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Numerical Cognition and Autism Spectrum Traits in Adults

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NUMERICAL COGNITION AND AUTISM SPECTRUM TRAITS IN ADULTS

by

Benjamin Covington

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Neuroscience

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UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Numerical Cognition and Autism Spectrum Traits in Adults

by

Benjamin Covington

Utah State University, 2021

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Evidence suggests that individuals with high-functioning autism spectrum disorder
(ASD) may be particularly inclined toward math proficiency, especially in adulthood.
There is also evidence, however, that many of those with an ASD struggle in math as
children compared to their typically-developing peers. These ostensibly inconsistent
findings may indicate that individuals with an ASD struggle with number sense, a
precursor to formal math, rather than with formal math *per se*. This account is compatible
with evidence of a specific form of neural dysregulation, excitatory/inhibitory imbalance,
in ASD that results in reduced signal-to-noise ratios (SNR) for processes that occur in
downstream neural regions (such as association cortex). Based on this view, formal math,
a task with enhanced SNR due to standardization, would likely be intact for individuals
with an ASD, while number sense, a domain localized to association cortex that lacks
SNR enhancement via standardization, would take longer to sufficiently refine and would
delay formal math acquisition for this population. The current studies examined whether
a neural dysregulation account of ASD effectively predicts and explains numerical

cognition performance across ASD traits. Experiment 1 examined whether scores on the *Autism-Spectrum Quotient* and the *Systemizing Quotient* predict performance on measures of numerical cognition consistent with a neural dysregulation account and in contrast to a traditional hyper-systemizing account of ASD. Experiment 2 examined whether strengthening the stimulus signal by presenting stimuli multimodally improves number sense performance across the range of ASD traits, as well as whether manipulation of high-level stimulus features affects multisensory integration in a manner consistent with a neural dysregulation account.

(126 pages)

PUBLIC ABSTRACT

Numerical Cognition and Autism Spectrum Traits in Adults

Benjamin Covington

Evidence suggests that individuals with high-functioning autism spectrum disorder (ASD) may be particularly inclined toward math proficiency, especially in adulthood. There is also evidence, however, that many of those with an ASD struggle in math as children compared to their typically-developing peers. These ostensibly inconsistent findings may indicate that individuals with an ASD struggle with number sense, a precursor to formal math, rather than with formal math *per se*. This account is compatible with evidence of a specific form of neural dysregulation, excitatory/inhibitory imbalance, in ASD that results in reduced signal-to-noise ratios (SNR) for processes that occur in downstream neural regions (such as association cortex). Based on this view, formal math, a task with enhanced SNR due to standardization, would likely be intact for individuals with an ASD, while number sense, a domain localized to association cortex that lacks SNR enhancement via standardization, would take longer to sufficiently refine and would delay formal math acquisition for this population. The current studies examined whether a neural dysregulation account of ASD effectively predicts and explains numerical cognition performance across ASD traits. Experiment 1 examined whether scores on the *Autism-Spectrum Quotient* and the *Systemizing Quotient* predict performance on measures of numerical cognition consistent with a neural dysregulation account and in contrast to a traditional hyper-systemizing account of ASD. Experiment 2 examined whether strengthening the stimulus signal by presenting stimuli multimodally improves

number sense performance across the range of ASD traits, as well as whether

manipulation of high-level stimulus features affects multisensory integration in a manner

consistent with a neural dysregulation account.

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Benjamin Covington

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<center>**Introduction**</center>

ASD and Mathematics

The mathematic abilities of individuals with high-functioning ASD[1] compared to the general population have been studied at length; however, the results of this research have produced an unclear picture (Iuculano et al., 2014; Oswald et al., 2016; see also review in Kim & Cameron, 2016). Numerous studies have suggested that there is a link between ASD and mathematical proficiency, especially later in life (Baron-Cohen et al., 2001; Baron-Cohen et al., 2007; Baron-Cohen et al., 2009; Baron-Cohen & Lombardo, 2017; Baron-Cohen et al., 2003; Iuculano et al., 2014; Wei et al., 2013). For example, Baron-Cohen et al. (2001) found that across social science, humanities, mathematics, and science students at Cambridge University, mathematicians scored the highest on the *Autism-Spectrum Quotient* (*AQ*, Baron-Cohen et al., 2001), a measure of ASD traits. Wei et al. (2013) also found abnormally high STEM participation by ASD students at the college level. Baron-Cohen et al. (2007) found that mathematics undergraduates were significantly more likely than undergraduates in social science, medicine, or law to be diagnosed with an ASD or have a relative with an ASD. A preliminary genomic study also found an association between math achievement and a single nucleotide polymorphism located in a region on chromosome 3q29, a region linked to ASD (Baron-Cohen et al., 2014; Sagar et al., 2013).

