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A Cascading Effects Model of Early Sensory Development in Autism

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Autism has historically been defined by the presence of differences in social communication and restricted, repetitive patterns of behavior, interests, or activities (RRBs). Since 2013 when the fifth edition of the *Diagnostic and Statistical Manual of Mental Disorders* was published, sensory features were added as one of the polythetic restricted and repetitive behavior diagnostic criteria of autism, though it has remained understudied. Here, we summarize theory and research to provide support for the perspective that early sensory functions and experiences play a primary role in autism and have downstream effects on social communication and repetitive behavioral features of autism. The goals of this article are to provide an understanding of the current sensory research landscape over the early developmental period; to contextualize our knowledge autism within a developmental framework; to delineate a cascading developmental model that provides testable hypotheses; and to identify current gaps in research that would allow us to further our understanding of the role, and primacy of sensory differences in the development of the autistic phenotype. We close by offering a set of recommendations for the field.

Keywords: autism, sensory, developmental cascades, developmental model

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continued

Autism spectrum disorder, which we refer to as autism¹ in the remainder of this article, is a complex neurodevelopmental condition, the causes of which have eluded researchers for nearly 80 years. It represents a behavioral phenotype characterized by atypical social communication and by the presence of repetitive behaviors, restricted interests, and sensory features (American Psychiatric Association, 2013). Current prevalence rates in the United States are 2.27% (Baio et al., 2018; Maenner et al., 2021), though meta-analytic evidence suggests a lower worldwide median prevalence of 1% (Zeidan et al., 2022), and recent global epidemiological rates are 1:127 (Santomauro et al., 2024). Rates of co-occurring conditions are high (Simonoff et al., 2008), with nearly 70% of autistic individuals meeting the diagnostic criteria for additional diagnoses, including attention-deficit/hyperactivity disorder in childhood (Antshel & Russo, 2019), and depression and anxiety in adolescence and adulthood (Simonoff et al., 2008).

Autism is associated with significant lifelong challenges to social, academic, and vocational success (Henninger & Taylor, 2013; Howlin et al., 2004; Howlin & Moss, 2012), and these outcomes are worse than would be predicted by an individual's cognitive abilities (Engström et al., 2003; Howlin, 2000). Further, current research does not permit a high degree of confidence in interventions targeting autism features (Sandbank et al., 2020). Together, these findings suggest that we are still a long way from understanding the pathogenesis of autism, its developmental course, and how best to support autistic individuals across the lifespan.

¹ We aim to avoid *albeit* language (Bottema-Beutel et al., 2021). We also use identity first (autistic person) and person first language (specifically the term "person on the autism spectrum") interchangeably throughout the article as these are most frequently preferred by autistic people (Bury et al., 2023; Keating et al., 2023; L. Kenny et al., 2016).

Experiences Questionnaire, Version 3.0, which are freely available and for which she receives no royalties; she has received grant funding from the NIH and other federal and foundation funders to study sensory features in autism; and she is employed by the University of Southern California Chan Division, which offers occupational therapy services and continuing education programs related to sensory processing and integration. Tiffany G. Woynaroski has received grant funding from the NIH and other internal and external funding sources to study sensory development in autism. She is additionally employed by the Department of Hearing and Speech Sciences at Vanderbilt University Medical Center, which offers occupational therapy services for sensory differences in autism via their outpatient pediatric clinic, and is a parent of a child on the autism spectrum. Zachary J. Williams has received consulting fees from Roche and Autism Speaks. He serves on the scientific advisory board of Hyperacusis Research Ltd. He has received grant funding from the NIH as well as other internal and external sources to study the sensory features of autism. He also serves on the Autistic and Neurodivergent Scholars Working for Equity in Research leadership committee of the Autism Intervention Research Network on Physical Health. Roseann Schaaf has received grant funding from the NIH and other internal and external funding sources to study sensory interventions in autism. She was the principal investigator of the project that supported the development of this paper, funded by the Nancy Lurie Marks Family Foundation. She is employed by the Department of Occupational Therapy, College of Rehabilitation Sciences at Thomas Jefferson University, and employed as research director for the Collaborative for Leadership in Ayres Sensory Integration. Heather L. Green has received grant funding from the NIH as well as other internal and external sources to study auditory processing in infants and children. She is employed by the Research Division of the Department of Radiology at the Children's Hospital of Philadelphia. Zoe Mailloux is coauthor of the Evaluation in Ayres Sensory Integration, a set of tests that measure sensory and motor functions in children, which are freely available and for which she receives no royalties; she is an instructor for a nonprofit organization, the Collaborative for Leadership in Ayres Sensory Integration which offers continuing education programs related to sensory integration, and receives teaching honoraria and royalties related to these programs. Nicolaas A. J. Puts is funded for work studying sensory differences in autism across the lifespan and is supported by a Simons Foundation Autism Research Initiative Human Cognitive and Behavioral Science award, through the Medical Research Council Centre for Neurodevelopmental Disorders, and by the National Institute for Health and Care Research Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King's College London. He has previously received funding from the National Institute of Mental Health as well as other external and internal funders to study tactile differences in autism. He is employed by

King's College London. Erica Wodka has received grant funding from the Organization for Autism Research as well as collaborated on other NIH grant-funded projects examining tactile attention and processing in autism and other neurodevelopmental conditions. She is employed by the Kennedy Krieger Institute and has a faculty appointment through the Department of Psychiatry and Behavioral Sciences at the Johns Hopkins University School of Medicine. The remaining authors have no conflicts of interest to disclose.

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The last 10 years has seen a renaissance of work focused on the sensory features of autism after a period of research in the 1990s and early 2000s that was strongly focused on the social communicative aspects of the disorder. In the 10 years between 1992 and 2002, a nonexhaustive, proof-of-concept literature search on Pubmed using “autism” and “sensory” as key terms yielded only 92 articles, while a similar search using “autism and language” and “autism and social” yielded 692 and 1,059 articles, respectively. At that time, sensory features were often seen as a secondary consequence of the primary social difficulties (Johnson et al., 1992; Minshew et al., 1994; Ozonoff, 1995; Tager-Flusberg et al., 1993, though see Bauman, 1991). However, clinical, and empirical evidence steadily accumulated suggesting that sensory difficulties in autism were prevalent, emerged early, persisted across development, and impaired daily functioning. This body of work led to fundamental changes to the diagnostic criteria of autism delineated in the *Diagnostic and Statistical Manual of Mental Disorders (DSM)*. For the first time in the modern diagnostic history of autism, the *DSM-5* (American Psychiatric Association, 2013) includes sensory features as a core diagnostic criterion. Currently, these sensory features are subsumed under the general criterion of restricted, repetitive patterns of behavior, interests, and activities, though this is without any consideration of its possible association with social communication challenges. Since then, the actual number of published articles that have a sensory component has increased; however, the same search terms as above for the years 2012–2022 suggest that the proportion of articles focused on this area has not changed, with the preponderance of research (~87%) still focused on the social communicative aspects of autism. Despite the co-occurrence of sensory and social difficulties in nearly every individual on the autism spectrum, they are generally studied in isolation.

Here, we develop a model that offers a different perspective than the traditional social communicative deficit framework and propose that owing to the developmental precedence of sensory organs, sensory receptors, and sensory experiences, as well as evidence that sensory differences may emerge prior to social communication challenges, differences in sensory structures, sensory functions, and sensory processes might be primary in autism, and have downstream effects on the social communication, repetitive behaviors, and other features of autism. This “sensory-first” account of autism has been proposed in the literature (e.g., Cascio et al., 2016; Y. J. Chen, Sideris, et al., 2022; Falck-Ytter & Bussu, 2023; Levit-Binnun et al., 2013; Robertson & Baron-Cohen, 2017). We take a step further and detail cascading developmental processes that may support a more comprehensive theory of sensory precedence. The goals of this article are to provide an understanding of the current sensory research landscape; to generate a framework and model to provide testable hypotheses and to identify current gaps in research that would allow us to further our understanding of the role, and potential primacy of sensory differences in the development of the autistic phenotype. To articulate this framework and our approach, we begin by providing some definitions followed by stating our assumptions and principles.

Definitions and Context

One challenge in the field has been the lack of consistency in terms used across (and even within) various disciplines to describe

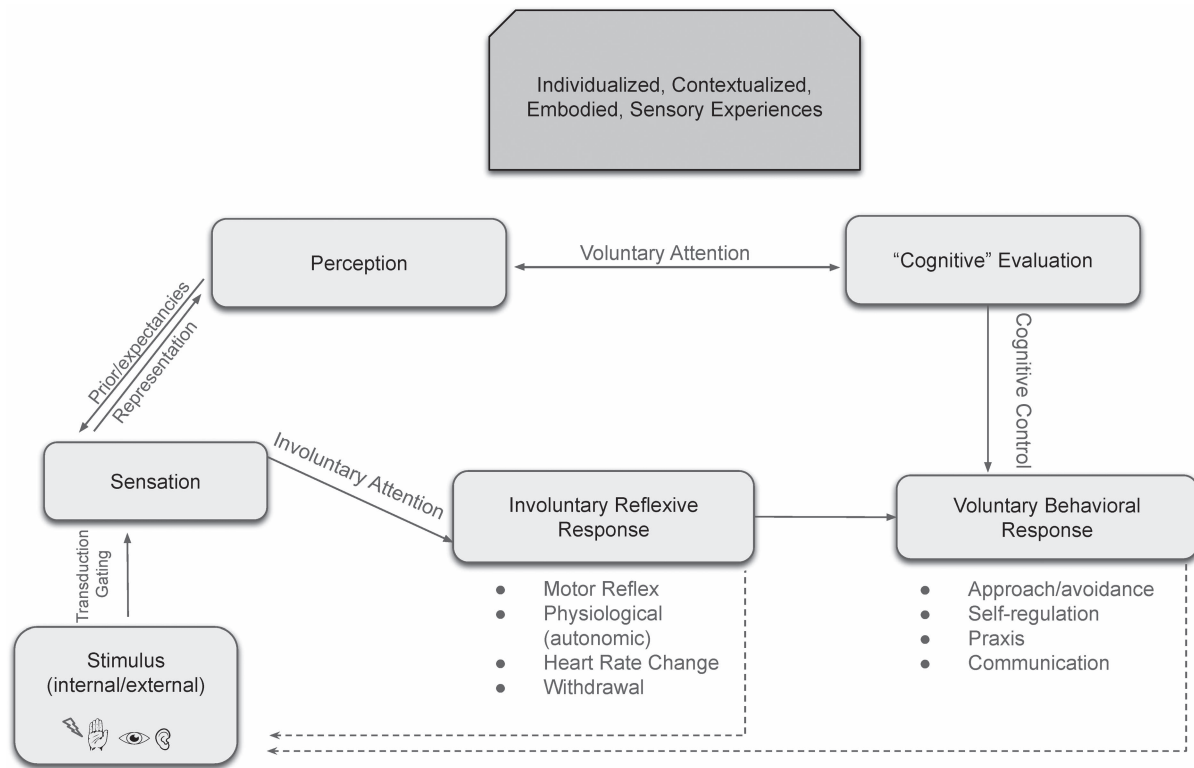
sensory experiences (Cascio et al., 2016; J. He et al., 2022; Kirby et al., 2017; Schaaf & Lane, 2015; Schauder & Bennetto, 2016; Uljarević et al., 2017). Likewise, in daily life, behavioral responses are often influenced by multimodal properties of convergent stimuli, making it difficult to isolate the relative contributions of specific modalities outside of an experimental situation. This makes the functional consequences of finding differences in autism on experimental tasks difficult to understand at times. The definitional challenges, the different perspectives on sensory features and their impact on science have been written about elsewhere (Cascio et al., 2016; J. He et al., 2022) and will not be reiterated here. However, what does bear mention is how we are conceptualizing “sensory” in the context of this article (Figure 1).

Sensory Conceptualization

Physical or chemical energy enters the nervous system and is transduced into neural energy by peripheral sensors (e.g., rods or cones for vision, mechanoreceptors for touch). The energy can arise from the external environment (e.g., vision, audition, touch, taste/smell) as well as the internal environment (e.g., interoceptive signals from heart, lungs, or gut; proprioceptive signals from muscle spindles and joints; vestibular input from semicircular canals and the otolith organs). These signals propagate through the peripheral and then multiple levels of the central nervous system, resulting in an internal experience that may or may not include attention, appraisal, or action, as in an observable behavioral response. *Each of these levels of processing may be affected in autistic people, but the common labeling of these components as “sensory” has led to confusion as well as seemingly incompatible findings in the field.* For example, behaviors such as putting one’s hands over one’s ears in response to sounds that others would not consider loud is a commonly described sensory feature in autism. Behaviorally, this response appears to function to decrease the negative impact of an external sound and would fall under the general heading of (auditory) hyperresponsiveness (Ausderau et al., 2014; Baranek et al., 2013). While this behavior demonstrates sensory hyperresponsiveness, from which clinicians and parents infer sensitivity, the *behavioral* readout may reflect differences in any of multiple stages of sensory, perceptual, attentional, cognitive, or affective processing. Further, even the earliest stages of sensory processing are subject to top-down influences of prior sensory experience. Thus, this behavioral response could be, *but is not necessarily*, a reflection of sensory or perceptual *sensitivity* (Aggelopoulos, 2015; de Lange et al., 2018; Dunovan & Wheeler, 2018). Conversely, differences in the same stages of sensory processing could yield different behavioral readouts across or even within individuals depending on the contexts.

While the genetics of autism are complex and likely impact multiple aspects of any sensory processing hierarchy, their examination is beyond the scope of this article (for reviews, see Dias & Walsh, 2020; Geschwind, 2011; Szatmari et al., 1998). However, there is emerging genetic support for the importance and relevance of sensory features in the pathogenesis of autism. For example, the majority of genes implicated in autism are expressed beginning in the early-to-mid prenatal period through very early postnatal development (Parikshak et al., 2013). These genes primarily play a role in basic neurodevelopmental processes in the cortex such as cell adhesion, synaptogenesis, and are associated with environmental

Figure 1
Conceptualization of Sensory Processing



sensory sensitivities (Assary et al., 2021, 2024). Further, sensory traits associated with autism are moderately heritable and share high genetic overlap with social traits of autism (Taylor et al., 2018), suggesting a link between these symptom domains. In addition, parents and siblings of autistic individuals report higher levels of sensory traits relative to the general population, and greater sensory sensitivities are observed in multiplex families at higher genetic liability for autism than in simplex families (Glod et al., 2017; Uljarević et al., 2014).

Two Assumptions and Three Principles

To clarify the perspective that frames our arguments, we highlight that our developmental model is based on two common assumptions about the phenotypic presentation of autism as well as three key principles of development.

