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Understanding sensory regulation in typical and atypical development: The case of sensory seeking

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ABSTRACT

Sensory regulation, the ability to select and process sensory information to plan and perform appropriate behaviours, provides a foundation for learning. From early in development, infants manifest differences in the strategies used for sensory regulation. Here, we discuss the nature and characteristics of sensory seeking, a key behavioural strategy for sensory regulation often described as atypical in children with Neurodevelopmental Disorders. We evaluate theoretical models proposed to clarify mechanisms underlying individual differences in sensory seeking and discuss evidence for/against each of these models. We conclude by arguing that the *information prioritization hypothesis* holds the greatest promise to illuminate the nature of individual differences in sensory seeking across participant cohorts. This proposal aligns to molecular genetic animal and human evidence, provides a coherent explanation for developmental findings, and generates testable hypotheses for future research.

Introduction

Information and knowledge about the world come to us through our senses. Since early in development, infants find themselves immersed in a cluttered sensory environment, whereby competition in sensory input is the rule rather than the exception (Amso & Scerif, 2015; Posner, 2011). To successfully navigate their multisensory world, infants must be able to select and process sensory information to plan and perform appropriate behaviours – a repertoire of skills often referred to as *sensory regulation* (Dunn, 2002, 2009, 2014). Sensory regulation is a prerequisite for adaptive functioning since it enables individuals to appropriately interact with and explore the world around them (Williamson & Anzalone, 2001).

Developmental research indicates that individual differences exist in the strategies infants and children use towards sensory regulation. Parent-reported measures of infants and children's sensory regulation (e.g., Infant-Toddler Sensory Profile, ITSP; Dunn, 2002; Sensory Profile, SP; Dunn, 1999) suggest that children differ in how they engage with sensory input or seek out sensory stimulation. For example, while some children enjoy the opportunity of "getting messy" at mealtime, others avoid experimenting with their food. Observational studies, whereby children's exploratory behaviour is recorded, also point to early individual differences in how infants approach novel objects or salient sensory stimuli (e.g., colourful toys) (Bornstein et al., 2013; Muentener et al., 2018; Sheese et al., 2008). While some infants display cautious exploratory strategies (e.g., slower reaching for toys and enhanced visual examination of them without touching), others favour more vigorous and fearless strategies (e.g., quicker reaching for toys and haptic

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exploration of them) (Sheese et al., 2008).

Individual differences in sensory regulation provide insight into the children's sensory processing needs and preferences. These differences are ubiquitous in early development, and they have been proposed to act as precursors of later temperament and personality traits (Aksan & Kochanska, 2004; Brock et al., 2012; Sheese et al., 2008). Although it is unclear if sensory regulation is an underlying component or dimension of temperament, or if it represents a distinct but related construct (Mammen et al., 2016), evidence suggests that associations exist between sensory regulation strategies and temperamental characteristics (see below) (Calkins et al., 1996; Fox et al., 2001; Li et al., 2020; Kagan & Snidman, 1991).

In the context of atypical development, evidence indicates that there are children who exhibit strategies for sensory regulation differing in quality or quantity from those manifested by age-matched typically developing children. These children frequently need unusually high or low levels of sensory stimulation to display a behavioural response (Ghanizadeh, 2011; Marco et al., 2011). Often, the behavioural response manifested differs from that observed in typically developing children. For example, children with Autism Spectrum Disorders (ASD) and infants at elevated likelihood of ASD frequently manifest reduced seeking of novel sensory input, coupled with engagement in restricted and repetitive behaviours (Garon et al., 2009; Harrop et al., 2014; Larkin et al., 2019). Conversely, elevated seeking of novel sensory input and enhanced distractibility are reported in children with Attention Deficit Hyperactivity Disorder (ADHD) (Donfrancesco et al., 2015; Melegari et al., 2015). These alternative sensory seeking strategies have further been linked to different temperamental outcomes in typically and atypically developing children. For example, reduced seeking of sensory input has been linked to higher temperamental negativity (DeSantis et al., 2011; Klein et al., 2008), whereas elevated sensory seeking has been shown to associate with enhanced temperamental positivity (Klein et al., 2008; Melegari et al., 2015).

The present review aims at evaluating the nature and characteristics of sensory seeking, a behavioural strategy towards sensory regulation, in populations with typical and atypical development. We begin by providing a definition of sensory seeking and discussing how the construct has been operationalized in the literature. We then summarise the theoretical models proposed to clarify mechanisms underlying individual differences in sensory seeking. In doing so, we evaluate evidence for/against each of these models and present a synthesis of the large body of work assessing parent-reported and experimental measures of sensory seeking in typically and atypically developing children. When discussing sensory seeking in atypical populations, we cover neurodevelopmental conditions such as ASD and ADHD, given that abundant research on sensory seeking in these disorders exists. We evaluate developmental changes in the manifestation of sensory seeking and discuss approaches for illuminating mechanisms underlying these changes. We conclude by presenting future directions of research that could enrich our understanding of this sensory regulation strategy in typical and atypical development.

Definition and construct operationalizations

A drive for novelty, that is a tendency to approach unfamiliar or incongruous stimuli, has been reported in many species, ranging from bees and cockroaches (Hughes, 1997) to non-human and human primates (Berlyne, 1950; Glickman & Sroges, 1966). Although species variation in novelty drives exists, with an increase in seeking novel and diversive sensory stimulation reported in primates relative to other species (Glickman & Sroges, 1966), it is commonly accepted that organisms possess a "need" for sensory change mainly satisfied by intrinsic exploration (Hughes, 1997). Research with humans provides support for this notion suggesting that, from early in development, infants display strategies to achieve sensory change (Kidd & Hayden, 2015). Among these strategies, sensory seeking encompasses a set of behaviours aimed at enhancing and/or diversifying sensory input through active engagement with the surrounding environment (Dunn, 1997; Dunn & Daniels, 2002; Piccardi et al., 2020). Infants described as *sensory seekers* commonly display acts, such as haptic exploration of objects, food playing or visual exploration of colourful or fast-paced stimuli, that do not appear instrumental in achieving a certain goal other than the enhancement or diversification of the input received. While variation in sensory seeking may manifest at a state-level, influenced by momentary fluctuations in the physiological, attentional, and emotional state of a given individual, as well as by the intensity and quality of stimulation, and by further contextual factors, trait-level variation has an early appearance in development, with some infants displaying a consistently higher tendency to approach unfamiliar or incongruous stimuli than others. Stable individual differences in novelty preferences in infancy have been further linked to later variability in cognitive abilities (e.g., explanation-based curiosity) during childhood (Perez & Feigenson, 2021; see also section 5). Thus, the preserved variation in infant's seeking of novel and diversive sensory stimulation points to its ecological significance within the human species.

