (Hadad et al., 2011; Knoblauch et al., 2001; Leat et al., 2009). Resolving competition at increasing levels of abstraction, and therefore within and across regions in the cortical hierarchy, becomes necessary as sensory development continues. Thus, attention may emerge from developmental changes in which features, objects, or locations are processed robustly enough to compete. Early in development, this may be driven by changes in sensory processing and perceptual learning via sensory experiences. Later in childhood, this may be driven by changes in working memory and cognitive demands via academic experiences. In either case, changes in competition are likely constrained by developmental changes in the structural and functional architecture of the cortex, including (1) cortical microstructure and excitatory/inhibitory neurotransmitter availability that drives within-region neuronal interactions, and (2) myelination within and across neural regions that allows for feedforward-feedback information flow.

Briefly, developmental changes in cortical architecture and functioning support typical behavioral improvements in attention (Oakes & Amso, 2018). Cortical development proceeds along the caudal-to-rostral axis, with prefrontal regions demonstrating the most protracted development (Amso & Scerif, 2015; Bunge & Zelazo, 2006; Charvet & Finlay, 2014; Gogtay et al., 2004). Both feedforward and feedback connections are established shortly after birth, with feedforward preceding feedback (Burkhalter, 1993; Kennedy & Burkhalter, 2004). Visual cortical neurons develop early in postnatal life (Huttenlocher & de Courten, 1987), but refinements in visual receptive fields continue into childhood (Gomez et al., 2018, 2019). Visuo-spatial integration improves across childhood and adolescence (Kovács et al., 1999), presumably through changes in feedback and local horizontal connections (Gilbert & Li, 2013; Liang et al., 2017). Recent developmental fMRI research shows that objects compete for representation in the visual cortex by age 5, with subsequent refinements based on spatial resolution (Kim et al., 2021). Thus, the current framework makes the prediction that the quality of sensory processing via local cortical architecture and feedforward-feedback information flow shapes the emergence and efficiency of attention across development.

This framework is also particularly valuable with respect to understanding different trajectories of attention development (Amso & Scerif, 2015). In particular, while individuals with Autism Spectrum Disorders (ASDs) are historically considered to have differences in social functioning (e.g., Baron-Cohen et al., 1985), recent research instead points to early sensory and attentional disruptions with consequences for social learning (Amso et al., 2014; Bertone et al., 2005; Johnson et al., 2021; Robertson & Baron-Cohen, 2017; Thye et al., 2018). Children with ASDs show differences in sensory processing broadly (e.g., Robertson & Baron-Cohen, 2017). Individuals with ASDs show poorer color processing in childhood and adulthood (Franklin et al., 2008, 2010; Maule et al., 2017), poorer texture processing but enhanced

orientation processing in adolescence and adulthood (Bertone et al., 2005), and atypical motion processing across childhood, adolescence, and adulthood (Annaz et al., 2010; Bertone et al., 2003; Koldewyn et al., 2010).

A variety of possible neural mechanisms that extend across the caudal-to-rostral cortical hierarchy may underlie early sensory processing differences in children diagnosed with ASDs. Elimination of unused synapses in sensory cortices follows an atypical developmental trajectory in children diagnosed with ASDs resulting in differences in experience-dependent plasticity than would be expected typically (Hansel, 2019; Tang et al., 2014). Differences in local excitation/inhibition balance may also influence sensory gating, either through reduced GABAergic inhibition or overactive glutamate neurons (Hussman, 2001; Rubenstein & Merzenich, 2003). Consistent with cortical microstructure (e.g., mini-column width) differences across the caudal-to-rostral cortical hierarchy (Casanova et al., 2006; McKavanagh et al., 2015), neuroimaging evidence suggests that both bilateral middle occipital gyrus and right cuneus cortical surface area is larger in 6–12 month-old infants at risk for ASDs, even before they are ultimately diagnosed (Hazlett et al., 2017). Differences in feedback and lateral connectivity may also contribute to differences in visuo-spatial integration in those diagnosed with ASDs (Jachim et al., 2015; Kéta et al., 2011; c.f., Gowen et al., 2020).