Assumptions

First, autism is assumed to reflect a set of neurodevelopmental conditions, the blueprints for which are present in the brain at birth but whose expression changes with development (for reviews on risk factors, see Elsabbagh, 2020; Kim et al., 2019; Modabbernia et al., 2017). That is, while the core differences between autistic and nonautistic people remain over the lifespan, the presentation of features changes with the different developmental tasks and challenges that individuals face as they age, reflecting the concept

of chronogeneity (Y.-J. Chen, Duku, et al., 2022). For example, while social communication is altered across the lifespan in autistic individuals, the specific expression of these differences changes as the social demands of our environments change, making development inextricable from our understanding of autism. The same is likely true for sensory features, although lifespan studies are needed to better understand the extent to which sensory processing functions change or whether coping strategies change the outward expression of behavioral manifestations of sensory processing differences.

A second assumption is that autism is heterogeneous across individuals, with some literatures referring in plural to “the autisms” (Y.-J. Chen et al., 2024; Geschwind & Levitt, 2007; Uljarević et al., 2017) and a common adage being “if you have met one person with autism, you have met one person with autism.” Accordingly, sensory features are also quite heterogeneous across autistic persons (Uljarević et al., 2017) and across sensory modalities even within the same person (Z. J. Williams et al., 2023). These assumptions, while seemingly epigrammatic, suggest that to understand autism, one must look for early underlying processes that on the one hand constrain, or alter, developmental trajectories in such a way as to lead to the expression of a specific core of clinical features, while at the same time allowing for individual differences that make up the vastly heterogeneous manifestations of those features across individuals and across development. For example, different clusters of phenotypes follow different sensory developmental trajectories in infancy and map on to different developmental outcomes that include autistic features (Y. J. Chen, Sideris, et al., 2022), adaptive

and maladaptive behavior; participation in developmentally relevant contexts (home, school, and community; Y.-J. Chen et al., 2024) and co-occurring anxiety (Dwyer et al., 2022).

Principles

Our first principle is that any model of autism must be informed by our current state of knowledge of developmental maturation. However, this is no small task as development itself is incredibly complex, our knowledge of exactly how it unfolds typically from a single cell is nowhere near complete, and our understanding of how different systems typically interact with one another to shape outcomes is even less complete. Nonetheless, our understanding of developmental maturation provides a benchmark for understanding when and where during the lifespan divergences might begin between those who do and do not go on to have autism.

Second, we operate under the general belief of the orthogenetic principle outlined by Werner (1957) which stated that, “wherever development occurs, it proceeds from a state of relative globality and lack of differentiation to a state of increasing differentiation, articulation and hierarchic organization” (p. 57). One implication of this principle is that an organism, and the behaviors it generates at any given time point reflect the cumulative end point of an organized, systematic developmental process, whether or not developmental trajectories are considered to deviate in some way from expectations. That is, the autistic brain, and the autistic person to whom this brain belongs, needs to be assumed to be organized in a manner that reflects adaptation. While practically, this means respecting neurodiversity, it also suggests that we should be focused on understanding trajectories of development in the way that we design and interpret research. Asking what this means about the development of the autistic person will get us farther than determining and labeling a phenomenon as “deficient,” because it is different from the group to which we are making comparisons. Thus, we also believe that you can learn more by understanding what an organism does and its adaptive utility, than by trying to understand why an organism does not do the things one thinks it should.

Our third principle, which follows from understanding development as complex and adaptive, stems from occupational science (Hocking & Clair, 2011; Wilcock, 2002). This approach foregrounds people’s choices in “doing” and stresses the transactional (Dickie et al., 2006) and situated nature of human “occupations,” which begin in infancy (Humphry & Wakeford, 2006). That is, situational context plays an inextricable role in shaping what an individual chooses to do (e.g., behaviors, activities), how they do it (e.g., performance patterns, habits, routines), with whom (e.g., social relationships and structures), and what meaning it has to them (e.g., personal, cultural; Wilcock, 2002). It is also of note that there is some overlap between this perspective and that of embodied cognition, which considers the holistic nature of behavior and development within an integrated brain–body framework, as opposed to focusing solely on the brain (Foglia & Wilson, 2013).

Early in development, contexts supporting children’s engagement in daily life occupations (e.g., playing or eating) are largely physical (e.g., the infant’s opportunities for sensory exploration and navigation of natural and built environments) and social (e.g., caregiver responsiveness to the infant’s affective or communicative signals and addressing basic needs; peer interactions and models), but over time, cultural, spiritual, and historical contexts become progressively

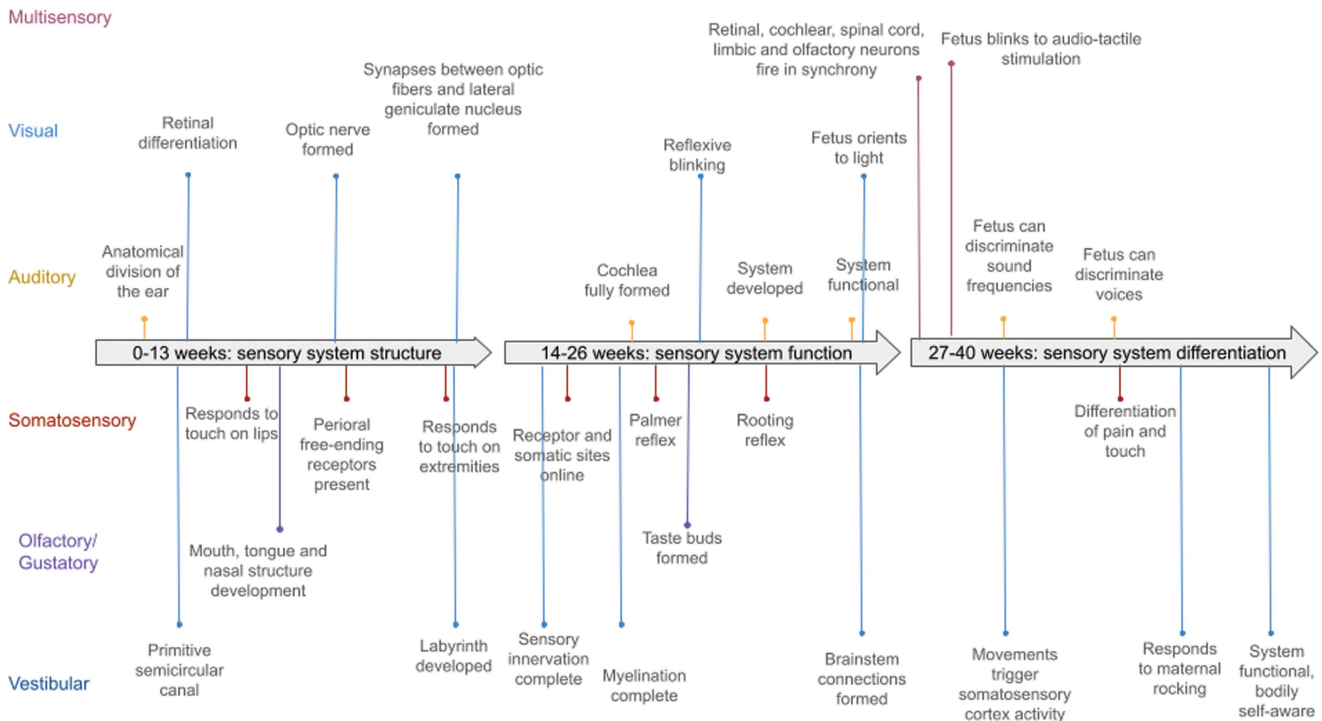
more salient (Bronfenbrenner, 1986; Yerxa, 1990). This principle guides our understanding of (a) individual differences in developmental patterns of engagement with the physical and social worlds, (b) “sensory experiences” as unique lived experiences with contextually relevant adaptations, (c) potential facilitators and barriers to meaningful engagement and development, and (d) more holistic approaches to early and supportive interventions that build capacities (not just address incapacities) for autistic individuals and their families.

Stemming from a need to anchor our knowledge in development, we focus on reviewing the sensory systems and processes as they typically unfold over the first few years of life. Here, we rely not only on empirical findings but also the theoretical models of developmentalists. This review provides a backdrop for framing our much more limited understanding of the development of autism over this same developmental time frame and for generating developmental cascades that could help us understand the role that sensory organs, functions and behaviors, and their contextual interactions play in the development of autism (Early Behavioral Manifestations of Altered Sensory Development in Infants at Elevated-Likelihood of Autism section). Critically and unfortunately, we omit olfaction and taste from this review, in large part, because work on these topics in autism are limited to a very small number of studies (e.g., Ashwin et al., 2014; Bennetto et al., 2007; Crow et al., 2020; Dusing, 2016; Koehler et al., 2018; Parma et al., 2013, 2014; Rozenkrantz et al., 2015; Sweigert et al., 2020). Further, although a detailed review of motor development per se is beyond the scope of this article, we recognize the inextricable links between sensory and motor aspects of development (Dusing, 2016), and therefore highlight important examples within specific sections below. The Pre- and Postnatal Sensory Development section will address the development of sensory systems and their integration in humans from fetal life onward; the Early Behavioral Manifestations of Altered Sensory Development in Infants at Elevated Likelihood of Autism section will address behavioral manifestations of altered sensory processing in infants at elevated likelihood of autism; in the Developmental Model section, we propose a developmental model that incorporates normative and autistic sensory development, with examples of putative “cascading” effects of sensory differences on the broader clinical–behavioral phenotype of autism. Each of these cascades represents a testable hypothetical framework intended to inspire future work in this area.

Pre- and Postnatal Sensory Development

Prenatally, the development of sensory systems sets the stage for all “experience-dependent” neurodevelopment (Rubenstein & Merzenich, 2003). Sensory systems develop in a specific order in utero and come online at different points in fetal development with all the senses demonstrating functional ability before birth (though vision is limited, see Figure 2). Broadly, sensory structures develop during the first 13 weeks, sensory functions emerge between 14 and 26 weeks, and sensory differentiation and integration begin in Weeks 27–40. Given this tight and orderly developmental timescale, potentially small changes in how and when the senses and/or their circuitry develop and interact can have cascading impacts on all aspects of functioning. One hypothesis proposed by Turkewitz and Kenny (1982) suggests that sensory systems are built sequentially so as to allow periods of uninterrupted unisensory development and

Figure 2
Typical Timeline of Fetal Sensory Development as a Function of Modality



Note. Broadly, the first 13 weeks reflect development of sensory structures, the next 13 weeks reflect the onset of sensory functions, and the last 13 weeks reflect sensory differentiation and integration. The sensory systems are presented on the y-axis, and the major sensory developments are color-coded and connect to the sensory modality they reflect. See the online article for the color version of this figure.

organization. The order of these developmental operations decreases the need for intersensory competition during embryonic development and confers behavioral advantages. For example, the first embryonic responses to stimulation are from the skin (e.g., the mouth) during which time other systems are still undeveloped and unresponsive. This allows the embryo to organize its behavior around that modality without competition from other inputs. This uninterrupted time paves the way for the development of the sucking reflex, which is a sensory–motor function critical to survival. Later, vestibular processing comes online and leads to a reorganization of the cutaneous sensory system to now include vestibular inputs. This iterative structure–function loop provides uninterrupted time for some *intrasensory* development and organization, prior to the need for *intersensory* integration and competition. Turkewitz & Kenny’s hypothesis suggests that small differences in the timing or organization of sensory structures, or their interaction with one another and with motor systems during early development, could have cascading impacts on distal sensory, perceptual, and cognitive experiences. This hypothesis, which is supported by animal studies (e.g., Kenny & Turkewitz, 1986; Lewkowicz, 2014), is also in line with current findings of differences in early sensory brain structures in autism (e.g., Hazlett et al., 2017). The authors also noted that earlier development or greater development or connectivity is not necessarily advantageous, suggesting that departures from expected brain growth trajectories in either direction may impact the developmental balance in cascading ways.

Over the first year of life, the infant’s sensory world opens up exponentially. No longer in the muted sensory environment of the womb, infants begin to explore their proximal world and begin to understand where their bodies end, and the external environment begins. Accordingly, post birth, there is a necessary reorganization of sensory systems that now needs to incorporate an external multisensory context that is ever changing and evolves over space and time.

In the first 6 months of life, neurodevelopment continues and becomes further integrated with the sensory experiences of the infant, now interacting more broadly with their external environments by rolling, reaching, and sitting upright. The sensory world of the infant is rich with input, including the presence of new uni-sensory stimuli, temporal coincidence across sensory modalities, haptic and oral exploration of the self, others, and objects through active engagement, interoceptive inputs, and their regulation by skin-to-skin contact. With ongoing exposure, frames of reference begin to change, and perceptual narrowing processes begin (Lewkowicz, 2014; Lewkowicz & Ghazanfar, 2009; Maurer & Werker, 2014). Infants have a lot to take in as they begin the process of making associations across and within sensory modalities, and acting upon the physical and social world through increasingly more complex and volitional behaviors (e.g., crawling toward toys or people; gestural communication), which further canalizes experiences and developmental trajectories (e.g., L. B. Smith & Thelen, 2003). However, as most infants are not yet walking independently until 12–18 months of

age, there are still limitations to the stimuli they are exposed to and in their ability to fully explore the sensory affordances within broader environments.

The whole world of the infant changes again once they are able to ambulate, though previous developmental constraints carry forward. Neurodevelopment during this period is slower relative to the infant stage, while sensory exploration continues and sensory preferences emerge, further shaping the environments and interactions children self-select into. Language production generally begins during this time as do key social cognitive behaviors such as joint attention. Both of these key developmental tasks emerge through a focus on objects the child is interacting with, such as labeling of objects and people and the referencing of these to others. While the world is in essence getting bigger, the types of sensory experiences, behaviors, and preferences are getting increasingly more solidified and hierarchically integrated into current developmental tasks. It is roughly at this point that common early signs of autism such as lack of joint attention and simple pretend play actions are noted, and some diagnoses can be reliably rendered by expert clinicians, even though the average age of diagnosis is much later. Unfortunately, from an autism sensory research perspective, this is generally where the empirical data begin.

While a few research groups have examined sensory development in infants at elevated likelihood of autism (ELA) either through familial or community risk (e.g., Y.-J. Chen et al., 2024; França et al., 2024; Piccardi et al., 2021), the vast majority of sensory research in autism is conducted with cognitively able, speaking individuals between the ages of 6 and adulthood, limiting the conclusions that can be drawn regarding the role of sensory processes, broadly construed, on our understanding of the development of autism (though see França et al., 2024). While some groups are focusing on neurobiological aspects of autism, and the emergence of social differences in the first year of life, few are focused specifically on sensory aspects of autism despite their critical importance to autism-relevant development. As such, we still have limited knowledge of what happens from a sensory perspective among children who go on to receive and autism diagnosis. Accordingly, to inform our model, we now turn to a detailed overview of the development of each sensory modality and their integration over the course of the first few years of development. We then move on to an examination of sensory *behaviors* in young autistic children and our limited knowledge of sensory neurobiology in autism before presenting our developmental model and recommendations.