Research has also demonstrated, however, that individuals diagnosed with an ASD tend to struggle with math in childhood. For example, Bae et al. (2015) found

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[1] The current studies focused on high-functioning ASD (HFA), also referred to as ASD without intellectual disability (the cutoff for which is standardly an IQ of 75). All references in the current study to ASD refer to this population unless otherwise specified.

significantly lower word-problem performance for fourth- and fifth-grade children with an ASD than for typically-developing (TD) children. Aagten-Murphy et al. (2015) found that 8- to 13-year-old children with an ASD performed below TD peers on the Mathematical Reasoning and Numerical Operations subtests of the *Wechsler Objective Numerical Dimension* (*WOND*; Rust, 1996). Chen et al. (2019) found that children 7 to 12 years old with an ASD scored significantly lower on Numerical Operations and Mathematical Reasoning subtests of the *Wechsler Individual Achievement Test* (*WIAT-II*; Wechsler, 2001) than did controls matched for age and full-scale IQ.

It is important to note that when learners do show math deficits, many studies indicate these deficits are not static (Barnett & Clearly, 2015; Bullen et al., 2020; Gevarter et al., 2016; Wei et al., 2015). Wei et al. (2015) found that even though approximately one-third of their sample (6- to 9-year-old children with an ASD) showed mathematical abilities two standard deviations below the national average, these abilities increased across three timepoints. Similarly, although Bullen et al. (2020) found that math performance for ASD children (8 to 15 years old) was significantly lower than their TD peers across a 30-month period, they also reported growth over time and that this rate of growth was comparable to TDs. In addition, reviews of math interventions for learners with an ASD indicate that these learners' mathematic skills can improve with assistance (Barnett & Cleary, 2015; Gevarter et al., 2016; King et al, 2016).

Numerical Cognition

Number Sense. These findings taken together may indicate that individuals with an ASD are not impaired in formal math *per se,* but may experience difficulty with an early numerical perceptual ability on which formal math may be predicated. This ability

is referred to in cognitive psychology and neuroscience literature as numerosity or number sense (Dehaene, 2001; Eger et al., 2003; Von Aster, 2000).[2] Number sense, which has been detected in non-human primates and in infants as young as 50 hours old, allows individuals to perceive with some accuracy the quantity property of a set of discrete objects without the use of symbols or counting (Izard et al., 2009; Nieder, 2016).

Without this ability to represent non-symbolic quantity, it is unclear how successfully an individual can acquire formal math (Butterworth, 1999; Dumontheil & Klingberg, 2011; Hubbard et al., 2005; Libertus et al., 2011; Mazzocco et al., 2011; Starr et al., 2013; Szucs et al., 2013). Butterworth (1999) proposed that the ability to learn abstract, linguistic representations of quantity depended first on the accurate perception of small quantities. In a study designed to test this idea, Penner-Wilger et al. (2007) found that first graders' performance on a numerical perception task (enumerating 1 to 6 red circles) was concurrently predictive of their calculation skill, as measured by the *Woodcock-Johnson*. Fischer et al. (2008) gave 7- to 17-year-olds with and without arithmetic deficit, as measured by either the *Zareki* or *DEMAT*, a similar measure (enumerating 1 to 8 circles) and found that those in the group with deficit were slower and less accurate for all quantities. Libertus et al. (2011) measured acuity for quantities 5 to 22 as well as formal math ability and verbal skills for 3- to 5-year-olds. The authors found that numerical perception acuity was predictive of scores on the *Test of Early Mathematics Ability, Third Edition* (*TEMA-3*; Ginsburg & Baroody, 2003) even when

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[2] It warrants noting that the term "number sense" is used more broadly in other domains. For example, educational psychology literature uses the phrase "number sense" to refer to a collection of adaptive skills and concepts surrounding not only quantity as a specific parameter, but also computational fluency and conceptual cohesion of the number system (Anghileri, 2000; Shumway, 2011). The present study deals specifically with the concept of intuitive number sense investigated in cognitive neuroscience. It is also worth noting that in this latter domain, number sense and numerosity are often used interchangeably, an approach adopted in the present study as well.

controlling for a child's age and verbal ability. Similarly, Mazzocco et al. (2011) observed that preschoolers' discriminability in a forced-choice, numerosity-array comparison task (quantities 1 to 14) predicted performance on the *TEMA-3* two years later. Importantly, the study found that this predictive power held uniquely for math achievement and not for other non-numerical domains of cognitive performance.