Although novelty preferences have been the staple of infancy research, variation in the tools used to study these preferences has clouded our understanding of the underlying mechanisms. Notably, novelty preferences in infancy were studied through habituation procedures, capturing shifts in infants' looking from repeated to novel sensory stimuli (Colombo & Mitchell, 2009), observational coding of infants' exploratory behaviour (Baranek et al., 2007; Bornstein et al., 2013; Muentener et al., 2018), or parent-reported measures, i.e., in infancy: Infant-Toddler Sensory Profile, ITSP, (Dunn, 2002); Infant-Behaviour Questionnaire, IBQ, (Gartstein & Rothbart, 2003); in early childhood: Sensory Profile, SP, (Dunn, 1999, 2014); Sensation Seeking Scale for Young Children, SSSYC, (Morronegiello et al., 2010); Early-Childhood Behaviour Questionnaire, ECBCQ (Putnam, Gartstein & Rothbart, 2006). Variation in the adopted methods led to a plethora of construct operationalizations and theoretical models put forward to clarify the mechanisms underlying individual differences in the seeking of novel and diversive sensory stimulation. The following section critically evaluates these theoretical models.

Mechanisms of sensory seeking: Theoretical models

The optimal stimulation hypothesis

One of the first models proposed to explain individual differences in sensory regulation is the *optimal stimulation hypothesis* (Zentall & Zentall, 1983). This hypothesis is rooted in traditional homeostatic models, according to which there is an optimal level of stimulation towards which organisms strive (Berlyne, 1950; Schneirla, 1959; Wachs, 1977). It follows that any deviations from optimal stimulation lead to aversive states for which individuals need to compensate. Sensory seeking is here hypothesised to represent a compensatory strategy aimed at preserving homeostatic balance. Thus, reduced sensory seeking is predicted to manifest in those individuals that are either exposed to intense stimulation or that respond too strongly to sensory input (i.e., exhibiting sensory hypersensitivity). Conversely, elevated sensory seeking is predicted to appear under conditions of sensory deprivation or in individuals who are hyposensitive to sensory input.

The optimal stimulation hypothesis largely draws on research with atypically developing populations. For example, children with ASD frequently display a pattern of behavioural responses characterized by passivity, reduced seeking of novel and diverse sensory input, withdrawal from arousing sensory or social contexts and overfocused attention (Johnson et al., 2015; Liss et al., 2006). The optimal stimulation hypothesis explains the behavioural profile of children with ASD as resulting from sensory hypersensitivity. By limiting stimulus input, either through reduced seeking of novel stimulation, or by engaging in restricted, repetitive and often self-produced activities, children with ASD would compensate for their sensory hypersensitivity and preserve an optimal level of stimulation. In line with this explanation, increased behavioural (e.g., Baranek et al., 2007) and neural response to sensory stimulation (e.g., Cascio et al., 2012, 2015; Ferri et al., 2003; Hudac et al., 2018; Lepistö et al., 2007, 2008; Miyazaki et al., 2007; Samson et al., 2012; Takarae et al., 2016) were reported in children with ASD. Further, Donkers et al., (2015) documented a relationship between neural hypersensitivity to auditory stimulation (indexed by enhanced P3a responses to novel tones) and lower sensory seeking behaviours (indexed by combined observational and parent-reported indicators) in 4–12 years old children with ASD.

Children with ADHD frequently display manifestations of hyperactivity, impulsivity and distractibility (Biederman, 2005; Johnson et al., 2015). The optimal stimulation hypothesis explains this behavioural profile as consequent to sensory hyposensitivity. By increasing stimulus input, either through elevated seeking of novel sensory stimulation or enhanced activity, children with ADHD would compensate for their sensory hyposensitivity. Supporting this explanation, reduced behavioural (e.g., Scherder et al., 2008), and neural responses to sensory stimulation were reported in children with ADHD (e.g., Yamamuro et al., 2016; Zhang et al., 2020). Although sensory seeking and hyperactive-impulsive manifestations in ADHD were proposed to act as modulators for high sensory thresholds (i.e., sensory hyposensitivity; Keating et al., 2021; Liss et al., 2006; Zentall & Zentall, 1983), experimental support for this notion is lacking.

Taken together, evidence from atypically developing populations provides some support for the optimal stimulation hypothesis. However, three limitations underlie this theoretical model. First, while the optimal stimulation hypothesis appears useful to understand some sensory manifestations in children with ASD or ADHD, it has so far revealed limited explanatory power in studies with typically developing populations (Carrol et al., 1982; Piccardi et al., 2020). This lack of explanatory power challenges the optimal stimulation hypothesis, given that ASD and ADHD-related sensory traits are believed to lie on a continuum in the general population, with clinical manifestations representing the extremes of this variation (Panagiotidi et al., 2018, 2020; Robertson & Simmons, 2013). Second, the optimal stimulation hypothesis appears unable to clarify the heterogeneity in sensory profiles characterising children with ASD or ADHD. By ascribing a profile of sensory hypersensitivity to children with ASD and hyposensitivity to children with ADHD, this model fails to explain why co-occurrence in sensory hyper/hyposensitivity frequently manifests in these conditions (Ben-Sasson et al., 2019; Green et al., 2016; Keating et al., 2021; Marco et al., 2011). Third, and most important, the testability of the optimal stimulation hypothesis is questionable given that this theoretical model fails to provide a formalization of the factors determining an individual optimal level of stimulation.

Dunn's model of sensory processing

Building on the optimal stimulation hypothesis is *Dunn's model of sensory processing* (Dunn, 1997), and its more recent conceptualization, *Dunn's sensory processing framework* (Dunn, 2014). Like the optimal stimulation hypothesis, this model posits that behavioural responses towards sensory regulation serve a homeostatic function. However, a more precise formalization of the factors determining behavioural responses is offered by this model. Differences in sensory profiles are here conceptualized to result from individual neurological thresholds which, in turn, drive alternative behavioural responses. Children with low neurological thresholds require less stimulation to display a behavioural response: these children notice and respond to stimuli easily, thus displaying manifestations consistent with sensory hypersensitivity. Conversely, children with high neurological thresholds require more stimulation to manifest a behavioural response: these children fail to notice and respond to sensory stimuli frequently, thus displaying manifestations consistent with sensory hyposensitivity. Behavioural responses are hypothesized to result from these neurological thresholds and range from active to passive. Among the active behaviours, the model includes sensory seeking and avoiding, which are aimed to enhance or minimise sensory stimulation. Conversely, sensory sensitivity and low registration are described as passive behaviours, leading to enhanced responsiveness or failure to detect sensory stimulation.