Development of the Somatic Senses

The somatic senses—including touch, proprioception (sensory input from muscles, tendons, and ligaments signaling body position), and interoception (sensory input from the viscera signaling body condition)—are among the earliest to develop in utero (Hooker, 1952; Humphrey & Hooker, 1959; Piontelli et al., 1997), as the fetal body itself and the immediate physical environment (e.g., the maternal body) are the primary sources of sensory input prior to birth. In the prenatal environment, contact with the uterine wall, movement within the amniotic sac, continual displacement of lanugo on the surface of the fetal body by the amniotic fluid (Muller et al., 1991), sensations from developing organs beginning to come

online, and self-contact (e.g., hand-to-mouth; de Vries et al., 1982) combine to provide a rich tapestry of input about the body within its environment.

The submodalities of touch, interoception, and proprioception rely on discrete peripheral receptors and labeled lines to communicate with the central nervous system and have thus historically been studied separately. However, we consider them here holistically for two reasons: (a) the extant literature on their development, and in particular their disruption in autism, is much smaller than that for audition and vision, thus combining them allows for a more integrated view of the state of the literature; and (b) this inclusive approach facilitates presentation within the context of an emerging reconceptualization of the somatic senses into separate but converging “streams” of information that ultimately convey a holistic experience of bodily awareness.

In their 2017 chapter, Bremner and Spence described the development of three distinct types of somatic perception: (a) haptics (cutaneous touch and proprioception for continuous, fine-grained modification of touch dynamics during active manual sensing and discriminative exploration of the external environment); (b) self/body sensing with respect to the external environment (cutaneous touch and proprioception for defining the body and its boundary with extracorporeal space); and (c) affective touch (touch with affective relevance, e.g., for social and/or interpersonal contexts). In this review, we extend this third category by integrating Bremner and Spence’s framework with that of Craig (2002, 2009), who proposed that affective touch is part of a broader system of slowly conducting peripheral fibers (small, unmyelinated C-type fibers, contrasted with larger, myelinated A-type fibers for proprioception/discriminative touch). C fibers carry signals related to the physiological condition of the body, inclusive of pain, affective/social (pleasant) touch, temperature, and interoceptive signals from the viscera. Thus, haptics and self/body sensing combine touch with proprioception to process what is in the physical world, how the body relates to it and how one physically interacts with it, whereas affective touch combines touch with interoception to process changes in the physiological state of the body brought about by emotionally relevant stimuli on either side of the physical boundary of the skin. Though there is considerable cross talk between these streams, we will consider the development and neurobiological basis of each in turn, before addressing what is known about their integration.

Development of the Somatic Senses for Tactile Discrimination and Haptic Exploration

Early in gestation, fetuses move away from objects with which they come into contact, while later they move toward them (Valman & Pearson, 1980). This suggests that during gestation, developmental processes supporting active exploration of the environment begin to emerge. Although haptic exploration in adults is primarily performed with the hands, in infants and toddlers, much exploration of the world is performed with the mouth. Within the first few days of life, neonates measurably modify manual pressure based on the texture of objects placed in their hand (Jouen et al., 2012; Molina & Jouen, 2003), suggesting that the ability to discriminate texture is already present at or shortly after birth.

The ability to discriminate the shape of objects manually is also evident in neonates (Streri et al., 2000) and even in preterm infants as young as 28-week gestation (Marcus et al., 2012). A. J. Bremner and Spence (2017) argued that this responsiveness of tactile “reflexes” such as the palmar grasp reflex suggests that they extend to involve cortex, and thus more conscious perceptual processing than the term suggests. Between 3 and 5 months, reaching behavior emerges, followed by grasping as fine motor control of the extremities catches up to gross motor control of the limbs (Needham et al., 2015). Between 4 and 7 months of age, role-differentiated bimanual manipulation emerges (Ittyerah, 2017), in which one hand is used to stabilize an object while the other is used to explore it. Though handedness may not be firmly established until 4–6 years of age (Bryden et al., 2000; McManus, 2002), eventual hand preference is strongly correlated with bimanual role differentiation laterality between 9 and 14 months (Babik & Michel, 2016). The motor abilities for haptic exploration reach adult levels between 3 and 5 years of age (Bushnell & Boudreau, 1993; Kalagher & Jones, 2011a, 2011b), as does haptic discriminative ability (Bushnell & Boudreau, 1993). Thus, haptic perception begins very early in prenatal development and is largely mature by early childhood (A. J. Bremner & Spence, 2017).

Development of the Somatic Senses for Self-Identification/ Delineation From External Environment and Bodily Awareness

Newborn infants are able to detect synchrony between touch and vision, when this coincident input has body relevance (Filippetti et al., 2013). In the first 2–3 months of life, supine neonates engage in high rates of self-touch in addition to surface touch (e.g., floor) that provide input as to the boundaries of the bodily self (DiMercurio et al., 2018). Over the first 6 months, self-touches proceed from being localized mainly to the head and trunk to more caudal targets, mirroring motor development (B. L. Thomas et al., 2015) and driving reciprocal sensorimotor plasticity progressively more distally from the central axis of the body. In infancy, it is important to note that the processes for bodily awareness become much more multisensory, combining touch, proprioception, and vision to delineate the body from the world it inhabits (A. J. Bremner, 2016). This multisensory processing is apparent in cortical responses to video feed of one’s own movements in infants as young as 5 months (Filippetti et al., 2015). By 20 months, toddlers accurately locate common body parts, evidence of an internalized representational map of the body (Brownell et al., 2010; Waugh et al., 2015). The neural basis for this cognitive ability is in place by at least 7 months of age, as evidenced by spatial separation of evoked responses to touch on the hand versus the foot as measured by electroencephalography (EEG; Saby et al., 2015).

Piaget (1954) suggested that infants initially use a body-centered (egocentric) frame of reference to integrate these multisensory cues, and then through experience exploring and manipulating the environment, develop an external (allocentric) frame of reference that allows mapping to the external world more objectively. Some evidence suggests that this remapping occurs much earlier than Piaget originally believed (A. J. Bremner et al., 2008) and with more granularity (e.g., with evidence from Gilmore & Johnson, 1997, that between 4 and 6 months, the egocentric

reference shifts from retinal-centered to whole-head-centered). As infants become more mobile, the ability to update their frame of reference in response to changes in body posture emerges between 6 and 10 months (A. J. Bremner et al., 2008). Despite some debate about the timing of the emergence of allocentric coding, there is consensus that it is in place by the second year (Acredolo, 1978; J. G. Bremner, 1978; Lew et al., 2000). A rough full mapping of the body topography appears to be in place by approximately 30 months of age (Brownell et al., 2007, 2010) that continues to be refined as development continues (Camões-Costa et al., 2011). The rapid changes of the body’s size and shape during these years make this a continually computationally intensive effort.

Developmental Neurobiology of the Somatic Senses

Peripheral mechanoreceptors specialized for discriminative and haptic touch are optimized according to their adaptation profile which is in turn dictated by their morphology. Rapidly adapting mechanoreceptors are structurally optimized for detecting vibration and flutter, and slowly adapting mechanoreceptors for static touch. The development of these structures and the myelination of their innervating afferents begin prenatally and extend into the first year of postnatal life (Feito et al., 2018). While most research in humans has focused on the central aspects of somatosensory processing, work in animal models suggests that hyperexcitability of these peripheral mechanoreceptors may have a role in the behavioral tactile defensiveness that is common in autism (Orefice, 2020). Further, the location and nature of peripheral mechanoreceptor pathophysiology may give rise to heterogeneity in the developmental timing of behavioral hyperreactivity to touch (Tasnim et al., 2024). Centrally, the somatotopic organization of primary somatosensory cortex is already apparent in preterm infants (Dall’Orso et al., 2018). Behavioral habituation to repeated touch is observable in term-equivalent human neonates (Dumont et al., 2017), and recent work at the cortical level has shown that diminished somatosensory evoked responses to predictable, repeated touch (i.e., thalamocortical sensory gating), is measurable within the first year of life and predicts individual differences in sleep onset latency (De Laet et al., 2022). Increasingly sophisticated inhibitory phenomena within the primary somatosensory cortex, such as feedforward temporal adaptation of the cortical response based on prior sensory exposure and lateral inhibitory mechanisms for spatial localization have also been implicated in autism (Puts et al., 2014; Tommerdahl et al., 2007). These phenomena involve the interplay between excitatory and inhibitory function that has been proposed as an overarching theory of autism neurobiology (Hollestein et al., 2023), but the trajectory of their emergence in the early stages of human somatosensory development has not yet been characterized.

Development of the Somatic Senses for Affectively Relevant Touch and Interoception

While the peripheral fibers that support sensory processing for haptic exploration and movement must conduct signals quickly to allow for rapid, online adjustments in grip, gait, and posture, the somatic senses for affective touch and interoception operate on a slower timescale. The unmyelinated peripheral afferents that

mediate both interoception and affectively relevant touch have been described in detail by Olausson, Wessberg, Craig, and others (Ackerley et al., 2013; Morrison, 2012; Olausson et al., 2010). This slowly conducting fiber type appears to traverse the internal (visceral) and external (social-affective touch) sensory environments that converge to inform the perceived physiological state, and thus, the emotional state, of the body (Craig, 2008). For positive affective touch, these peripheral fibers, known as C-tactile (CT) fibers, are tuned to respond maximally to slow, gentle lateral movement across the skin (Wessberg et al., 2003). In infancy, such caregiving touch is intimately related to the maintenance of bodily homeostasis (Billner-Garcia et al., 2018; Fotopoulou & Tsakiris, 2017; Zoltowski et al., 2022), forming strong associative links between gentle, affiliative touch and positive somatic sensations such as clean skin, a full tummy, and the relaxation of sleep.

Even before these associations have time to develop, there is evidence of interaction between the positive and negative aspects of affective touch mediated by this system of slowly conducting fibers. Touch targeted to maximize CT fiber response, delivered in advance of a heel lance procedure, attenuates noxious-evoked brain activity in the first 1–3 days of an infant's postnatal life (Gursul et al., 2018). Gentle stroking in the first few weeks of life (Tuulari et al., 2019) elicits response from both primary somatosensory cortex, and the posterior insula, a primary cortical target of interoceptive, pain, and affective touch signaling that is well-established in adults (Löken et al., 2009). In the first few months of life, social touch demonstrably improves orienting to socially relevant stimuli in other sensory modalities (Della Longa et al., 2019; Lew-Williams et al., 2019; Rigato et al., 2019). Young infants also show implicit behavioral and neural evidence of interoceptive processing, exhibiting preferential looking to visual stimuli presented asynchronously with the heartbeat, and a heartbeat-evoked potential measured by EEG, at 5 months (Maister et al., 2017). At 9 months, infants show lower heart rate in response to CT-targeted touch than to slower or faster tactile stimuli (Fairhurst et al., 2014), suggesting a calming effect. At 12 months, response of the superior temporal sulcus to affective touch negatively predicts parent-reported aversive behavioral reactions to tactile stimuli (Miguel et al., 2019), whereas at 7 months, this brain region is not yet measurably responding to affective touch (Miguel et al., 2020).

It is important to note that the development of affective touch is not limited to CT-targeted, stroking touch. A prime example is the powerful impact of early skin-to-skin contact (Field et al., 1986; Maitre et al., 2017) which is more static (but likely also engages slowly conducting fibers with changes in skin temperature) on infant health and development. Various other somatic inputs have crucial roles in soothing and regulating infants, including vestibular (e.g., rocking, bouncing, swinging; Jahromi et al., 2004; Korner & Thoman, 1972) and rhythmic non-CT-targeted touch (e.g., patting) that may replicate in utero sensations such as translocation through amniotic fluid and maternal heartbeat. Deep pressure is also increasingly recognized for its calming properties (Grandin, 1992) and potential to signal the proximity of socially relevant conspecifics (Case et al., 2021). As infants develop the ability to recognize caregivers and contextualize social touch, many more complex factors converge with sensory input to influence the perception of affective touch (Cascio et al., 2019).

Integration of Somatic Information to Form a Holistic Body Percept

Though much extant research considers them separately, there is now some limited but growing information about how these “streams” of somatic sensory input for action, exploration, self-identification, and affective regulation integrate with each other and with other senses to provide a holistic perceptual experience of having a body in the world. As mentioned above, newborns can detect both spatial (Filippetti et al., 2015; R. L. Thomas et al., 2018) and temporal (Filippetti et al., 2013) multisensory congruence when aspects of the information are “body-relevant” (i.e., an upright vs. an inverted face), suggesting that prenatal experiences predispose infants to enter the world with a perception of their bodies already in place. This is corroborated by fetal behavior observed with 4D ultrasound (Hata et al., 2010) that shows organized hand-to-mouth movements, and by observations that neonates can differentiate stimuli that arise from outside versus within the body (Rochat, 2011; Rochat & Hespos, 1997). Rochat argued that an embodied sense of self as an organized and differentiated entity from other entities in the environment providing sensory input is the foundation for infant learning and development (Rochat, 2019).

Perception of interoceptive signals and their effects on body ownership may depend on individual abilities to regulate the balance of interoception and exteroception in given contexts (Crucianelli et al., 2018). Perceived body ownership is influenced by complex interactions between affective touch, proprioception, interoception, vision, and the vestibular system (Ponzo et al., 2018) that emerge in infancy in the context of iterative caregiver responses to infants' communication of their own bodily needs as well as bodily attunement with the caregiver (Montirosso & McGlone, 2020). Mundy et al. (2009, 2010) have noted the complex developmental interplay between neural systems for interoceptive and exteroceptive attention and their roles in joint attention, one of the earliest markers of the foundational social communicative skills affected by autism.

Development of Vestibular Sense

Closely related functionally to the sense of proprioception is the body's vestibular sense, which relies on signals from the inner ear to detect changes in head position in three-dimensional space. The vestibular labyrinth is continuous with the cochlea and comprises the semicircular canals and the otolith organs, which all signal movement via stimulation of hair cells, the same types of cells that respond to sound waves. Hair cells transmit signals via the vestibulocochlear cranial nerve to the cerebellum and to the brainstem vestibular nuclei. The vestibular system plays a critical role in the first months of life as the infant gains head and neck control and continues to support balance, postural stability, and movement throughout early childhood (Ornitz et al., 1979).

The semicircular canals primarily signal head rotation about each of the axes in three-dimensional space, while the otolith organs primarily signal changes in head position (e.g., linear or tilting movements). This system has strong and early developing connections with the oculomotor and skeletomotor systems, and the interaction of these systems manifest as a variety of reflexes that are often used to evaluate global neurologic function in infants. As central inhibitory influences come online, disappearance of certain

vestibular-mediated reflexes is also an important indicator of neurological health in the first months of life. Vestibular input in typical infancy (e.g., rocking, bouncing) is a primary mechanism of soothing (Korner & Thoman, 1972) and promotes skeletomotor and oculomotor development (Burns, 1985; Gregg et al., 1976) as well as auditory function (Korner et al., 1983; Neal, 1967). Rocking premature infants, an intervention that aims to recover lost prenatal input, improved motor, auditory, and visual function as well as increased weight gain in the treatment group (Neal, 1967). In children with developmental delays, vestibular stimulation improved motor skills and reduced stereotyped behaviors (MacLean et al., 1986). Thus, the role of vestibular input in early life is far-reaching as development progresses.