Such disruptions to the local neural architecture may influence neural computations carried out across the cortical hierarchy and in turn contribute to attention differences in children diagnosed with ASDs. Exactly how differences in local neuronal cortical architecture impact biased competition is a matter of inquiry. Infants at high-risk for ASDs (Gliga et al., 2015), and toddlers (Kaldy et al., 2011), children (Keehn et al., 2008; O’Riordan et al., 2001; Plaisted et al., 1998), and adults (O’Riordan, 2004) diagnosed with ASDs perform *better* on visual search attention tasks relative to their typically developing peers. Consistent with atypical visual feature processing (e.g., Bertone et al., 2005; Franklin et al., 2008), better search performance may stem from alterations to target-distractor discrimination in those diagnosed with ASDs (Joseph et al., 2009). We speculate that disruptions to the local neuronal connectivity and excitatory/inhibitory balance may influence receptive field tuning properties whereby the influence of and competition with adjacent stimuli is reduced. Reduced competition between competing stimuli may facilitate local biased competition computations in favor of target selection.

Similarly, when viewing 2D naturalistic social scenes, children diagnosed with ASDs disproportionately attend to winner-take-all visually salient regions relative to children without ASDs, regardless of whether the social content is also salient (Amso et al., 2014). Across the scene, visually salient regions and social stimuli may compete for selection within the priority map, where each visual field location carries a value that represents the priority that it be attended (Fecteau & Munoz, 2006). The proposed framework therefore raises the hypothesis that, due to differences in early sensory processing in children diagnosed with ASDs, visually salient regions may be weighted more heavily than social information, resulting in increased attention to salient locations. In parallel to “typical” development, the current framework makes the prediction that any disruption to sensory processing via cortical architecture, excitation/inhibition balance, and feedforward-feedback information flow will alter the developmental trajectory of attention.

5 | CONCLUSION

Extensive work over the past several decades has identified a set of neurobiological systems underlying attention (Corbetta & Shulman, 2002; Petersen & Posner, 2012). Recurrent connections carry information along the cortical hierarchy, from caudal sensory regions to rostral frontal regions (Felleman & Van Essen, 1991; Gilbert & Li, 2013). Stimulus-driven attention computations integrate visual features across the cortical hierarchy to determine which visual field locations are most salient (Itti & Koch, 2001). However, feedback connections simultaneously provide input from higher-order brain regions that convey behavioral context and goals (Gilbert & Li, 2013) and indirectly influence sensory processing via horizontal connections to resolve the information bottleneck. In this way, attention emerges at multiple levels of the cortical hierarchy, from caudal sensory representations to rostral hierarchical rule structure representations. At the lowest level of the cortical hierarchy, attention emerges from within the visual cortex with enhanced sensory processing for relevant stimuli and suppressed processing for irrelevant stimuli. At the highest level of the cortical hierarchy, attention emerges from within the frontal cortex with enhanced processing for the relevant action rule and suppressed processing for the irrelevant action rules.

In the framework we present, attention reflects the output of a complex biased competition neural computation that occurs within and across hierarchically embedded cortical regions. Differences in sensory processing, local cortical microstructure, excitatory/inhibitory neurotransmitter availability, and myelination can all impact the biased

competition computation and translate to differences in attention. Ultimately, considering attention from the perspective of its biology, evolution, and developmental origins will shed novel light on how adult stable states come to be so.

CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

AUTHOR CONTRIBUTIONS

Andrew Lynn: Conceptualization (equal); data curation (equal); investigation (equal); visualization (equal); writing—original draft (lead); writing—review and editing (equal). **Dima Amso:** Conceptualization (equal); data curation (equal); investigation (equal); supervision (lead); visualization (equal); writing—review and editing (equal).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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