Early studies examining the processing of small quantities in learners with an ASD have suggested a preference for serial counting over perceptual approximation, which lead to speculations that individuals with an ASD may be impaired in this area (Gagnon, et al., 2004; Jarrold & Russell, 1997; Russell et al., 1996). Some of the paradigms used, however, resulted in interpretative limitations (Gagnon et al., 2004).[3] In an attempt to address many of these limitations, Gagnon et al. (2004) gave fourteen individuals with an ASD ($\bar{X}_{age} = 15$) and fourteen age- and FSIQ-matched TD controls a quantity perception task (enumerating arrays of 2 to 9 squares) with no distractors and with instructions to respond as quickly and accurately as possible. The authors found comparable response times and error rates for both groups, with response times increasing as quantity increased, as expected. Although these results seem to suggest no ASD impairment, a closer examination of response times for quantities 3 to 5 revealed a slope difference between the two groups such that TDs showed a steeper change in response time than ASDs. This was taken to suggest that individuals with an ASD were more likely to default to a less efficient serial counting strategy instead of perceptual approximation even for small quantities.

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[3] These limitations include instructions to "count" stimuli rapidly in Jarrold and Russell (1997, p. 29), and inclusion of additional variables that were not controlled statistically or experimentally in Trick and Pylyshyn (1994).

The study by Gagnon et al., however, also has limitations affecting interpretation.[4] In an attempt to more effectively measure perceptual approximation, Aagten-Murphy et al. (2015) used a forced-choice display that instructed TD children and children with an ASD (8 to 13 years old) to choose which image displayed more marbles. Two side-by-side panels of dots were presented simultaneously for 500 ms and participants were instructed to touch the side of the screen with the higher numerosity. One of the panels always included the reference quantity of 48 dots, and the comparison panel numerosity varied by means of trial-by-trial update using Watson and Pelli's (1983) QUEST algorithm to estimate the point of subjective equality, a measure of the pairwise difference at which the panels are perceived to be equal. Weber ratios of numerosity discriminability were also computed for all participants. The authors found that children with an ASD were less precise than their TD peers (i.e., exhibited larger Weber ratios), requiring greater differences between the display quantities on average to accurately determine the larger quantity.

In a similar study, Hiniker et al. (2016) gave TD children and children with an ASD (7 to 12 years old) displays of green dots for 1500 ms that ranged in quantity from 2 to 9. The authors found that the ASD and TD groups did not significantly differ in response time; however, the ASD group was significantly less accurate and required greater differences in quantities to make accurate judgements. Thus, there does appear to be evidence suggesting that individuals with an ASD struggle with number sense

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[4] These limitations include excluded direct groupwise comparisons of ASD and TD participants regarding smaller numerosity ranges (partially addressed in O'Hearn et al., 2013) as well as a verbal response protocol that may conflate language processing and numerical cognition in response patterns.

compared to their TD peers (Aagten-Murphy et al., 2015; Gagnon et al., 2004; Hiniker et al., 2016).

These studies also demonstrate, however, that individuals with an ASD do not lack number sense; these learners appear able to perceive and approximate quantity, just not as precisely as their TD peers. In other words, learners with an ASD have mental representations for quantity on which they can map number symbols. Sufficiently acute representations, however, may take more time and/or effort for individuals with an ASD to acquire, resulting in symbolic number system and formal math acquisition delays, consistent with findings of growth in these abilities over time.