Dunn's model proposes sensory seeking to be an active behavioural response exhibited by children with high neurological thresholds. It follows that those children who are less sensitive to sensory stimulation would engage in behaviours maximising sensory exposure to compensate for their high neurological threshold. Such behaviours could include touching textured objects, fidgeting or

watching fast-paced TV shows (Dunn, 1997; Dunn & Daniels, 2002). The model emphasizes that sensory seeking may appear in both typically and atypically developing children and, taking a strength-based approach, suggests that one's sensory patterns (including sensory seeking) are features to be understood, not indicators of a deficit. It follows that understanding the level of seeking may help find the best activities and contexts to support individual learning.

Dunn's conceptualization represents a cornerstone of the sensory processing literature, and it has informed both clinical assessment and intervention planning (e.g., Dunn, 2007, 2008). The main strength of this model is that it does not ascribe a profile of sensory hypersensitivity to children with ASD and sensory hyposensitivity to children with ADHD, thus offering the opportunity to evaluate co-occurring sensory hyper/hyposensitivity in populations with atypical development (Ben-Sasson et al., 2009; Green et al., 2016; Keating et al., 2021; Marco et al., 2011). However, some limitations underlie this model. First, Dunn's model does not formalize a potential mechanism for the differences in neurological thresholds, nor for what may drive the need to implement a behavioural response to meet those thresholds. Second, empirical evaluation of the model's constructs has challenged some of its assumptions. For example, Metz et al. (2019) examined the neurological threshold and behavioural regulation axes of the model by evaluating them for scaling. Contrasting a tenet of the model, results indicated that the behavioural response axis may not reflect a construct with ordinal range. Thus, it is possible that a combination of behaviours (active and passive) may concurrently be exhibited by the same child across contexts (i.e., a child displaying enhanced sensory sensitivity may also manifest increased sensory seeking behaviours). Indeed, as acknowledged by Dunn (2002), the model provides only a rough characterisation of what is most likely the true interaction between neurological thresholds and behavioural responses. Further, the model does not offer a description of potential manifestations of sensory behaviours. As we will discuss in section 4, sensory seeking, as measured by instruments developed from Dunn's model (e.g., ITSP), could manifest as active search for novel and diversive sensory stimulation, or as repetitive and restricted seeking. While the former may have a protective function in early development and broaden opportunities for learning, the latter, while still serving an adaptive function, may restrict learning opportunities and contribute to later atypicality (Piccardi et al., 2021).

Information processing and sensory seeking

Information processing was also proposed as driver of individual differences in sensory regulation, with the speed of such processing hypothesized to be the mechanism underlying individual differences in the seeking of novel and diversive sensory stimulation. According to this theoretical model, engagement with a current sensory stimulus would depend on the amount of time required to process that stimulus (Colombo et al., 1991; Slater, 1995). Thus, the faster individuals would process incoming stimuli, the higher the number of stimuli they would afford to seek, and further process.

Indirect evidence for the *processing speed hypothesis* as a potential explanation for individual differences in the seeking of novel and diversive sensory stimulation emerged from traditional looking times familiarization tasks. In these tasks, paired stimuli are presented to infants repeatedly: one stimulus remains constant while the other stimulus changes from trial to trial (Fantz, 1964; Roder et al., 2000; Rose & Feldman, 1987). Processing speed is here captured by determining how many trials the infant requires to display a "novelty" preference, that is systematic¹ visual preference for the novel stimulus, based on the assumption that shifts in looking index encoding of the repeated stimulus properties and disengagement from it, once encoded (Clifford & Williston, 1993; Hunter & Ames, 1988; Sokolov, 2003). Studies employing these tasks revealed individual differences in infants' performance, with some infants more quickly displaying a novelty preference than others (Kail, 2000). Researchers traditionally interpreted variation in performance as resulting from processing speed differences: thus, short looking infants (i.e., infants requiring less time to habituate to visual stimulation, or shorter fixation periods to recognise novelty) were deemed faster at processing the available information (Colombo et al., 1991; Slater, 1995). The relative consistency of looking time over repeated assessments (Colombo et al., 1986) and its predictive relationship to later measures of IQ (Kail, 2000; Rose et al., 2008, 2011) were taken as additional sources of support for the hypothesis that processing speed may represent a stable and reliable factor underlying drives towards novelty.

Due to its relative simplicity and longitudinal explanatory power, the processing speed hypothesis has had a longstanding influence on the literature on early neurocognitive development. However, the extent to which cognitive ability drives the seeking of novel and diversive sensory stimulation remains debated (Powell & Nettelbeck, 2014; von Stumm et al., 2011). Moreover, while processing speed could represent a relatively simple mechanism for individual differences in seeking novel and diversive sensory stimulation, this mechanism falls short in explaining how infants move from something they have learnt to something new – i.e., what determines that enough of the "old" stimulus was learned. Research by Richards and collaborators (Richards and Casey, 1992; Richards, 1997) shed light on the physiological underpinnings of infants' beginning and terminating states of information processing, employing heart rate to define states when the infant is attentive (i.e., sustained attention) as opposed to states when the infant is inattentive (i.e., attention termination). According to this research, sustained attention is characterised by a maintained decrease in heart rate below pre-stimulus levels, while attention termination is accompanied by a return in heart rate to pre-stimulus levels coupled with continued looking at the stimulus. Richards and collaborators (Reynolds et al., 2010; Xie et al., 2018) further demonstrated that these states of information processing are accompanied by specific neural changes, including an increase in the amplitude of the ERP component NC, synchronization of the EEG theta rhythm and desynchronization of the EEG alpha rhythm during sustained attention relative to attention termination. While disclosing state-level brain-behaviour associations, this research does not shed light on individual differences and remains correlational in nature, thus not explaining what determines that enough of the "old" stimulus was learned. Although

¹ Systematic visual preference is typically determined by computing a novelty percentage, that is the sum of the durations of looking to the novel stimuli in the block divided by the sum of the durations of looking to both the novel and the familiar stimuli in the block.

information must be processed to disengage from a sampled stimulus and engage with a novel one, the speed of such processing may ultimately not be the only mechanism underlying individual differences in seeking novel and diverse sensory input.