Because the vestibular system is so tightly coupled with oculomotor, visual, and skeletomotor systems, its function is typically experienced as part of a multisensory event rather than a specific “vestibular” event (MacLean et al., 1986). As such, many clinical or experimental tests of vestibular function also include oculomotor function. A common variant is rotary chair testing, in which the vestibulo-ocular reflex is measured by turning the patient or participant in a chair. The eyes travel the opposite direction from the direction of movement in order to maintain a constant visual perspective. The speed and acceleration of the chair movement, as well as the lighting and thus the amount of visual input, can be varied to assess different aspects of vestibulo-oculomotor integration. Outcomes from this type of test include response gain (e.g., amount of eye movement relative to the amount of chair rotation), the timing and decay of the response, and suppression of the response while fixating a visual target. In neonates, the assessment is conducted by the examiner holding the infant upright at eye level and turning in a circle (Brazelton & Nugent, 1995), whereas for young children under age 5, this type of test is commonly done sitting in a parent’s lap while the parent sits in the rotating chair. In children 5 and older, more extensive and invasive testing can be done, including more rapid head movements, tight fitting goggles, and caloric testing in which water is delivered into the ear canal. Vestibular dysfunction in infancy impacts gross motor development, but long-term effects are still an area of active research. Together, these findings suggest that somatosensation, integratively constructed, provides a wealth of information to the infant about where they are in the world, where they end and others begin, and has far reaching influences on learning and early social development (Mailloux et al., 2014; Mundy et al., 2009, 2010).

Development of Audition

The maturation of auditory structures and functions lays a foundation for the acquisition of speech and language and subserves broader multisensory (e.g., audiovisual) processing. The development of the peripheral auditory system begins quite early, with differentiation of the auditory and vestibular systems occurring in the fourth week of gestation (Arnold & Lang, 2001) and the cochlea reaching adult-equivalent size as early as 17 weeks (Jeffery & Spoor, 2004). The auditory system is physically developed by 20 weeks and begins to function shortly thereafter, with evidence that the first fetal responses to sound are evident by 25 weeks of gestation (Igarashi & Ishii, 1980; Jutras et al., 2020). Although the fetal acoustic environment is somewhat impoverished (Abrams & Gerhardt, 2000), recent computational evidence simulating the

prenatal auditory environment suggests that the low frequencies that reach the fetus are particularly adaptive for integration of auditory input over long timescales which predicts later emotion recognition ability (Vogelsang et al., 2023). Further, exposure to speech sounds during the third trimester is theorized to facilitate future language learning (Gervain, 2018). By 30 weeks, the fetus can discriminate sound frequencies, which precede the ability of the fetus to discriminate its mother’s voice (B. S. Kisilevsky et al., 2009) and the emotional qualities of speech (S. Kisilevsky et al., 2004). At the time of birth, an infant’s peripheral auditory system is already adult-like in both structure and function, but central auditory structures continue to develop substantially throughout childhood and into early adulthood (Jutras et al., 2020; Powles-Glover & Maconochie, 2018).

Many countries have developed programs for early hearing detection and intervention that include neonatal screening regardless of risk factors for hearing loss. This produces a wealth of data that can be used to understand early auditory development. Otoacoustic emissions and the auditory brainstem response are common tests for neonatal hearing concerns and can be done at birth or later in infancy. A recent study demonstrated that, with analytic methods beyond what are used clinically, the auditory brainstem response can be used to differentiate neonatal intensive care unit neonates that will, versus will not, go on to develop autism, suggesting promising utility as a very early biomarker (Torres et al., 2023).

Auditory Detection, Discrimination, and Identification

The most basic auditory ability, sound detection, is present at birth; however, hearing thresholds are known to decrease considerably during the first 6 months of life (Olsho et al., 1988; Tharpe & Ashmead, 2001) and, to a lesser degree, throughout early childhood (Haapaniemi, 1996; Trehub et al., 1988). Notably, high-frequency thresholds (e.g., 4,000 Hz) reach adult levels much more quickly than low-frequency thresholds (e.g., 500 Hz), though the physiologic basis of this difference has yet to be determined (Litovsky, 2015). Another early emerging auditory function is stimulus discrimination, the general ability to perceive differences between two acoustic events on the basis of their spectrotemporal properties.

Electrophysiological studies indicate that infants can distinguish different frequencies within the first few days of life (Håden et al., 2015, 2016) allowing infants to discriminate their mother’s voice from that of a stranger (Beauchemin et al., 2011; DeCasper & Fifer, 1980). Frequency discrimination, however, is far from mature at birth. Rather, studies have demonstrated that this skill and its neural correlates continue to develop into adolescence (Bishop et al., 2011; Maxon & Hochberg, 1982). Other forms of auditory discrimination, such as those based on sound intensity or duration, are also evident in infancy (e.g., Sinnott & Aslin, 1985), though performance on such discrimination tasks improves substantially until early school age (Jutras et al., 2020; Litovsky, 2015). Auditory identification, the ability to recognize specific auditory stimuli, is another early emerging ability that has been observed even in utero (as early as 33- to 34-week gestational age) using maternal voice stimuli (Jardri et al., 2012; B. S. Kisilevsky et al., 2009). As with auditory detection and discrimination abilities, auditory identification (as measured using speech reception thresholds in quiet and noise) improves substantially with age, reaching adult-like performance

levels on most tasks by the age of 10–12 years (Koopmans et al., 2018; Leibold & Buss, 2019; M. C. Smith, 2019).

Auditory Temporal Processing

Auditory temporal processing is defined as the perception and interpretation of acoustic events distributed in time (Eggermont, 2015; Jutras et al., 2020). This ability is essential for multiple auditory functions, including speech understanding, sound localization, and communication in noisy environments. Moreover, neurophysiological studies have indicated that low-level temporal auditory processing ability during the first years of life is a significant predictor of language development throughout early childhood (Benasich et al., 2002; Benasich & Tallal, 2002; Choudhury & Benasich, 2011; van Zuijlen et al., 2012). Psychoacoustically, auditory temporal processing can be subdivided into auditory temporal *integration* (e.g., the ability to more easily detect sounds of a longer duration; Solecki & Gerken, 1990), auditory temporal *resolution* (e.g., the ability to follow temporal changes in sound patterns; Moore, 1985), and auditory temporal *sequencing* (e.g., the ability to identify the order in which stimuli were presented; Szymaszek et al., 2006), and each of these abilities exhibits a distinct developmental trajectory.

Auditory Temporal Integration and Resolution

Based on a study of 7-month-old infants, auditory temporal integration abilities are believed to mature rather early in development (Berg & Boswell, 1995), although inefficiency in temporal integration in school-aged children relative to adults has been demonstrated under some experimental conditions (Fox et al., 2010; S. He et al., 2010). Gap detection thresholds in noise, commonly used to index auditory temporal resolution, have been shown to decrease substantially from infancy to childhood (Trehub et al., 1995), and while some children demonstrate adult-like temporal resolution as young as 5 years of age, individual differences in maturational trajectories can be substantial and differ according to stimulus parameters (Buss et al., 2017; Gay et al., 2020). The developmental course of temporal sequencing is less clear, as tasks routinely used to tap this auditory skill are often unable to be completed successfully by individuals under approximately 6 years of age (Berwanger et al., 2004). The extant literature that has been conducted to date, however, suggests that this ability continues to develop gradually until adult-like performance is reached between the ages of 10 and 12 years (Berwanger et al., 2004; Jutras et al., 2020; Wang & Yang, 2018).

Binaural and Spatial Hearing

Binaural integration, the ability to process and combine the different information simultaneously being processed by each ear, is a key auditory function that supports sound localization and source segregation in the auditory environment. Integration of binaural signals is present in newborns, with studies demonstrating evidence of this phenomenon as early as 4 days of age (Bertoncini et al., 1989). Sound localization, which primarily relies on binaural cues such as interaural level and time differences (Akeroyd, 2006), has been demonstrated in newborn infants hours after birth (Muir et al., 1989).

Auditory Scene Analysis

In real-world listening scenarios such as classrooms, home environments, and public spaces, individuals encounter a complex array of auditory stimuli that vary in content, location, spectro-temporal characteristics, and behavioral relevance. To successfully navigate these environments, individuals must be able to organize the “auditory scene” into discrete percepts that can be further integrated with information from other sensory modalities. Perceptually, auditory scene analysis requires a listener to determine which sounds do and do not “belong together,” and this grouping and segregation of various sound sources (known as “auditory streaming”) lay the foundation for the creation of more abstract “auditory objects” (Litovsky, 2015; Winkler et al., 2009). Auditory streaming is poorly developed in infants, who have particular difficulty attending to one voice in the presence of competing speech sounds (Newman, 2009). Together, these findings suggest very early sensory development of auditory inputs has important downstream impacts on the development of language and social function.

Development of the Visual System

Normative development of the visual system results in a highly complex, modular, hierarchical system at maturity. The cardinal developmental principle of critical or sensitive periods arose, in part, from studies of the visual system (Hubel & Wiesel, 1963; Wiesel & Hubel, 1963a, 1963b). While the visual system is less mature at birth relative to other modalities, in part because of the limited light available in the intrauterine environment, there is still considerable evidence for prenatal visual development.

Prenatally, the visual system is the last to develop with retinal differentiation beginning around 5 weeks (Hendrickson et al., 2008; Kelley et al., 1995) and the optic nerve forming around 8 weeks prenatally. The retina is partially functional by 13 weeks with synapses between optic fibers and lateral geniculate nucleus developing around this time. Reflexive blinking has been seen by 16 weeks, but the eyelids remain closed until 22 weeks. Retinal and subcortical structures develop prenatally, which is thought to be a result of spontaneous firing of retinal cells (Wong, 1999). These cells fire in coordinated waves of activity, traveling across the retinal surface and propagating systematically to higher areas of the visual system, giving rise to retinotopic mapping even in the absence of visual stimulation. While retinal cells are present by 23 weeks and myelination of the optic nerve begins by 24 weeks, it is not until 26 weeks that neurons are present in the visual cortex and can respond to light (K. Dunn et al., 2015) and that fetuses orient with both eye movements (Donovan et al., 2020) and head movements (Reid et al., 2017) toward or away from light shined on the maternal abdominal wall. Orienting toward visual stimuli is coordinated in part by prenatal development of the superior colliculus, which integrates multisensory input with somatic maps to drive head, eye, or body movements toward the stimulus (Pitti et al., 2013). An intriguing study suggests that fetuses may orient preferentially toward visual stimuli configured similarly to faces relative to an inverted configuration (Reid et al., 2017), but methodological concerns (Scheel et al., 2018) and lack of independent replication thus far temper confidence in this finding.

Orienting and Habituation to Visual Stimuli in Infants

As described above, subcortical mechanisms for orienting the head, eyes, or body toward a visual stimulus are already in place by birth. More volitional control emerges by 2–3 months postnatally and depends on oculomotor abilities to hold fixations and saccade to new targets (also see the role of vestibular system in oculomotor control; Carson et al., 2017; Fukushima & Kaneko, 1995). Covert orienting to visual or other exteroceptive stimuli can also be indexed without movement, by autonomic readouts such as pupil dilation or the cardiac orienting response or by visual evoked responses (VERs). Pupil dilation is mediated by the sympathetic autonomic system and allows more light to reach the retina, while cardiac orienting is a deceleration of heart rate, mediated by the parasympathetic system, in response to a stimulus of interest (Colombo, 2001; Sokolov et al., 2002). This cardiac orienting response is thought to direct oxygen away from the periphery and toward the central nervous system to facilitate information processing. Cardiac deceleration in response to visual stimulation has been demonstrated in infants as young as five months (Lewis et al., 1966, p. 199). At birth, neonates demonstrate a pupillary constriction response to light and a behavioral orienting response, which infant researchers have leveraged to develop paradigms that measure preferential looking at one stimulus compared to another to infer visual discrimination (Tronick & Clanton, 1971). Using VERs, evidence for covert visual orienting is present by 4.5 months of age (Richards, 2005). Visual habituation, measured behaviorally using reduced looking to repeated stimuli, is evident in neonates (Slater et al., 1983, 1984), though this response continues to develop over the first months of life (for a thorough review, see Colombo & Mitchell, 2009). VER evidence of habituation is evident within the first month postnatally (González-Frankenberger et al., 2008; Matuz et al., 2012).

Development of Visual Stability and Motion Sensitivity

As infants gain mobility, keeping the representation of the visual field stable is important. The compensatory vestibulo-ocular reflex in which the semicircular canals trigger eye movements to oppose head movement, and the optokinetic reflex, which stabilizes the visual image during movement through the environment using saccades, are both functional at birth, but gradually mature over the first year. Optic flow sensitivity and smooth pursuit eye movements may not develop until after 6 months, alongside development of independent locomotion (e.g., scooting, creeping, or crawling). While an in depth review of this subcortically mediated integration between vision, vestibular sense, and the oculomotor system is beyond the scope of the article, it is worth pointing out that these phenomena, which serve vision-for-movement, contribute to the delineation of the dorsal visual stream (Mishkin & Ungerleider, 1982), through which visual information relevant for navigating and interfacing with the environment travels. This stream flows from the primary visual cortex (V1) in the occipital lobe to the parietal cortex where visual information is integrated with somatic sensory information to guide motor exploration and navigation of the environment.

Development of Visual Acuity

Early in the neonatal period, infants begin to actively scan the visual environment (Haith, 1980), focusing preferentially on edges or other areas of high contrast or motion. Visual acuity, contrast sensitivity, color sensitivity, and sensitivity to direction of motion all improve in the early neonatal period (Banks & Salapatek, 1983). Many of the driving influences for improved acuity throughout infancy can be attributed to peripheral structures: Acuity improves in infancy as receptor cells migrate toward the center of the retina and elongate to absorb more incoming light. At the same time, the eyeball physically increases in size which improves the lens' power. These occur concurrently with central changes including faster and more efficient signal transmission attributable to myelination, synaptogenesis, and pruning (Stanley, 1991). Heavy synaptogenesis and arborization in V1 peak between 8 months and 2 years (Huttenlocher et al., 1982), and pruning that refines visual receptive fields and delineation of cortical columnar units contributes to increased acuity throughout middle childhood.