Using foraging theory to understand sensory seeking

An alternative perspective towards explaining individual differences in seeking novel and diverse sensory stimulation is offered by classic *foraging theory* (Addicott et al., 2017; Calhoun & Hayden, 2015; Hills et al., 2015; Stephens, 1987). Foraging theory is a branch of behavioural ecology explaining how animals seeking resources make decisions. According to this theory, foraging behaviours are regulated by a trade-off between exploitation of the resource at hand and exploration of novel resources (i.e., *exploration–exploitation trade-off*). While familiar resources have a known reward value, novel resources are unfamiliar and, thus, carry an unknown reward value. It follows that a problem individuals must face is deciding between exploitation of a familiar resource with a known reward value or exploration of an unfamiliar resource which may be more, or less rewarding than the familiar one. Efficient performance is achieved through decisions that maximise the rate of obtained rewards and minimise costs (e.g., time, effort, or money).

Foraging theory relies on a set of basic principles, proving ideal to explain behaviour in diverse species, from insects (e.g., Anreiter & Sokolowski, 2019), to non-human and human primates (e.g., Pearson et al., 2014). Further, while foraging is commonly understood as the search for resources, such as food, territory or mates, it in fact encompasses a broad range of behaviours supporting survival (Calhoun & Hayden, 2015). Thus, one could hypothesize that sensory stimulation may be sampled in a similar way as other resources. Engagement with a current sensory stimulus would be regulated by an exploration–exploitation trade-off: individuals would engage with a current sensory stimulus (i.e., exploitation) until the effort needed to extract further information from it would outweigh the effort required to extract information elsewhere (i.e., exploration). At that point, individuals would display a shift in the allocation of their attentional resources, leading to seek novel and diverse sensory input. Individuals may switch from exploitation to exploration depending on the environment, but evolution also introduced individual variation so that when environmental conditions change abruptly, some individuals can readily trade off great effort to explore for novel resources.

In humans and other species, individual variation in foraging biases was linked to modulation of the neurotransmitter dopamine (DA). Specifically, animal research indicated that DA drives exploratory behaviour in novel environments (Dulawa et al., 1999) and novel stimuli excite DA neurons located in the ventral midbrain (Bromberg-Martin et al., 2010; Horvitz, 2000). Inhibition of the DAT transporter in monkeys was shown to enhance novelty-seeking behaviour by increasing the initial reward value assigned to novel stimuli (Costa et al., 2014). Intriguingly, research with human infants also highlighted the role of DA for assigning reward value to novel and diverse stimuli. Notably, the DRD4 receptor gene exists in two forms: the 4-repeat variant and the 7-repeat variant. The 7-repeat variant of this receptor gene is two times less potent in mediating DA influences than the 4-repeat form, and infants as young as 12 months with the longer version of the allele are reported to be less anxious and driven towards novelty than infants with the shorter version of the allele (Lakatos et al., 2003). Long-term influences of DRD4 polymorphisms were also documented, with enhanced exploration of visual scenes in 3-month-old infants with the 7-repeat form of DRD4 longitudinally predicting novelty seeking scores measured at 15 years of age (Laucht et al., 2006). Altogether, this evidence supports the notion that novelty may act as an intrinsic reward and be, sometimes, preferred over extrinsic rewards (Blanchard et al., 2015; Kang et al., 2009; Sethi et al., 2018). Computational work has provided further support for this notion, demonstrating that novelty can increase the efficiency of exploration and expedite learning when extrinsic rewards are sparse (Jaegle et al., 2019).

While classic foraging theory is instrumental in attributing reward value to resource foraging, it fails to quantify the variable to which reward value is associated – i.e., novelty. We previously suggested that situational or individual variation in the reward value of learning progress will lead to individual differences in seeking novel and diverse sensory stimulation (Piccardi et al., 2020). Thus, individuals that assign high reward value to smaller amount of learning progress will continue exploiting the ongoing resource and be less willing to disengage from it to move on to new information. Conversely, individuals that assign low reward value to smaller amount of learning progress will be less willing to put effort into the ongoing information resource and more willing to disengage from it to explore novel stimuli. Although the same individuals may also vary in their rate of learning progress (i.e., processing speed), it may ultimately be variation in information prioritization that determines differences in the seeking of novel and diverse sensory stimulation. We refer to this proposal as the *information prioritization hypothesis*.

Investigating information prioritization in infancy

Evidence in support of the information prioritization hypothesis has emerged from looking times familiarization tasks (Fantz, 1964; Roder et al., 2000; Rose & Feldman, 1987). As reviewed in section (c), traditional models interpreted shifts in infants' looking from the repeated to the novel stimulus to index encoding of the stimulus properties and subsequent disengagement from it, once encoded. Early studies provided support for this notion (Colombo, 1993; Colombo et al., 1988, 1991; Colombo & Mitchell, 1990), suggesting that infants who manifest brief visual fixations during familiarization (i.e., short lookers) are more likely to display evidence of recognition memory during subsequent stimulus exposure than infants who manifest long visual fixations (i.e., long lookers). However, contrasting evidence emerged from later studies. For example, de Barbaro et al., (2011) micro-analysed 6–7-month-old infants' looking behaviour while attending to multiple spatially distributed targets (videos) in a naturalistic environment. The authors evaluated several features of infants' looking behaviour, including fixation durations, reorientation speed, and time spent looking at the videos. Results indicated that infants who manifested faster orienting to the peripheral videos, also displayed a lesser decrease in looking time to these videos, following repeated orienting, over trials. These results contrast evidence from earlier studies, further questioning the idea that short

lookers learn faster thereby more rapidly habituating to repeated sensory stimulation.

Early stimulus disengagement in infants as young as 6 months was linked to enhanced vigilance (Aston-Jones & Cohen, 2005) – a physiological state under the influence of the DA derivative neurotransmitter norepinephrine (NE) (Aston-Jones et al., 1999; Skosnik et al., 2000). Indeed, de Barbaro et al., (2011) found an association between vigilance state and looking behaviour in 6–7-month-old infants, whereby high vigilant (but not low vigilant) infants displayed short looking and enhanced distractibility (i.e., high vigilant infants were more driven by unpredictable peripheral stimuli). These results fit with evidence from pharmacological investigations indicating that the neuromodulatory state of an organism can account for individual differences in exploratory drives (Aston-Jones et al., 1999; Skosnik et al., 2000). Further, these results suggest that a link may exist between vigilance (as a state) and drives towards seeking novel and diverse sensory stimulation (as a trait). In support of this notion, molecular genetic animal and human research documented associations between cortical NE activity in the locus coeruleus (LC) and the medial prefrontal cortex (MPFC) and drives towards novel and diverse sensory stimulation. For example, NE neurons in the LC of awake rats, cats and monkeys are particularly responsive to novel sensory stimulation (Aston-Jones et al., 1991; Rasmussen et al., 1986; Sara et al., 1994) and pharmacological inhibition via clonidine of NE neurons in the LC abolishes novelty seeking behaviours in rats (Sara et al., 1995), suggesting that the activation of these neural populations is necessary for the behavioural expression of novelty seeking drives. Importantly, the role of NE in mediating the expression of drives towards seeking novel and diverse sensory stimulation is not independent of DA (and vice-versa). NE is a DA derivative neurotransmitter and, particularly in the MPFC (which receives dense NE projections from LC and contributes to novelty detection; Dias & Honey, 2002; Rebec et al., 1997), extracellular DA is regulated by the NE transporter. Although NE and DA have typically been studied as separate systems, they overlap in multiple domains (e.g., receptors non-specificity, transporter affinity and signalling pathways) (Ranjbar-Slamloo & Fazlali, 2020). Thus, it is likely that NE and DA systems concurrently mediate drives towards novel and diverse sensory stimulation.

Further evidence in support of the information prioritization hypothesis has emerged from an EEG study we recently conducted (Piccardi et al., 2020). In this study, 10-month-old infants were presented with the same cartoon clip, randomly interrupted by sudden-onset checkerboards (Fig. 1B). Modulation of the frontal EEG theta rhythm (4–6 Hz) during repeated video viewing was quantified as a measure of learning progress (i.e., processing speed), based on literature highlighting the role of this frequency band in mediating information processing and active learning in adults (Klimesch, 1999) and infants (Begus & Bonawitz, 2020). For example, oscillations in this frequency band during object manipulation were reported to predict infants' subsequent object memory (Begus, Southgate & Gliga, 2015), and sustained frontal theta power was observed during the initial phase of learning arbitrary visuo-motor associations, and declined as adult participants improved performance (Clare et al., 2018). Modulation of the occipital P1 peak amplitude to the briefly flashed checkerboard was quantified as a measure of responsiveness to incoming stimulation (i.e., orienting to novel

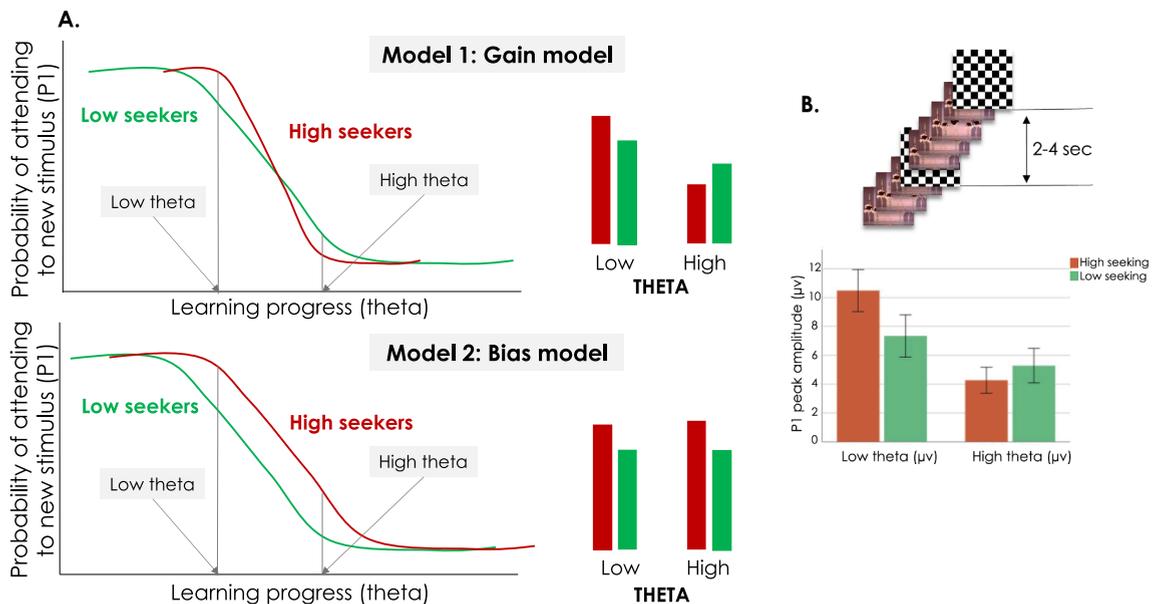


Fig. 1. [A] The likelihood of disengaging attention from the current stimulus to engage with new stimulation depends on how engaged we are with the former. Individual (or situational) variation in this function could result from either modulating the slope of this association (model 1 = *gain model*) or shifting the intercept (model 2 = *bias model*). The *gain model* would predict high seeking infants to manifest a sharper decrease in the likelihood of orienting to incoming sensory stimulation as their learning about the video accelerates; the *bias model* would predict high seeking infants to be always more likely to orient to incoming sensory stimulation; [B] Bar chart illustrating the P1 peak amplitude to incoming sensory stimulation (a briefly flashed checkerboard presented with an inter-stimulus interval varying randomly between 2 and 4 s) as a function of the amplitude of theta band activity during video viewing for high seeking infants (red) and low seeking infants (green). Novel re-analysis of data from Piccardi et al., (2020). Red = high seeking infants; Green = low seeking infants. Error bars represent + -1SE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

information) based on literature highlighting the role of this ERP component in indexing sensory stimulus selection (Lunghi et al., 2019; Luck, 2014; Hillyard et al., 1998). These neural measures were used to evaluate the explanatory power of theoretical models proposed to clarify the nature of individual differences in infants sensory seeking (i.e., optimal stimulation hypothesis, processing speed hypothesis, information prioritization hypothesis). Under the optimal stimulation hypothesis, we predicted higher parent-reported visual sensory seeking to associate with hyposensitivity to sensory stimulation (as indexed by weaker *P1* peak amplitude to the incoming checkerboard). Under the processing speed hypothesis, we predicted higher visual sensory seeking to associate with faster information processing (as indexed by a stronger decrease in frontal EEG theta amplitude with video repetition). Finally, under the information prioritization hypothesis, we predicted higher visual sensory seeking to associate with stronger modulation of responsiveness to incoming sensory stimulation (as indexed by *P1* peak amplitude modulation) based on relative engagement with the repeated video clip (as indexed by frontal EEG theta amplitude modulation).