Development of Binocularity

The independence and mutual cooperation of both eyes is a complex and multifaceted phenomenon that develops postnatally. The development of ocular dominance columns (e.g., vertical columns of cortex that respond to input from only one eye or the other such that neighboring columns respond to opposite eyes) in the primary visual cortex (V1) is experience-dependent and requires binocular function over the first few postnatal years. The establishment of ocular dominance columns is thought to require both neurotrophic factors and Gamma-aminobutyric acid (GABA)-mediated lateral inhibitory activity (Elliott & Shadbolt, 2002). The integration of information from these separate columns forms the basis for stereopsis, the development of which depends on a critical period that begins around 4 months of age (Birch et al., 1985) and lasts between 1 and 3 years (Banks et al., 1975). A recent study found an increased incidence of strabismus in infants who went on to have an autism diagnosis (Eyoh et al., 2023), suggesting that early altered binocular input could in part explain reports of altered binocular rivalry in autism (Robertson & Baron-Cohen, 2017; Robertson et al., 2013; Spiegel et al., 2019).

Foundations of Visual Categorization and Separation of the Dorsal and Ventral Visual Streams

The counterpart to the dorsal visual stream described above is the ventral stream—extrastriate cortex in the ventral temporal lobe that is dedicated to fine visual detail and form perception of static stimuli such as objects, faces, and alphanumeric characters (Mishkin & Ungerleider, 1982). Parts of this visual stream were long thought to be innately category-selective, for example, specialized a priori to process faces or objects, but the relative roles of innate proto-organization and visual experience-driven plasticity are still contested (Cabral et al., 2022). Accumulating evidence suggests that this category selectivity depends to a large extent on visual experience and intensive processing with exposure and learning of commonly overpracticed categories of stimuli (Bi et al., 2016; Gauthier et al., 2014). There is evidence for this stream's separation

from the dorsal stream as early as 4 months postnatally. In 4-month-old infants, preferential looking to actionable objects varies with object location (looking for action, dorsal stream) but not identity, while looking to nonactionable objects varies with object identity (looking for detailed perceiving, ventral stream) but not location (Mareschal & Johnson, 2003). Before acquiring independent mobility, the most frequent visual stimuli to which infants are exposed are faces (Jayaraman et al., 2015; Jayaraman & Smith, 2019), while visual exposure to other stimuli such as objects may be more limited. Accordingly, exposure to mostly familiar faces trains feature discrimination during the first year (Sugden & Moulson, 2020). This is reinforced by nonhuman primate work demonstrating an association between face processing and ventral visual connectivity in the first 2 months (Ford et al., 2023). After the first 6 months, infants are increasingly able to hold objects and bring them in front of their own face for visual inspection, promoting both dorsal (vision for reaching and grasping) and ventral (object discrimination) development (Atkinson, 2017). They may also be exposed to a wider range of caregivers and continue to learn facial feature discrimination with less familiar faces. Between 6 and 18 months, as independent locomotion (e.g., scooting, crawling, cruising, and later also walking) emerges, the dorsal stream undergoes intensive development (Atkinson & Braddick, 2020). This is consistent with research describing a positive association between visual motion perception and gross motor development (Thompson et al., 2017).

Development of Multisensory Integration (MSI)

The external world is complex, inherently multisensory, and we, from birth onward, must extract regularities from information impinging on our senses in this unfamiliar, ever changing spatial and temporal environment, in order to learn. While all of our senses are functional, though not completely developed, at birth, evidence from studies of animals and human infants converge on the finding that the integration of sensory information is an experience-dependent process that tunes itself to the parameters of its environment over time (Stein et al., 1993; Stein & Stanford, 2008). Studies of human infants have, in general, focused on how amodal properties (information that is not uniquely represented across modalities such as rate and intensity) and unique sensory qualities (e.g., color is only available to the visual system) are used by infants (Bahrick & Lickliter, 2000, 2012; Bahrick & Watson, 1985). While other researchers focus on temporal integration (Hillock-Dunn & Wallace, 2012; Powers et al., 2009; Stevenson & Wallace, 2013) and whether and when children weight sensory inputs optimally (Burr & Gori, 2012; Ernst & Banks, 2002; Gori et al., 2008), for example, these types of studies are focused on children that are school-aged and older.

The Rules Guiding MSI

MSI, defined in the strict sense (Stein & Stanford, 2008), reflects the notion that the integration of information from multiple sensory modalities lead to supra-additive benefits that statistically supersede the sum of the unisensory responses (Besle et al., 2004; Brandwein et al., 2013). Important developmental questions focus on when and how this integration emerges, the rules that govern its optimal occurrence and how it can be demonstrated

experimentally. While supra-additivity suggests that the whole is (statistically) greater than the sum of its parts and has been demonstrated across multiple systems that include single unit recordings (Meredith et al., 1987; Meredith & Stein, 1983, 1986; Nagy et al., 2006), local field potentials (Ghazanfar et al., 2005; Kayser et al., 2008; Montemurro et al., 2008), and at times electrophysiological responses (Brandwein et al., 2013; Russo et al., 2010) and blood-oxygen-level-dependent (BOLD) responses (Calvert et al., 2000, 2001), though see (Beauchamp, 2005), this strict quantification is not always observed, nor is it always necessary for demonstrating that integration has occurred. For example, behaviorally, MSI is reflected in findings that accuracy for multisensory stimuli is greater than would be predicted by probability summation, while for response times, race models are commonly used to quantify whether integration has occurred (e.g., for a review, see Stevenson et al., 2014). Despite differences in how MSI is quantified, there is evidence to suggest that contrary to what was once thought, multisensory inputs are integrated early in the processing stream, in primary sensory cortices that were originally considered to be unisensory (Meredith & Stein, 1983; Stein & Stanford, 2008). As examples from animal studies, cells that respond to multisensory stimulation are found in the deep layers of the superior colliculus, while more anterior layers respond to visual inputs alone. Further, the borders between sensory cortices are highly responsive to multisensory stimulation (e.g., secondary somatosensory cortex of rat integrates auditory–somatosensory inputs, Menzel & Barth, 2005). Evidence from studies of humans supports a similar profile, with, for example, auditory cortex being active during audio-visual letter presentation (van Atteveldt et al., 2004) and findings that among adults MSI occurs as early as 50 ms for auditory–somatosensory (Foxe et al., 2000; Murray et al., 2005) and audio-visual (Giard & Peronnet, 1999; Molholm et al., 2002) stimulus combinations over sensory regions, when measured with ERPs. Together these findings suggest that brains are more multisensory than was once thought, and that MSI occurs earlier in the processing stream than was once believed.

The field of MSI has been guided by three rules that suggest that the presence of stimuli from more than one modality leads to some sort of facilitation, be it behavioral (e.g., increased accuracy, decreased response time) or neuronal (e.g., larger BOLD response). These rules are referred to as the temporal, spatial, and inverse effectiveness rules, and help an organism develop a unified percept of an event, despite getting different types of information from different sensory modalities that travel at different speeds and provide both redundant and unique information. The temporal rule holds that MSI is more likely when the component unisensory stimuli occur within relatively close temporal proximity, the limits of which can extend hundreds of milliseconds (Hillock et al., 2011; Powers et al., 2009; Stevenson et al., 2011; Stevenson & Wallace, 2011). The spatial rule holds that facilitation occurs when component unisensory stimuli emanate from the same general spatial location (Kadunce et al., 1997; Meredith & Stein, 1986, 1996; Spence, 2013; Wallace & Stein, 2007), though see Spence (2013). Finally, the inverse effectiveness rule suggests that MSI is more likely to occur when the component stimuli elicit a small response or are harder to perceive (Ghazanfar et al., 2005; Lakatos et al., 2007). This is evidenced in studies, for example, that show that individuals are more accurate at detecting a word presented in noise when they

have access to visual information such as the speaker's lips then when they simply have access to the auditory input, which is not necessary in situations where there is no noise in the signal. However, the veracity with which these rules hold beyond individual neurons or brain regions is unclear (Spence, 2013). That is, while neuronal spiking increases significantly in response to a multisensory stimulus relative to its component unisensory stimuli in a manner consistent with the rules stated above, human neural measures such as BOLD responses, ERPs, and behavioral metrics such as response times generally do not meet this strict criterion despite facilitative effects of MSI being present and measurable. It is also important to note that, given known differences in fine motor control (Choi et al., 2018) and resulting inter-trial variability (Z. J. Williams et al., 2019) in autism, response time differences should be interpreted cautiously. Further, other than a few studies which we review below, there is nearly no empirical data on how and whether these rules apply to infants. Rather, theoretical and empirical accounts of MSI in infants have focused on how infants use sensory information.

How Does Multisensory Development Unfold?

Newborns seem to come equipped with, or have developed in utero, some ability to take in information from one sensory modality and transfer that information in a meaningful way to another. While there is debate about the veracity and replicability of findings (e.g., Maurer et al., 1999; Meltzoff & Borton, 1979), there is evidence to suggest that within hours of birth infants are able to visually recognize a shape that they had felt and transfer texture information from vision to touch and touch to vision (Sann & Streri, 2007). Multisensory neurons are active very early in development among nonhuman animals (e.g., Stein et al., 2013), but the evidence is less clear for the developing human. Limited in utero evidence from sonographic monitoring of fetal eye movements suggests possible auditory–somatosensory MSI by 28 weeks (Petrikovsky et al., 2003). Response times or psychophysical measures are difficult to acquire from infants such that evidence of MSI is garnered either from looking time or from neural measures such as EEG and functional magnetic resonance imaging. However, there is a strong body of work that supports the notion that infants attend to the amodal redundancies of their environment.

The work of Lorraine Bahrack and Robert Likliter has been at the forefront of our understanding of how infants make sense of a multisensory world. They propose the *intersensory redundancy hypothesis* that suggests that infants begin to develop top-down attentional control from using amodal properties of objects and environments to guide their attention. These amodal properties include temporal and spatial synchrony, rhythm, tempo, and intensity and are available from each sensory modality. When these amodal properties co-occur across modalities, not only are their perception facilitated, but these properties/events are selectively processed and attended to, which can be seen in infants as young as 4 months of age (Bahrack et al., 1981). Interestingly, this facilitation is evidenced in 4-month-olds for information that is both social and nonsocial, suggesting that these might be governed by the same domain-general mechanisms (or emerge at the same developmental time). In addition, Bahrack and Likliter also suggested that when the information specified by an event is unique to a modality (e.g., color is a feature that is unique to vision), then

infants attend to it more than when that same information is presented in a bimodal or multisensory context. For example, the color of an object would be better attended to when presented alone, then when paired with a sound. That is, the perception of unique unisensory information is facilitated by the absence of nonredundant salient features. Likliter and Bahrack proposed that there is a “salience hierarchy” in which amodal features are detected first, followed by properties that are modally specified. This hierarchy is evident moment to moment as well as maturationally and provides a basis for understanding the nature of how sensory inputs guide the maturing infants' perceptions and attention, in a bottom-up, feature-based manner. Further, the authors suggested that in the face of complexity (new developmental tasks), there will be a return to previous or earlier forms of functioning whereby unisensory and multisensory inputs serve different facilitative functions in different contexts. These hypotheses are in line with developmental accounts of differentiation and increased specification of the developing organism (e.g., Gibson, 1969; Werner, 1957), perceptual narrowing associated with social communication and language (Lewkowicz & Ghazanfar, 2009; Pons et al., 2009) and also dovetail nicely with theories focused on the development of MSI over larger swaths of developmental time (Murray et al., 2016).

There is preliminary support that supra-additivity and temporal integration are present early in development. For example, Hyde et al. (2010) found that 3-month-old infants showed supra-additive responses to a compound audiovisual stimulus beginning around 400-ms poststimulus onset as measured by event-related potentials (though the sample was small and the more than 50% of their original sample had to be excluded making replication necessary). In addition, Neil et al. (2006) demonstrated the presence of supra-additivity in infants between 8 and 10 months of age, using head turn time as their metric. Infants can also perceive temporal synchrony for both nonspeech and speech sounds at birth. However, the development of MSI along with the optimal use of sensory inputs are quite protracted and do not reach adult like levels until children are around 10 years of age (Barutchu et al., 2009; Brandwein et al., 2013; Burr & Gori, 2012).

Together, the examination of sensory structures, functions, their development, and their interaction provides a backdrop for understanding sensory development in autism and the role that early sensory differences may play in the emergence of higher order functions and behaviors consistent with an autism diagnosis. What is clear from this review is that sensory development is well underway in the first postnatal year, and while developmental refinements, recalibrations, and performance improvements on tasks continue, most of the data suggest that by the school-age development is almost “adult-like.” Infants in their first year perceive affective touch, have a full mapping of body topography, can discriminate, detect, and identify sounds, can effectively process temporal information, have an emerging ability to categorize visual information, can detect audiovisual temporal synchrony and rely on sensory cues (unisensory, multisensory, and amodal patterns) to learn about and act upon their environment. These are the building blocks not only of sensory development and processes but also form the basis of language and social development, which are critical features to our understanding of autism. That is, there are important developmental changes in the processing and integration of unisensory and multisensory inputs that

occur prior to and can predict social communication abilities in typically developing individuals. While there is still much to know about sensory development in nonautistic populations across development, the data in autism clearly demonstrate a central role of sensory alterations in the early *behavioral* manifestations of autism. After we review these early behavioral manifestations of autism, we present our model as well as some plausible developmental hypotheses and conclude with a set of recommendations for research moving forward.

Early Behavioral Manifestations of Altered Sensory Development in Infants at Elevated Likelihood of Autism

In alignment with the orthogenetic principle, the study of early behavioral indicators of sensory differences in autism is generally less differentiated by sensory modality than are studies of school-aged children, adolescents, and adults. While there is an emerging literature on the neurobiology of early sensory differences among infants who were at elevated likelihood of, and went on to develop autism, which we discuss below, there is a relatively large body of work focused on the early behavioral manifestations of sensory features in this population. There is ample evidence documenting various behavioral manifestations of sensory features in autism across the lifespan (Ausderau et al., 2016; Ben-Sasson et al., 2007; Ben-Sasson, Hen, et al., 2009; Cline et al., 2016; Crane et al., 2009; Lane et al., 2014; McCormick et al., 2016; Philpott-Robinson et al., 2016; Wiggins et al., 2009), which is comprehensively summarized in many review articles (Barbaro & Dissanayake, 2009; Ben-Sasson, Carter, & Briggs-Gowan, 2009) as well as book chapters (Baranek et al., 2014). We use the word “features” as opposed to symptoms since specific behavioral manifestations may reflect enhancements, not just deficits, in sensory processing functions, and sensory experiences may be personally reported as positive or negative by different people in different contexts.

Prevalence rates and manifestations of sensory features vary based on the age of the participants studied, as well as based on measures and units of analysis (e.g., item-, modality-, or domain-level) used in the studies (Ausderau et al., 2014; Baranek et al., 2006; Ben-Sasson et al., 2007; Kern et al., 2006; Kientz & Dunn, 1997; Le Couteur et al., 1989; Leekam et al., 2007; O'Donnell et al., 2012; Ornitz et al., 1977; Tomchek & Dunn, 2007; Watling et al., 2001). The existing literature, which is primarily cross-sectional in methodology, emphasizes the vast behavioral heterogeneity of sensory features inherent in this population, especially in older children and young adults, and to a lesser extent, prodromal features that manifest early in development (e.g., before features are fully manifested and can be reliably diagnosed, Ausderau et al., 2014; Baranek, 1999; A. E. Lane et al., 2010, 2014; Patten et al., 2013; Uljarević et al., 2016). Only recently have we begun to focus more on understanding longitudinal development (change or stability) in sensory features over time (Baranek et al., 2019; Y. J. Chen, Sideris, et al., 2022; S. A. Green et al., 2012; McCormick et al., 2016; Perez Repetto et al., 2017). Although sensory features are included in the clinical diagnosis of autism (*DSM-5*; American Psychiatric Association, 2013), there is limited information about their early mechanistic underpinnings. Thus, we focus on sensory features evident behaviorally during the first 2 years of life.