A threefold set of results emerged. First, a non-linear modulatory profile occurred for theta amplitude during video viewing and *P1* peak amplitude time-locked to checkerboard onset. Specifically, theta amplitude manifested an initial increase, followed by later decrease, suggestive of initial engagement and later disengagement with the repeated video scene. Conversely, the *P1* peak amplitude to the sudden onset checkerboard displayed an initial decrease, followed by a later increase, indicating initial suppression of, and later orienting to the incoming stimulus. Second, the two neural measures displayed an inverse relationship, whereby the higher the theta amplitude during video viewing, the lower the *P1* peak amplitude in response to the checkerboard, suggesting that a trade-off in infants' attention distribution to incoming relative to ongoing stimulation was being captured. Third and most important, neither infants' rate of learning progress (i.e., processing speed, indexed by the decrease in frontal EEG theta amplitude with video repetition), nor stimulus selection (indexed by *P1* peak amplitude to the incoming checkerboard stimulus) predicted parent-reported visual sensory seeking, failing to support the processing speed and optimal stimulation hypotheses as putative explanations for variation in sensory seeking drives. Conversely, it was infants' relative responsiveness to the incoming checkerboard stimulus based on engagement with the ongoing video scene that predicted parent-reported visual sensory seeking at 10 and 16 months – a result indicating that infants whose modulation of the *P1* peak amplitude to the checkerboard was stronger than expected based on their frontal EEG theta amplitude modulation to the repeated video also displayed enhanced parent-reported visual sensory seeking. Of note, this set of results was documented concurrently (i.e., 10 months) and replicated longitudinally (i.e., 16 months), reinforcing the idea that a stable and reliably reported trait was being captured. Taken together, this evidence supports the idea that variation in the reward value of learning progress underlies individual differences in the seeking of novel and diversive sensory stimulation.

An important issue left undiscussed in the study by Piccardi et al., (2020) concerns the putative mechanism underlying variation in the reward value of learning progress. As Fig. 1 illustrates, variation may be achieved by modulating the gain (i.e., model 1: *gain model*), or by directly modulating the reward value of learning progress (i.e., model 2: *bias model*). The gain model assumes information processing to be an act of balancing competing signals in accordance with situational and individual demands (Hauser et al., 2016; Lawson, Rees & Friston, 2014). Elevated gain would enable strengthening highly informative ongoing signals at the expense of less informative incoming stimulation. Conversely, lowered gain would enhance the likelihood of detecting less informative incoming stimulation at the expense of highly informative ongoing signals. When leveraged to explain individual differences in sensory seeking, the gain model would predict high seeking infants to manifest a high gain information processing style, thus displaying a sharper decrease in the likelihood of orienting to incoming stimulation (e.g., sudden onset checkerboard) as their learning about ongoing signals (e.g., repeated video) accelerates. Conversely, low seeking infants would be expected to manifest a low gain information processing style, thus being more likely to disengage from highly informative ongoing signals in the presence of incoming sensory stimulation. Differently from the gain model, the bias model does not assume information processing to be an act of balancing competing signals. It follows that the bias model would predict high seeking infants to be *always* more likely to orient to incoming sensory stimulation, irrespective of the information content of the current source.

We recently evaluated the explanatory power of the gain and bias models as putative explanations for individual differences in sensory seeking by conducting novel re-analysis of data from Piccardi et al., (2020). Results from this work confirm that the gain model optimally fits with data from our research, demonstrating that high seeking relative to low seeking infants displayed higher *P1* peak amplitude to incoming sensory input when theta amplitude during video viewing was low (but not when theta amplitude was high; see Fig. 1). The gain model also optimally fits with evidence from molecular genetic animal and human research on the functional role of NE and DA. Indeed, these neurotransmitters are thought to mediate drives towards novel and diversive sensory stimulation by modulating neural signal gain (Hauser et al., 2016). Thus, under high neural gain states, an increase in NE and DA would concurrently act to strengthen tuning to highly informative ongoing signals and attenuate the processing of incoming sensory stimulation. Conversely, under low neural gain states, a decrease in NE and DA would suppress tuning to ongoing signals, favouring the selection and processing of incoming stimulation.

Based on this evidence, we conclude that the information prioritization hypothesis holds promise to clarify the nature of individual differences in seeking novel and diversive sensory stimulation. Thus far, however, research has solely evaluated its explanatory power in typically (but not atypically) developing populations. Thus, the extent to which this hypothesis may explain the spectrum of sensory seeking manifestations in children with ASD or ADHD remains an open question.

Leveraging the information prioritization hypothesis to understand sensory seeking in typical and atypical development

As reviewed, several measures have been used to study sensory seeking manifestations during development. These measures range from assessment of infants' visual preferences in looking times familiarization tasks (e.g., Colombo & Mitchell, 2009; Fantz, 1964; Roder et al., 2000; Rose & Feldman, 1987), to observational coding of infants' object exploration (e.g., Bornstein et al., 2013;

Muentener et al., 2018; Sheese et al., 2008), to parent-reported measures used either in isolation (e.g., Dunn, 2002, 2007), or in combination with neural measures (e.g., Donkers et al., 2015; Piccardi et al., 2020). These measures have been instrumental in illuminating the ubiquity of individual differences in sensory seeking. However, variation in the tools used has also clouded our understanding of the underlying mechanisms.