Given the definitional challenges described above, as well as the ways these features have been studied in young autistic children, in

this section, we focus our behavioral descriptions on three overarching pan-modal constructs or “sensory response patterns”—sensory hypo-responsiveness (e.g., attenuated or absent responses to stimuli; HYPO, also referred to as hyporeactivity, or under-responsivity), sensory hyper-responsiveness (e.g., averse or avoidant responses to stimuli; HYPER, also referred to as hyperactivity or over-responsivity), and sensory interests, repetitions, and seeking behaviors (SIRS, e.g., showing intense craving for, or fascination with, particular sensory experiences; SIRS; Ausderau et al., 2016; Baranek et al., 2013). We acknowledge that theoretically, motor challenges such as dyspraxia may stem from sensory processing differences, particularly in the somatosensory or multisensory realms (Ayres & Robbins, 2005; S. J. Lane et al., 2019; Roley et al., 2015; Schaaf & Mailloux, 2015), but description of these motoric features is beyond the scope of this article. There are also emerging psychometric findings from extant parent-report measures with autistic children over the age of 3 years (Z. J. Williams et al., 2023), suggesting that further subcategorization by modality (e.g., HYPER-Tactile; HYPER-Auditory, HYPO-Tactile, HYPO-Auditory, etc.) may add value in characterizing sensory features and testing mechanistic hypotheses. However, these findings are limited to parent-report measures, and there are no studies replicating this work with infants and toddlers who are at elevated likelihood of autism.

The evidence for early behavioral presentations of sensory features in infants and toddlers who go on to later be diagnosed with autism stems primarily from (a) personal narratives (mainly parent recollections of their infant's development; Clifford & Dissanayake, 2008; Sivberg, 2003; Vostanis et al., 1998; Young et al., 2003), (b) clinical chart/case reviews (Dahlgren & Gillberg, 1989), (c) retrospective video analysis (home movies; Adrien et al., 1993; Baranek, 1999; Clifford & Dissanayake, 2008; Colgan et al., 2006; Osterling & Dawson, 1994; Poon et al., 2012), (d) prospective studies of infants at familial risk of autism (Bryson et al., 2007; Feldman et al., 2021; Lee et al., 2019; Mulligan & White, 2012; Ozonoff et al., 2010; Sacrey et al., 2015; Wolff et al., 2019; Zwaigenbaum et al., 2005), and more recently, (e) prospective studies of community samples and screening for ELA (Baranek et al., 2015, 2022; Ben-Sasson & Carter, 2013; Y. J. Chen, Sideris, et al., 2022; Turner-Brown et al., 2013).

Birth to 6 Months

Overall, there are few empirical studies characterizing specific sensory features in infants at elevated likelihood of autism below 6 months of age in either community or familial risk samples. Some researchers have suggested that neurobiological changes may be evident before the onset of behavioral symptoms in this age range (e.g., Wolff et al., 2017); however, given the paucity of robust measures of sensory features across this age range, it is also possible that developmental deviations may have been missed by existing clinical measures or parent report. Parents of infants who go on to be diagnosed with autism may be more likely to notice general disruptions in sleep–wake cycles, or temperamental challenges, which could reflect sensory processing differences (Baranek et al., 2013; Bryson et al., 2007; MacDuffie et al., 2020; Nguyen et al., 2018), but this requires systematic study.

A robust finding that emerges by 6 months of age in infant sibling studies is decreased visual fixation to faces (Chawarska et al., 2013),

or more specifically to eyes, which appears to progressively decline from 2 to 6 months of age (Jones & Klin, 2013). Future replications are needed with community samples to track phenotypic similarities or differences, as well as to determine the extent to which social versus nonsocial factors (or some combination) may be affecting the emergence of these differences in ELA infants. For example, if nonsocial sensory information captures attention more than social information, if multisensory information is confusing, or if stimuli are experienced as aversive or painful, the infant may disengage from a social interaction, thereby constraining their learning and participation, which may trigger a developmental cascade.

Delayed or absent behavioral responses to sensory stimuli (e.g., *hyporesponsiveness*) are often operationalized with measures that tap orienting to novel sensory stimuli. The use of standardized neonatal assessments during early postnatal periods and their correlations with later outcomes showed that the integrity of early sensory orienting mechanisms is critically important to development (Lester & Tronick, 2004). Behavioral orienting is typically measured through eye/head movement in the direction of a sensory stimulus such as the shaking of a rattle or movement of a bright object. Decreased orienting to visual and auditory stimuli on the Neonatal Behavioral Assessment Scale (Brazelton & Nugent, 1995), a standardized measure, as well as parent reported auditory hyporesponsiveness (low registration) on the Infant-Toddler Sensory Profile (W. Dunn & Daniels, 2002) at 2- to 7-day postpartum among infants born full term each predicted more failures on the Modified Checklist for Autism in Toddlers screening for autism at 18 months. Further, infants with familial risk of autism (as a group) had fewer visual fixations to inanimate as well as animate (social) stimuli at 2–3 months of age compared to infants at low likelihood of autism (Bradshaw et al., 2020), suggesting that decreased attention to sensory information is associated with increased likelihood of autism.

Separate from orienting, standardized neonatal assessments also measure the integrity of an infant's responses to repeated sensory stimuli (habituation), visual tracking, and other self-regulation functions that depend upon intact sensory processing. Some studies have applied these methods to the study of premature infants, who are known to be at higher likelihood (~7%) of developing autism later in life (Agrawal et al., 2018).

Gaze aversion during face-to-face encounters between infants and caregivers has been suggested as a manifestation of hyperresponsiveness—that is, overstimulation causes the infant to look away from the caregiver, and looking away results in lower heart rate (Field et al., 1986). Thus, the capacity to regulate gaze patterns may serve a sensory regulating function; infants who are overaroused by visual information may avert their gaze from caregivers as a protective mechanism during highly stimulating face-to-face interactions. In the autism literature, gaze differences are often reported with toddlers at elevated likelihood of autism, but researchers disagree whether lack of eye contact points to overarousal or indifference to specific social cues (Moriuchi et al., 2017). Interestingly, premature infants (at term-equivalent age) who showed *less* gaze aversion were found to have a *greater* likelihood of a later autism outcome, indicating that perhaps early regulatory mechanisms were atypical for these infants (Pineda et al., 2015). Such findings underscore the importance of deciphering the underlying functions of observable behaviors and may explain why patterns of hypo- or hyperresponsiveness, and fluctuations between

the two, are evident in at-risk populations that may vary as a function of development and result in cascading effects on social interactions and other outcomes (see Campi et al., 2023 for a description of the optimal engagement band for further explanation). In sum, more research related to the development of sensory orienting/attention, and habituation mechanisms pre- and postnatally may facilitate our understandings of specific sensory response patterns observed behaviorally and their connection to later autism outcomes.

6–12 Months

By 6–12 months of age, behaviors thought to indicate sensory *hyperresponsiveness* have been noted across modalities (e.g., touch aversion, intense reactions to visual stimuli, covering ears to sound, overreactivity to sensory toys) in infants who are later diagnosed with autism in both community samples (Baranek, 1999; Baranek et al., 2022; Y. J. Chen, Sideris, et al., 2022) and familial risk samples (Clifford et al., 2013; Wolff et al., 2019; Zwaigenbaum et al., 2005). There is also considerable evidence that points to sensory *hyporesponsiveness*, as measured by failure to orient to auditory or visual stimuli, in infants with familial risk (Elison et al., 2013; Falck-Ytter et al., 2018; Sacrey et al., 2015), as well as those from community samples who are later diagnosed with autism (Baranek, 1999; Freuler et al., 2012). Specifically, sensory (and motor) concerns (by 6 months of age) that included increased staring at objects after they had been reached for, preceded social communication concerns as reported by parents of infant siblings who were later diagnosed with autism (Sacrey et al., 2018). Further, infant siblings of autistic children showed longer visual orienting latencies to images of faces and objects on an eye tracking task at 7 months of age (Elison et al., 2013). Although many studies focus on the visual modality, there is evidence to suggest that these findings extend to the tactile modality with findings that 12-month-old infants who showed slower initial responses (potentially hyporesponsiveness) to caregiver touch during playful interactions, and then disengaged more abruptly (potentially hyperresponsiveness) were more likely to be later diagnosed with autism (Kadlaskar et al., 2019). These findings suggest that infants at elevated likelihood of autism have narrower bands of optimal engagement with sensory stimuli that may appear as both hypo- and hyperresponsive behaviors within the same infant, which thereby constrains opportunities for social engagement and results in further developmental cascades (Campi et al., 2024).

Reports of heightened *sensory interests or engagement in repetitive sensory play* with objects (e.g., rubbing hands repetitively on an object, unusual mouthing/sniffing, visually fixating on objects that move or spin) have also been noted by 6–12 months of age in studies utilizing observational methods (Baranek, 1999; Freuler et al., 2012; Osterling & Dawson, 1994; Ozonoff, 1995; Ozonoff et al., 2008; Zwaigenbaum et al., 2005) as well as parent report (Bryson et al., 2007; Dahlgren & Gillberg, 1989; Guinchat et al., 2012). Some of these sensory focused behaviors were reported to precede social communication symptoms (Sacrey et al., 2013). Interestingly, some researchers have hypothesized that sensory hyporesponsiveness and SIRS in infancy may be related to challenges disengaging attention manifested by the end of the first year of life (Baranek et al., 2018; Elsabbagh et al., 2013), although more controlled research linking these constructs is needed.

12–24 Months

By the second year, sensory features are commonly reported in infants who later receive an autism diagnosis, especially for behaviors thought to indicate *hyporesponsiveness* and *sensory seeking behaviors* (Ben-Sasson et al., 2008; Eeles et al., 2013); prospective longitudinal studies in recent years have added confidence to these findings (Philpott-Robinson et al., 2016; Ryckman et al., 2017; Wolff et al., 2019). For example, Grzadzinski et al. (2020) prospectively followed a community sample deemed to be at higher likelihood of autism based on the First Year Inventory (Baranek et al., 2003) and demonstrated that from 14 to 23 months, an increasing trajectory of sensory *hyporesponsiveness* across tactile, auditory and visual modalities as measured with the Sensory Processing Assessment (Baranek, 1999) was associated with higher autism symptom severity during the preschool years. Further, 24-month-old infant siblings with a later diagnosis of autism (at 36 months) had more auditory processing problems and poor registration (*hyporesponsiveness*) across modalities as measured by parent report (Germani et al., 2014). One possible explanation for hyporesponsive behaviors after 12 months of age could be related to visual disengagement deficits, also called “sticky attention” (Elsabbagh et al., 2013; Sacrey et al., 2015). For example, on an eye-tracking task, infant siblings who were later diagnosed with autism showed longer latencies of attentional disengagement to visual stimuli (objects) at 14 months of age, but interestingly, not at 7 months of age (Elsabbagh, Fernandes, et al., 2013). Similarly, longer latencies to disengage visual attention starting at about 12 months of age, which continued through 15-, 18-, and 24-month assessment time points for infant siblings later diagnosed with autism at 36 months of age have also been documented (Sacrey et al., 2015) suggesting that persistent challenges with visual disengagement across the second year of life negatively impact later cognitive abilities.

Behaviors thought to indicate hyperresponsiveness to sensory stimuli have been shown to increase in frequency and/or intensity in the early toddler and preschool years for children at greater likelihood of developing autism (e.g., Guinchat et al., 2012; Zwaigenbaum et al., 2005). One possible explanation may be that hyperresponsive behaviors lead to greater avoidance of specific sensory activities, which provides these children with fewer opportunities to learn to modulate their responses over time. However, it is also possible that as children age, they become more effective at communicating their sensory discomfort, which may result in caregivers endorsing more obvious hyperresponsive behaviors on questionnaires. Although SIRS are also observable, many sensory-focused actions are quite typical in early development (e.g., mouthing objects, playing with water) and may not concern parents until such a time that they seem different from peers or interfere with adaptive behavior. Over time, the environmental stimuli to which toddlers are exposed and expectations for self-regulation from caregivers increase, and thus caregivers may become more aware of sensory differences as children age and the child’s behavior looks progressively different from peers. Caregivers are also apt to endorse more symptoms, including sensory features, once they learn of a diagnosis (Lord, 1995).

The presence of *sensory interests*, *repetitions*, and *seeking behaviors* is well-documented by 18–24 months of age in both infant

sibs and in community samples of infants later diagnosed with autism. This includes, for example, reports of increased licking and sniffing behaviors during the Communication and Symbolic Behavior Scales at 18–24 months of age in a community sample of children later diagnosed with autism (Watt et al., 2008). Further, *sensory interests*, *repetitions*, and *seeking behaviors* in the toddler period may have negative downstream effects on later social development with findings that infants with familial risk of autism demonstrated more *sensory seeking* behaviors on the Sensory Processing Assessment for Young Children (Baranek, 1999) at 18 months, and these features were significantly associated with the severity of later social symptoms measured by the Autism Diagnostic Observation Schedule at 36 months of age; this association was found to be mediated by deficits in social orienting behaviors (Damiano-Goodwin et al., 2018). Using a community sample, Baranek et al. (2018) replicated Damiano-Goodwin et al.’s (2018) study and noted similar cascading patterns of SIRS at an earlier age point (e.g., 12 months) to later autism symptoms, with partial mediation through social orienting. Thus, stronger social orienting skills may help to attenuate the negative impact of SIRS on later autism severity.

In a large community sample that was tracked prospectively from infancy through school age (Y. J. Chen, Sideris, et al., 2022), growth trajectories of the three sensory response patterns (e.g., higher levels of hyporesponsiveness, hyperresponsiveness and SIRS over time) significantly predicted the severity of autistic traits as measured by the Social Responsiveness Scale by 6 years of age. Overall, the findings from studies of the behavioral manifestations of sensory differences in autism suggest that they are present early, measurable and predict autism outcomes among participant groups that are at elevated likelihood of autism through infant sibling studies as well as among community samples. Critically these behavioral manifestations are often seen before the presence of other higher level indicators of autism and differentially predict the presence of repetitive behaviors and restricted interests as well as social communication challenges, thereby supporting the inherent value of assessing and understanding sensory features as a means of understanding autism.

While the behavioral manifestations are clearly evident in the first 2 years of life, their underlying neurobiology is still in the early discovery phases. Nonetheless, neuroimaging studies of infant siblings at elevated likelihood of autism have provided clues to the neurobiological differences that may underlie these early alterations in sensory and attentional processes. By 6 months old, several structural brain differences have been identified in infants later diagnosed with autism, including atypical development of white matter tracts (Wolff et al., 2012), greater cerebral spinal fluid (Shen et al., 2017), and increased corpus callosum area and thickness (Wolff et al., 2015). Between 6–12 months, infants who go on to have autism show hyperexpansion of cortical surface area, primarily in sensory cortical regions (Hazlett et al., 2017). Some mouse models of brain overgrowth also show sensory hyperresponsiveness, suggesting that hyperexpansion of sensory cortical regions might underlie sensory, motor, and attentional orienting deficits, though this has not been directly examined in human infants. At 8–9 months, EEG studies have demonstrated that infants at elevated likelihood of autism have reduced habituation to deviant tones (Guiraud et al., 2011), and infants later diagnosed with autism show reduced repetition suppression (increased cortical activity) to repeated tones

(Kolesnik et al., 2019) and tactile pulses (Piccardi et al., 2021), suggesting that early deficits in habituation to sensory stimuli precede later emergence of full autism symptoms. How these map on to behavioral indices is currently unknown, but these findings suggest that there are neuronal differences specific to sensory processes that precede evidence of social communicative deficits.

In summary, emerging data from studies of infant siblings of autistic children indicate that alterations in sensory relevant biological processes that may eventually manifest as the classic social and communication symptoms of autism emerge long before these behaviors are evident. Atypical sensory processes are likely the earliest behavioral manifestations of the altered neurobiological development that begins by the mid-fetal developmental period. Many of the structural and functional brain changes that have so far been identified in human infants who go on to have autism are also linked to sensory, motor, and attentional functions. However, the studies to date are limited by small sample sizes and methodological challenges in measuring sensory functions across the first year, as well as on their reliance on infant sibling samples rather than also focusing on community samples of infants with ELA.

Early emerging sensory processes and their spatial and temporal integration are critical foundations to supporting language, cognitive, and social development. The slow maturation of sensory processes, their context-dependent learning, and their fundamental importance for the processing of both internal and external environments make sensory features, sensory neurobiology, sensory processes, and sensory development critical areas for further study. The field needs studies that systematically characterize the emergence and developmental trajectories of heterogeneous sensory features from birth through 2 years of age. These would ideally assess how individual differences are associated (concurrently and predictively) with social communication, cognitive, motor, and adaptive outcomes in both familial likelihood and community samples of infants at increased likelihood of a later diagnosis of autism. While differences in behavioral responses to sensory stimuli, such as orienting to, or disengaging from sensory stimuli, are documented by 6–12 months of age in infants who are later diagnosed with autism (Baranek, 1999; Clifford et al., 2013; Sacrey et al., 2018), it is unknown exactly *when* these sensory differences emerge or *how* they change over time. Further, prospective studies beyond infant siblings samples are just beginning to emerge (e.g., Y. J. Chen, Sideris, et al., 2022) and show that individual differences in sensory response pattern trajectories (e.g., hypo-, hyperresponsiveness and SIRS) map onto dimensional traits associated with autism in the general population; however, more research is needed to better understand to what extent these relate to neurobiological differences. More prospective studies spanning larger developmental ranges and using stable observational measures of sensory constructs along with measures of social communication and cognitive outcomes are also needed.

While we are still a long way away from being able to determine with certainty the role that sensory features may play in developmental cascade to a diagnosis of autism, the data are clear that these are early emerging and cover multiple and inter-related sensory systems. Further, there is substantial research tying early differences in sensory response patterns (including hyporesponsiveness, hyperresponsiveness and SIRS) differentially to later social communication and restricted and repetitive behavior outcomes, suggesting that differences in

sensory development might provide a unifying framework for understanding these frequently differentiated symptom classes in autism. Early occurring sensory differences could constrain developmental trajectories such that they lead to the expression of a specific core of clinical features, while also allowing for heterogeneous manifestations of those features across individuals, and across development.

Developmental Model

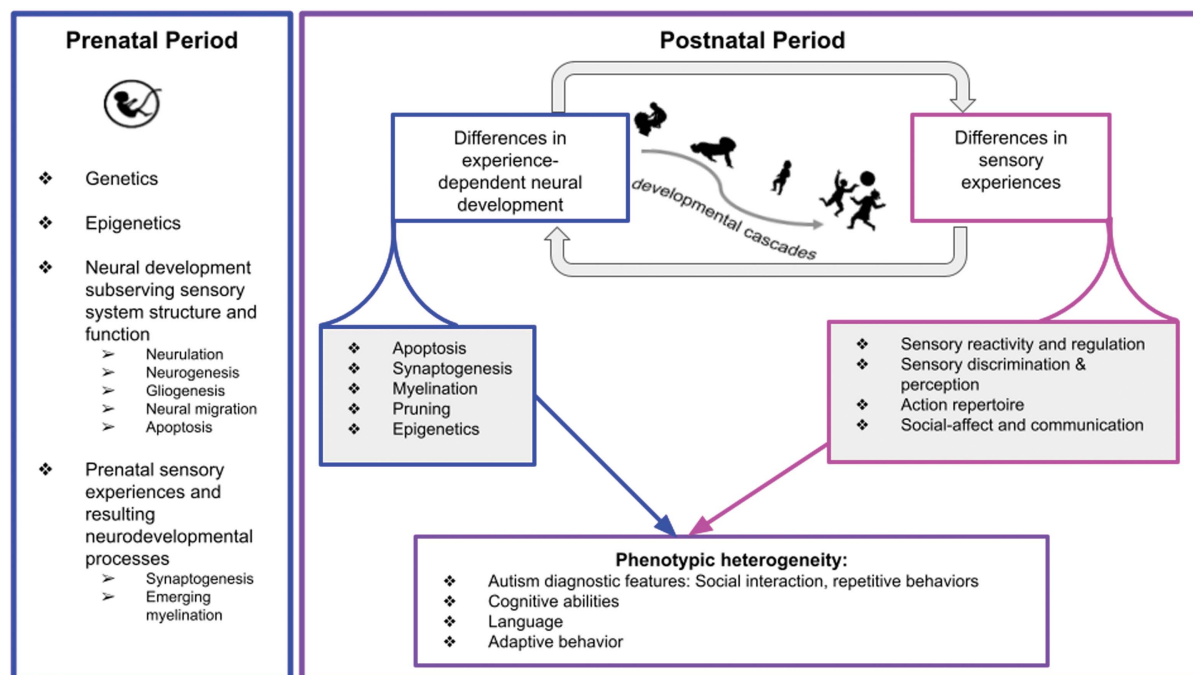
The model we provide below (Figure 3) is meant to underscore the balance and interaction between sensory experiences and neurodevelopment and their changes over time. In the womb, sensory experiences are more limited than they are postnatally but are nonetheless critical in this phase of neurodevelopment. Individual differences in the structure, timing, or integration of neural development subserving sensory systems and their functions may have cascading effects. After birth, sensory experiences with the external environment make up a larger part of infant's world, while neurodevelopment continues. With time, the pace of neurodevelopment slows while the sensory experiences a growing child is exposed to expands and gets intertwined with the child's preferences and environments in larger and larger ways that also lead to important individual differences. The development of cognitive abilities is wholly dependent on parsing an ongoing stream of sensory input, and the brain appears to employ both prospective statistical prediction of sensory events and retrospective reconstruction of perceptual and cognitive events arising from this stream (Polyanskaya, 2022). Further, sensory exposure over the course of development provides "priors" for both of these processes and coalesces to determine the prestimulus neural activity upon which new stimuli are imposed (Zaretskaya, 2024), underscoring the iterative nature of how sensation informs higher order processes over developmental time.

The cascades provided are theoretically based and have connections to both typical development and autism. These do not always have direct empirical and developmental evidence for their causative links to autism but nonetheless are plausible links that could be explored to further our understanding of the role that sensory processes, broadly construed, have in the pathogenesis of autism.

Plausible Developmental Cascades

Prenatal Foundations and Early Neural Development

From Prenatal Body Maps to Social Cognition. In the first trimester, by approximately 7 weeks, most sensory input is somatic, setting up a template for bodily exploration (e.g., hand to mouth or feet) and the beginning of a representation of one's self (e.g., body maps). This also sets up associations between movement and tactile experience. Further MSI is rapidly incorporated postnatally, with neonates demonstrating the ability to detect synchrony between touch and vision when this coincident input has body relevance (Filippetti et al., 2013). These associations and multisensory integrative processes in turn lay the foundation for the development of body maps and self–other distinctions which are necessary for the later development of social cognition (A. J. Bremner & Spence, 2017; Chagnaud et al., 2017; Rochat, 2003). Evidence from developmental scientists suggest that joint attention reflects the coordinated action of sensory–motor systems in nonautistic

Figure 3*Model of Sensory Development and Its Potential Impact on the Autism Phenotype*

Note. In the prenatal period (blue), there is considerable sensory input, although much less than postnatally. Genetically determined processes interact with sensory experiences in prenatal brain development. Postnatally, a sharp increase in the amount, intensity, and complexity of sensory experiences amplifies and diversifies the processes of shaping the structure and function of the nervous system (pink). This includes sensory reactivity and regulation, sensory discrimination and perception (e.g., enhanced perception, acuity), action repertoires such as sensory-seeking, motor performance and praxis, and social affect and communication (including joint attention and orienting responses). This continues throughout development in a reciprocal and recursive manner. In autism, differences in both aspects of these processes produce developmental cascades that propagate and lead to the autism phenotype centered on reduced or divergent social communication and patterns of repetitive, restricted behaviors, in addition to other associated features (purple). See the online article for the color version of this figure.

infants (Yu & Smith, 2017), a hypothesis that has not been tested in infants with or at elevated likelihood of autism. However, joint attention is one of the earliest social milestones known to be delayed in autism (Malesa et al., 2013), appears on most screeners and diagnostic measures for toddlers (Dumont-Mathieu & Fein, 2005), and is currently attributed not to sensory or sensory-motor differences but rather to social communication challenges.

From Divergent Development of Auditory Cortex Subdivisions to Enhanced Perception and Atypical Language. The human auditory cortex is divided into three parts, the core, the belt, and the parabelt. The core responds optimally to pure tones while the other two regions respond selectively to complex sounds. The core is considered a true primary cortex and has strong projections from the thalamus, while the other two regions have secondary sensory cortical features and show more direct connections to the prefrontal cortex. For a detailed description of the anatomic organization of human auditory cortex, see Hackett (2015). Neurophysiological evidence suggests infants' processing of low-level speech sounds (e.g., syllable/ba/) during the first years of life predicts language development throughout early childhood (Benasich et al., 2002; Choudhury & Benasich, 2011; van Zuijen et al., 2012). The ability of young infants to process (nonspeech) sounds presented in quick succession predicted language development at 36 and 48 months of age, suggesting

a role for both low-level auditory processes and temporal processing in the development of language, in addition to known roles for more complex auditory processing. Neural evidence of hyperfunctionality of the core/basic processing division of auditory cortex comes from longitudinal magnetoencephalographic data, which demonstrates rapid early maturation in young children with autism (H. L. Green et al., 2023). In autism, there appears to be a distinction whereby the perception of pure tones is enhanced while the perception of complex tones does not differ between autistic and nonautistic groups (Bonnell et al., 2003, 2010). Thus, divergent developmental trajectories within subdivisions of auditory cortex may be related to the paradoxical combination of enhanced perception of simple auditory stimuli, and difficulty with more complex auditory properties that are needed for linguistic processing that is impacted but developmentally malleable in autism (Eigsti & Fein, 2013).

Early Postnatal Integration and Sensory Motor Interactions

From Sensory Network Structural Inefficiencies to Social Function. At 6 months, infants who go on to have a diagnosis of autism show network inefficiencies in regions involved in low-level sensory processing. Further, these structural differences predict

autism symptom severity at 24 months. This suggests that early differences in sensory processing may give rise to foundational network differences that impact later social communication abilities (Adolphs, 2010; Nowell et al., 2020; Wallace et al., 2020). In addition, among children and adolescents with autism, sensory cortices appear connected more strongly with one another than in nonautistic individuals (Belmonte et al., 2004; Courchesne & Pierce, 2005; Hong et al., 2019; Rudie & Dapretto, 2013), a finding that may suggest compensatory changes in response to diminished connectivity in the earliest stages of infancy though further study on the connectivity among sensory areas and to other areas of cortex are needed.

From Midbrain MSI to Social Orienting. The superior colliculus integrates multisensory input for rapid orienting to potentially salient stimuli before in-depth processing has a chance to occur and to position the sensory apparatuses of the body to receive more detailed information about the stimulus (Pitti et al., 2013). In nonhuman primates, superior collicular neurons with central receptive fields respond preferentially to face-like patterns of visual features within the first 50 ms of stimulus onset (Le et al., 2020), implicating the superior colliculus as a rapid face detection system. Dysfunction in this structure affecting MSI could delay or impede the development of orienting to faces in very young infants and cascade to thus impact social development more broadly (Jure, 2022).

From Cortico-Subcortical Connectivity in the Thalamus and Basal Ganglia to Repetitive Behaviors and Restricted Interests. Recent work with older adolescents with and without autism finds that autistic children show greater connectivity between unisensory visual and auditory regions and the basal ganglia and the thalamus (Cerliani et al., 2015). The basal ganglia, a group of GABA mediated nuclei, play an important role in motor and cognitive actions which relies on the integration of sensory information (Reig & Silberberg, 2014; Subramanian et al., 2017). The basal ganglia have been associated with repetitive behaviors in mouse models of autism (Subramanian et al., 2017) as well as across disorders associated with repetitive movements including obsessive compulsive and tic disorders. The basal ganglia have been implicated in autism with postmortem findings of atypical cell density and volume (Wegiel et al., 2014). In addition, in autistic adolescents, greater connectivity between the basal ganglia and visual and auditory regions was associated with greater repetitive and stereotyped behaviors, providing a link between sensory neurobiology and repetitive behaviors (Maximo & Kana, 2019). While these data were acquired in older children and warrant replication with younger samples, they provide putative neuroanatomical connections.

Sensory Responsiveness and Social Development

From Imbalances in Excitatory/Inhibitory Signaling to Sensory Overwhelm. GABA-mediated inhibition is a critical mechanism throughout the nervous system for keeping excitatory projections in check, filtering sensory information, spatially tuning neuronal receptive fields, and enabling adaptation to repeated stimulation. In the visual system, autistic individuals show longer durations in ambiguous perceptual states during binocular rivalry (J. L. He et al., 2021; Robertson et al., 2013; Wood et al., 2021), a process that depends on GABA-ergic inhibitory function in visual

cortex. In the somatosensory system, GABA mediates adaptation of cortical neurons to low-level stimuli, a response that is also affected in autism (Puts et al., 2017, p. 20). The evidence base for altered GABA signaling in autism is mixed (Hollestein et al., 2023; Song et al., 2023; Thomson et al., 2024; Tokatly Latzer et al., 2023) but has not yet been measured in infants at ELA who are followed prospectively. If present in the first few years of life, these differences and other similar GABA-mediated processes could converge to produce a sensory experience that is unstable, less precise, and less able to filter irrelevant or redundant input, leading to sensory overwhelm and associated hyper- or hyporesponsiveness.