Traditional measures, namely assessment of infants' visual or object exploration (captured through experimental designs or parental reports), have a common limitation, that is they conflate individual variation in the rate of learning progress (i.e., processing speed) during the session and variation in prioritization of incoming sensory stimulation. Specifically, in looking times familiarization tasks, the dependent variable of interest is the time (i.e., number of trials) infants require to manifest a shift in looking from the repeated to the novel stimulus. Similarly, in observational studies of infants' object exploration, the dependent variable of interest is the time infants require to shift manipulation from an old to a new object, or the number of different objects touched during the session. Although these variables can disclose individual differences in infants' sensory seeking behaviours, none of them sheds light on the potential mechanisms underlying these differences. In the absence of a direct measure of information processing, the time required by an infant to shift looking or the number of different objects touched represent mere correlates of an underlying neural activity that could mediate either exploitation of the resource at hand, or exploration of incoming sensory stimulation. This issue may explain the many non-replications in the literature on early visual disengagement in ASD (for a review, see Sacrey et al., 2014). Indeed, while some studies reported slower disengagement in children with ASD (e.g., Landry & Bryson, 2004), others failed to replicate this finding (e.g., Fischer et al., 2016). Drawing on the information prioritization hypothesis, we argue that the inconclusive nature of this research results from its limited attempt to quantify information content and variation in its prioritization. If low gain characterises information processing in children with ASD, we would predict these children to be faster at disengaging from highly informative content but slower at disengaging from less informative content.

We previously provided an objective marker of individual differences in visual sensory seeking, whereby exploitation of the ongoing resource (i.e., learning progress on the task) and exploration of incoming sensory stimulation could be disentangled at a neural level (Piccardi et al., 2020; described in section 3e). Compared to prior measures, the advantage of our neural measure lies in its ability to quantify infants' likelihood to "let go of the old information" to explore incoming sensory stimulation, temporarily determining the exact time in the individual learning progress when this shift manifests. We suggest that similar paradigms can be adopted to assess sensory seeking manifestations in other sensory modalities, such as touch or audition, and/or to evaluate qualitative differences in sensory seeking behaviours between children with atypical relative to typical development.

Collecting data that is as close as possible to the hidden constructs that may clarify the underlying mechanisms (i.e., learning progress and prioritization of incoming sensory stimulation) is important, particularly if we aim to evaluate qualitative changes in the manifestation of sensory seeking in atypically relative to typically developing children. Indeed, while much of the sensory processing literature assumes sensory regulation strategies to be relatively stable over time, with a preferred strategy determining an individual's way of conducting life (e.g., Dunn, 2002), limited research has evaluated the typical and atypical developmental trajectory of sensory regulation strategies, including sensory seeking. In a meta-analysis of 14 studies, Ben-Sasson et al., (2009) noted that infants and toddlers younger than 3 years of age, but not children with ASD, were more frequently displaying reduced sensory seeking compared to age-matched typically developing children; chronological age was reported as the only factor explaining variability in seeking profiles. Later studies adopting parent-reported and observational methods replicated the profile of reduced sensory seeking in infants at elevated likelihood of ASD (Mulligan & White, 2012; Piccardi et al., 2021) and enhanced sensory seeking in children with ASD (Lane et al., 2010; Simpson et al., 2019; Tomchek et al., 2018). This evidence contrasts the notion of stability in sensory seeking manifestations in ASD, pointing instead to a developmental transition. But what could explain this transition? To answer this question, it is fundamental to note that elevated sensory seeking in children with ASD manifests as repetitive and restricted seeking, such as hand flapping, or spinning a wheel on a toy car. Drawing on the information prioritization hypothesis, we propose that this developmental transition may reflect learning that another strategy to limit incoming novel and diverse sensory stimulation (which children with ASD may experience as distressing, Mulligan & White, 2012) is to repetitively and restrictively seek sensory stimulation that is often self-produced. Such transition would reflect a process of *ontogenetic niche construction*, enabling children with ASD to select a sensory environment which is best suited to process and generating behaviours that maximise sensory information that can be processed (Johnson, 2017). From an empirical perspective, this proposal is supported by evidence that early exploratory drives are weaker in infants at elevated likelihood of ASD (Gluga et al., 2018), that the prevalence and severity of restricted and repetitive behaviours increase during childhood in ASD (Harrop et al., 2014; Richler et al., 2010), and that diagnostic traits and symptoms related to restricted and repetitive behaviours are not measurable in the same way in early relative to later years (Courchesne et al., 2021).

Our theoretical proposal also argues for a primarily reciprocal role of causation, where individual differences in children's information prioritization would shape their preferred sensory environments, and vice versa. Thus, selected sensory environments may also influence children's information processing styles, narrowing or widening learning opportunities. This notion emphasizes the importance of context for characterizing children's sensory seeking behaviour, acknowledging that everyone has contexts that may promote sensory seeking and contexts that may be too rich, or sparse to support individual ways of finding out about the world.

Preliminary support for this idea has emerged in a recent study (Piccardi et al., 2021), whereby tactile sensory seeking at 10 months was shown to moderate the association between early tactile sensory processing (i.e., suppression of repeated tactile stimulation) and later ASD traits. Specifically, 10-month-old infants who displayed elevated tactile sensory seeking despite their concurrent sensory processing difficulty (i.e., limited neural suppression of repeated tactile stimulation), also manifested fewer ASD traits at 24 months. Although not conclusive, this evidence suggests that elevated tactile sensory seeking in early development may act as a protective factor, helping to shape an environment that could widen opportunities for learning and socialization. Despite this evidence, the extent to which early elevated sensory seeking in infants at elevated likelihood of ASD may influence neural responsiveness to sensory

stimulation (e.g., mitigating early atypical neural activity over the course of development) remains an open question.

In sum, we argue that current measures conflating exploitation of the resource at hand and exploration of incoming sensory stimulation are unlikely to advance our understanding of the mechanisms underlying individual differences in sensory seeking. We believe, instead, that developing measures that separate learning progress and prioritization of incoming sensory stimulation is necessary. These measures would benefit our understanding of this sensory regulation strategy in typical and atypical development.

Conclusion and future directions

We aimed to evaluate the nature and characteristics of sensory seeking, a behavioural strategy for sensory regulation, in populations with typical and atypical development. To this aim, we presented several theoretical models proposed to clarify mechanisms underlying individual differences in sensory seeking, critically assessing evidence for/against each of these models. Following our synthesis of the work examining sensory seeking manifestations in populations with typical and atypical development, we argued that the information prioritization hypothesis holds the greatest promise to advance our understanding of this sensory regulation strategy across participant cohorts. Drawing on this theoretical model, we now offer some areas for future research: the first prompts examination of the potential effects of sensory seeking on brain plasticity; the second motivates evaluation of linkages between measures of sensory seeking and information seeking.