From Sensory Exploration to Social Communication. Toddlers actively explore their physical environments, and opportunities for social interactions with caregivers arise from this sensory-motor exploration (e.g., shared attention and “follow-in” utterances; Grzadzinski et al., 2021; Kinard et al., 2017). Sensory hyporesponsiveness including lack of orienting to salient stimuli and/or sensory avoidance due to hyperresponsiveness may limit this exploration and thus results in fewer opportunities for social communication (Baranek et al., 2013; Bruckner & Yoder, 2007; McDuffie et al., 2012; Yoder, 2006). Further, hyperresponsiveness is also linked to higher levels of restricted/repetitive behavior in toddlers (Boyd et al., 2010), which then further limits the diversity of exploratory play and opportunities for social communication. Cascading effects of altered sensory responsiveness on social (Baranek et al., 2018; Damiano-Goodwin et al., 2018) and communication (Feldman et al., 2022) skills have been demonstrated in infants at elevated likelihood of autism.

From Sensory Hyperresponsiveness to Repetitive Behaviors Through Anxiety. Emerging theoretical (K. L. Williams et al., 2021) and empirical work suggests that sensory hyperresponsiveness predicts anxiety among infants and young children at ELA (Masters, 2023), toddlers with autism (S. A. Green et al., 2012) as well as among typically developing preschoolers (Carpenter et al., 2019). Anxiety, in turn has been shown to impact the presence of restricted and repetitive behaviors (RRBs) both among children with autism and among autistic children (Joosten et al., 2009; Rodgers et al., 2012; Sukhodolsky et al., 2008). Direct links between these three constructs have been noted in at least one study in which the relation between hyperresponsiveness (and hyporesponsiveness) and RRBs in autistic youth between 8 and 16 years of age was mediated by anxiety (Wigham et al., 2015). Together these findings suggest that sensory hyperresponsiveness may lead to anxiety, perhaps because of a sense of decreased control over an unpredictable environment, which in turn leads to increased repetitive behavior to serve as a coping mechanism in children with autism.

From Altered Sensory Connectivity to Social, Linguistic, and Cognitive Abilities. Converging evidence from both structural and functional neuroimaging implicates hyperconnectivity within sensory pathways in children and adults with autism at multiple levels of the processing hierarchy, including brainstem (Surgent et al., 2022), thalamus (Fu et al., 2019), and cortex (França et al., 2024). Alongside this, elevated thalamic-primary sensory cortical connectivity in infants at high familial likelihood of autism is associated with reduced connectivity with higher order brain regions (Wagner et al., 2023), suggesting a trade-off that may bias the nervous system toward lower level processing and away from complex social stimuli. While overconnectivity of sensory systems has been reported frequently in individual studies, a mega-analysis

of individuals 5–58 years old (Ilioska et al., 2023) with perhaps the largest sample to date suggests that some (though not all) sensory networks are underconnected in autism, measuring connectivity both within the networks and between the sensory and other networks. A notable exception was hyperconnectivity between thalamus and the somatomotor network. This may reflect more time for compensatory changes in this network, which is among the earliest to mature.

These findings are complemented by functional findings that autistic individuals activate sensory regions more so than their typically developing peers when completing cognitive tasks (Russo et al., 2010; Sahyoun et al., 2010; Soulières et al., 2009). While the developmental precursors of these findings are less well understood, recent evidence suggests that these connectivity patterns can be seen in 2-year-olds with autism (Xiao et al., 2023). Specifically, in nonautistic toddlers, connectivity between temporal cortex and frontal, and anterior cingulate cortex, was associated with language and social communication, patterns that were not seen in autistic toddlers. Rather, in 2-year-olds with autism, it was differences in connectivity between temporal cortex and visual regions that was related to social and linguistic processing. Whether and how this greater sensory connectivity in toddlerhood relates to findings in infancy of hyperexpansion of sensory regions is an open question but these data do suggest that sensory regions of the cortex likely impact social, linguistic, and cognitive development in autism.

These cascades continue to influence development and are known to have impacts on peer relationships (social), emotion regulation (anxiety/arousal; Dwyer et al., 2022), academic performance (cognitive/learning), and broader community participation (Y.-J. Chen et al., 2024). In addition, there are also strengths that develop because of sensory differences that may have positive influences on occupations-specific interests/hobbies, skills, savant abilities, and vocational opportunities.

Conclusions and Recommendations for Future Research

In reviewing the experimental field of sensory/perceptual processing in autism, there is a striking gap in approaches to science across ages and developmental levels. For example, there is an emerging body of research on infants and toddlers with autism using passive techniques (e.g., resting state magnetic resonance imaging, eye-tracking), observational tools, or parent reports that suggest that sensory features of autism are present, measurable, and meaningful predictors of outcomes. These studies are generally inclusive of community participants who range in socioeconomic status, sex, and support needs (Y. J. Chen, Sideris, et al., 2022; Lee et al., 2022) or include younger siblings of autistic children who are at elevated likelihood of an autism diagnosis and community comparison participants. However, after the age of 6, the focus of sensory autism science, though it was not reviewed here, seems to shift to more experimental, computer-based studies that aim to isolate sensory modalities and specific aspects of function. While it offers precision in measurement to a certain extent, it is unclear if the findings from these studies are generalizable to the entire spectrum of autism nor how findings relate to or predict symptoms. As we begin to develop experimental paradigms for younger children/toddlers, there are important lessons garnered from this work that can be used to guide the field. One such area relates to task demands and their impact on autism research. For example, paradigms requiring overt motor

responses such as a button press especially those indexing responses time as a measure of perceptual ability (Z. J. Williams et al., 2019) are confounded by deficits in motor execution and coordination in autism. Tasks that demand sustained attention and verbal task instructions carry similar limitations. Many studies do not adequately account for nonsensory differences such as response criterion in detection paradigms; people with autism exhibit more conservative criteria than neurotypical peers for responding “yes” when they are uncertain about the presence of stimulus (Quinde-Zlibut et al., 2020). These methodological limitations may lead to an overestimation of sensory or perceptual *deficits* in autistic people and an underestimation of autistic *strengths* in visual discrimination (Hagmann et al., 2016; Kopec et al., 2020; O’Riordan et al., 2001), tactile spatial localization (Tommerdahl et al., 2007), and pitch discrimination (Bonnell et al., 2003, 2010; Heaton, 2003). If experimental tasks place high motor or language demands on participants, which reflect areas of challenge in autism, the presence of enhancements in perception may be obscured, leading to null findings or even findings of erroneous deficits.

The vast majority of autism research has historically focused on the social and linguistic aspects of autism. That body of literature has appropriately utilized longitudinal designs to understand the role of development in social communication in a developmental disorder. Given the expense and complexity of these designs and the lack of sensory paradigms that are valid for young infants, few sensory researchers have followed this example. Nearly all of the neuroscience-informed sensory research has instead been patterned after standards in experimental psychology and psychophysics, employing cross-sectional designs. While this is of value, the relative absence of a developmental perspective in behavioral and neuroscience focused sensory research thus far has left us with large gaps in our understanding of the primacy and centrality of sensory differences relative to the clinical features of autism. This is compounded by the reality that few of these paradigms are appropriate for infants and very young children, or for people with limited cognitive or verbal abilities, reducing our knowledge base to a small swath of the autism spectrum. This leads to several recommendations for research. The first recommendation is to adopt prospective longitudinal designs that begin recruitment of infants very early in life and follow them through at least school age. The second recommendation is to develop and validate paradigms and measures of sensory constructs that are appropriate across a wide range of ages, cognitive and linguistic abilities.

While social communication centers on observable behaviors that rapidly develop over the first few years of life, sensory function begins to develop prenatally. It is yet unknown how early these processes diverge from a neurotypical developmental trajectory. However, given the ontological primacy of sensory structures and function for all other behaviors, we find it highly likely that relevant sensory differences may be happening much earlier than previously thought, and an understanding of how and when this occurs has the potential to unify our understanding of the social communication and repetitive/restricted behavior aspects of autism in an unprecedented way. Thus, a third recommendation is for researchers to learn and/or develop and validate methods for assessing sensory reactivity and regulation in utero, and in young infants and to ensure that sensory focused items are included in developmental assessments and screening tools.

A major breakthrough was a return to including sensory features in the diagnostic nosology for autism, with their addition in *DSM-5*. However, the assignment of sensory reactivity differences to the category of restricted and repetitive behaviors creates an expectation that they are more related to those features than to social communication, which we see as a false dichotomy. A steady accumulation of basic and applied science suggests that early sensory development and sensory processes are critical building blocks to the development of language (Bahrick & Lickliter, 2012), social communication (Watson et al., 2011) and predict the presence and intensity of repetitive behaviors and restricted interests (Boyd et al., 2010). Further, emerging evidence suggests that hyporesponsiveness at 6–16 months is associated with increased levels of social communication impairments at 6 years while hyperresponsiveness was associated with increased levels of RRB's in a community sample including children with autism (Y. J. Chen, Sideris, et al., 2022). Thus, a fourth recommendation is for researchers to adopt a more holistic approach to studying the etiology of the two separate diagnostic domains, with sensory processes as a potential unifying framework.

While developmental studies focused on populations with higher probability for autism (e.g., infant siblings of older children with autism) has been fruitful, there are several limitations that have not been addressed that would allow the field to fully generalize findings to the population at large. One consideration is to expand this work to also include children of autistic parents (Crane et al., 2021). In addition, one major limitation rests on the assumption that infant siblings and community sample infants (without older siblings with autism) would have similar phenotypic presentations. This is unlikely to be true given the vast heterogeneity in symptom expression at any single point in time, chronogeneity in developmental trajectories, varied etiological factors at play (e.g., genetic, epigenetic, in-uterine environmental risk or protective factors), as well as contextual factors (e.g., lived experience of having an older sibling with autism). Another limitation is the differential base rates in high risk versus community populations from which studies sample, thereby affecting the probability of early detection, and the conclusions made regarding the validity of available screening tools or methods. The design and implementation of prospective longitudinal community-based studies is more complicated and resource intensive than a focus on those at higher probability of autism. Nonetheless, our fifth recommendation is that researchers move beyond a methodological focus on infant sibling samples and embrace methods for detection and recruitment of infants with elevated likelihood of autism from community samples that are more generalizable.

Research on sensory processing in autism has proceeded for some time with clinical/observational and neuroscience/experimental expertise largely being applied in parallel. There is a consensus that researchers would like to understand sensory processing across levels of measurement, from neurophysiology to perception to behavior. The benefit of this consensus is that, increasingly, research groups are gathering data at multiple levels of measurement in the same samples (Wodka et al., 2016). A drawback is that, at times, researchers may use methods that are not native to their area of expertise improperly. A cardinal example is the use of self- or parent-report questionnaire measures without awareness or consideration of how they were developed or for whom they are valid. This may result in noisy or even invalid data about one level, which is then difficult to link to data

at other levels of measurement, resulting in missed opportunities to advance our knowledge and waste of time and resources. Thus, a sixth recommendation is for researchers to work in cross-disciplinary teams comprising experts in each method they employ to facilitate meaningful and coherent integration across levels of measurement (e.g., from behavior to brain).

This article has focused on empirical findings regarding the development and cascade of sensory differences in autism and now sets the stage for the translation of this work into meaningful and impactful intervention. The design of effective screening tools and early interventions addressing sensory reactivity and regulation for infants at elevated likelihood of autism below age 2 years is critical to supporting families and promoting optimal development, as well as long-term outcomes for health, well-being, and social participation. There are relatively few studies of infants/toddlers at elevated likelihood of autism that have focused on the sensory domain as a key ingredient of intervention (Baranek et al., 2015; Watson et al., 2017). One smaller randomized clinical trial focusing on parent coaching strategies in the sensory as well as social communication domains demonstrated significant improvements in infants' sensory hyporesponsiveness, language, and socialization skills. The second larger randomized clinical trial failed to replicate the main effects (both the treatment and control groups made progress) but found that improvements in parent responsiveness mediated child outcomes for both groups. Further, emerging evidence suggests that addressing sensory responsiveness may have positive impacts on language and socialization (Grzadzinski et al., 2021) especially for children that demonstrate sensory hyporesponsiveness at baseline. Critically, coaching parents to attune to their infant's sensory reactivity and regulatory capacities may facilitate developmental trajectories across a variety of domains. Future studies are needed to also address moderators of interventions (such as demographic variables as well as cognitive function differences) to understand the key ingredients and approaches that best serve specific subsets of children and their families. Although clearly, we know from other populations of infants and toddlers that addressing sensory differences early in life may have positive benefits on motor, language, and cognitive skills as well as parent well-being (Blanche et al., 2016; Jaegermann & Klein, 2010; Pineda et al., 2021), there may be other nonsensory approaches or combined approaches that are plausible theoretically and should be tested. Thus, a seventh recommendation is for researchers to pursue and funding agencies to support, well-designed, conceptually sound and ecologically valid early interventions that prioritize the role of sensory processing in addition to social communication. In so doing, a focus on using sensitive behavioral, physiological, and neural outcome measures at both proximal and distal time points is needed. This would allow for not only the identification of key intervention ingredients but also provide a direct assessment of the malleability of sensory features and processing and their impact on social communication and RRB features of autism. This could help not only to optimize outcomes but could be beneficial in testing the cascading effects model more directly.

Conclusion

Across all these recommendations, the sensory developmental framework highlighted here can facilitate the field's understanding of the experience-dependent plasticity that shapes the neurodivergent

brain at any given point where measurements are taken in the lab. Behavioral or neural differences in autism reflect adaptations developed over time to individual experiences of altered sensory or perceptual phenomena. Despite positive advances and findings that sensory differences predict social communication and RRB's and precede their development ontologically, there are still major gaps in our knowledge that need to be filled prior to a full reconceptualization of autism as a sensory difference with cascading effects on social development that impact function and participation. While we have listed what we think are a reasonable set of plausible developmental cascades, these questions need to be contextualized into the current landscape of our science.

It is clear from numerous studies that the biological processes underlying autism begin long before any behavioral symptoms are evident, and sensory processes and their associations with motor development are likely the first behaviors affected by these preliminary neurodevelopmental differences beginning by the mid-fetal developmental period. In this article, we have laid out the current evidence linking early neurodevelopmental differences with heterogeneous phenotypic outcomes by proposing a novel cascading developmental model of autism that centralizes the primacy of sensory functions. We invite healthy and robust discourse and propose this conceptual model not as an end point but as a starting point from which to build, deconstruct and rebuild our knowledge of autism.

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