Sensory seeking and brain plasticity

Brain plasticity refers to the ability of the nervous system to change its activity in response to environmental input by reorganizing structure, functions, or connectivity patterns (Mateos-Aparicio & Rodríguez-Moreno, 2019). Over the past century, research has indicated that brain plasticity is a fundamental property of many species, from insects to non-human and human primates (for reviews see, Duffau, 2006; Mateos-Aparicio & Rodríguez-Moreno, 2019). For example, in the human brain, reorganization was reported in the visual cortex of congenitally blind skilled Braille readers (Pascual-Leone et al., 2005), or in the posterior hippocampi of professional taxi drivers (Maguire et al., 2000). While brain plasticity has been reported throughout the life span, evidence also indicates that there are periods of sensitivity during early development whereby the extent of brain plasticity is maximal (Knudsen, 2004).

Considering this evidence, an area that warrants examination concerns the potential effects of sensory seeking behaviours on brain plasticity in typically and atypically developing populations. We argue that differences in sensory seeking behaviours may lead to changes in the post-natal environment experienced by children, in turn affecting brain plasticity through learning. As a strategy to compensate for sensory processing difficulties in the early development of ASD, reduced sensory seeking may also restrict learning opportunities, further reinforcing neurodevelopmental changes leading to later atypical development. Conversely, elevated sensory seeking in the face of existing sensory difficulties may be a protective factor in early development, widening opportunities for learning and socialization, and mitigating the effect of neurodevelopmental changes on later outcomes. This prediction could be empirically assessed by means of longitudinal designs, whereby the same measures of neural processing to sensory stimulation and sensory seeking are collected at various points in development. We would expect sensory seeking to act as a longitudinal moderator, such that infants

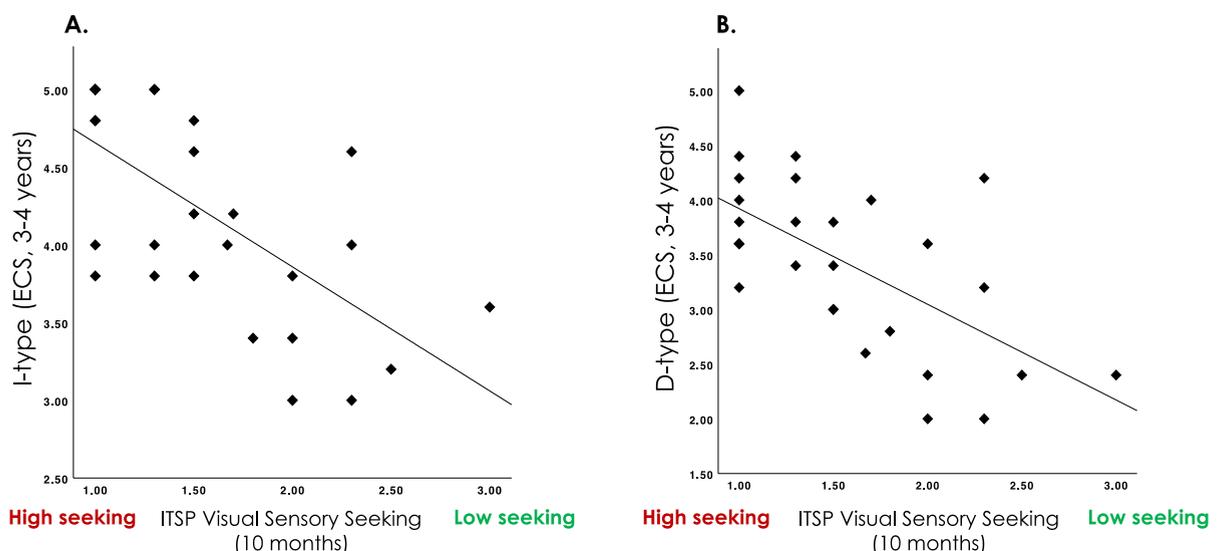


Fig. 2. Scatterplots illustrating the significant associations between ITSP visual sensory seeking scores at 10 months and **[A]** Epistemic curiosity (Interest-type; $\rho = -0.691$, $p < .001$), **[B]** Epistemic curiosity (Deprivation-type; $\rho = -0.606$, $p < .001$) scores at 3–4 years of age. The higher the parent-reported visual sensory seeking scores at 10 months (assessed through the ITSP; Dunn, 2002), the higher the parent-reported epistemic curiosity at 3–4 years (assessed through the Epistemic Curiosity Scales for Young Children; Piotrowski et al., 2014). See SM for further details.

manifesting enhanced sensory seeking despite early atypical neural responsiveness to sensory stimulation would restore typical neural responsiveness later in development.

Linkages between measures of sensory seeking and information seeking

Although developmental research has investigated the constructs of sensory and information seeking separately, evaluation of potential linkages between these constructs remains limited. Measures of information seeking have mostly focused on examining individuals' drives towards learning something new – a concept known as *epistemic curiosity* (Litman, 2008). In early development, behaviours such as pointing, or questioning have been employed as a proxy for children's information seeking drives (Begus & Southgate, 2012; Kurkul & Corriveau, 2018). On the other hand, measures of sensory seeking have spanned several behavioural manifestations. In early development, behaviours such as visual, or haptic exploration of objects have been used as a proxy for children's sensory seeking drives (Sheese et al., 2008; Dunn, 2002). A link is likely to exist between drives towards novel and diversive sensory stimulation and measures of epistemic curiosity, however developmental research in this area remains scarce (e.g., Perez & Feigenson, 2021). We are currently undertaking longitudinal research examining links between measures of sensory seeking in infancy and epistemic curiosity in early childhood (based on two dimensions: Interest – capturing the desire of obtaining new knowledge capable of producing positive experiences of intellectual interest; Deprivation – capturing the desire of reducing unpleasant experiences of information uncertainty) (Piotrowski & Litman, 2014). Our hypothesis is that continuity exists between measures of information seeking (interest and deprivation) and the seeking of novel and diversive sensory stimulation, with the latter scaffolding the former over development. A recent study by Perez and Feigenson (2021) provided support for this hypothesis, demonstrating that individual differences in novelty preferences at 11 and 17 months predict explanation-based curiosity at 3 years. Emerging results from our research also support this hypothesis, indicating that elevated parent-reported visual sensory seeking at 10 months longitudinally predicts higher parent-reported epistemic curiosity scores (interest and deprivation) at 3–4 years of age (see Fig. 2 and SM for study details). Further, drawing on the information prioritization hypothesis, we propose that common mechanisms may underlie information seeking and the seeking of novel and diversive sensory stimulation: i.e., learning progress and prioritization of incoming information.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dr.2022.101037>.

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