Aagten-Murphy et al. (2015) and Hiniker et al. (2016) also examined the relationship between the number sense acuity of children with an ASD and their formal math performance. This pattern, however, is less clear. Although Aagten-Murphy et al. found that children with an ASD performed significantly below TD peers on Mathematical Reasoning and Numerical Operations subtests of the *WOND* they found no significant correlation between number sense acuity and math performance for either TDs or individuals with an ASD, nor did they find number sense significantly predictive of math performance using a regression model. In contrast, Hiniker et al. (2016) found no difference in math performance between 7- to 12-year-old TD children and children with an ASD of the same age and IQ. The authors did, however, find a significant partial correlation between number sense acuity (given as Weber fractions) and composite math score (derived by combining the Mathematical Reasoning and Numerical Operations subtests of the *WIAT-II*) for both TDs and children with an ASD while controlling for symbolic number acuity.

Symbolic Number System. It is postulated that once number sense has been sufficiently developed learners are able to map a symbolic number system onto their representations of quantity (Wang et al., 2016; Rathé et al., 2019). Recruiting the concept of quantity for use in solving complex problems benefits greatly from mapping quantities onto standardized symbols (Ashcraft & Krause, 2007). For example, manipulating quantity concepts requires overcoming limitations of memory (e.g., sensory memory duration, working memory capacity), which is why mental arithmetic is more difficult than written arithmetic (Ashcraft & Krause, 2007; Dehaene, 2011; Raghubar et al., 2010). In addition, the use of concrete manipulatives for quantity, even small objects (e.g., beads), requires overcoming limitations of space (Dehaene, 2011). For example, performing calculations with large numbers or several steps can be unwieldy on an abacus. Consequently, working with large quantities and solving complex problems is considerably improved by the acquisition of an efficient written notation system (Dehaene, 2011). While the types of numerical relationships expressed throughout systems differ substantially, all such systems are predicated on successfully creating corresponding symbols for the abstract numerosities being utilized.

Consistent with this view, measures of children's performance on tasks requiring the symbolic number system suggest that it is predictive of later formal math performance (Hiniker et al., 2016; Hornung et al., 2014; Jordan et al., 2007; Jordan, Glutting, and Ramineni, 2010; Jordan, Glutting, Ramineni, & Watkins, 2010). Jordan, Glutting, and Ramineni (2010) found that first-graders' performance on a number sense battery, including comparison of symbolic numbers, predicted third grade math performance. Similarly, Sasanguie et al. (2013) measured symbolic comparison

performance for 6- to 8-year-olds and found that scores on this task predicted

performance on both a timed arithmetic test (*Tempo Test Rekenen*, *TTR*; De Vos, 1992)

and a curriculum-based math achievement test. Desoete et al. (2010) showed that among

kindergarteners, symbolic comparison of Arabic digits significantly predicted simple,

procedural calculation ability two years later. Similarly, Scalise and Ramani (2021) found

that preschoolers' symbolic magnitude comparison abilities significantly predicted their

procedural addition skills three to four months later.

The relationship between symbolic number ability and formal math has been less

explored for learners with an ASD. Aagten-Murphy et al. (2015) found that children (8 to

13 years old) with an ASD made significantly more errors on a symbolic numberline

tasks than TD peers. Although the authors did not find a significant relationship between

number sense and formal math, they did find that ASD performance on these spatial,

symbolic measures significantly correlate with mathematical performance, even when

age and IQ were controlled. The authors also found that performance on one of their

numberline tasks (1-1000) was significantly predictive of their math composite score

(Mathematical Reasoning and Numerical Operations from the *WOND*) in a regression

model that included age, IQ, and diagnostic status.

Hiniker et al. (2016) found that children (7 to 12 years old) with an ASD showed

no difference than TDs in accuracy, RT, or Weber fraction on an Arabic symbols

comparison task. The authors also found that symbolic Weber fractions significantly

correlated with a math composite score (*WIAT* subscales) for both TD children and

children with an ASD. Regression analyses controlling for age and IQ indicated that

neither number sense nor symbolic number acuity predicted math performance for TD

children; however, both measures remained significant for children with an ASD, with symbolic number acuity showing the stronger relationship. The authors further found that a model for symbolic number acuity added predictive power for math performance over a number sense model, however, the reverse was not true.

Hiniker et al. (2016) also conducted mediation analyses examining the relationship among symbolic number, non-symbolic number and formal math performance for each group. Hiniker et al.'s (2016) findings suggest that while both non-symbolic number acuity and symbolic number acuity predict formal math performance for children with an ASD, the dominant predictive factor was symbolic number acuity. This, however, was not found for TDs. A closer examination of the series of regressions supporting this finding shows that the standardized β coefficients for these two predictors in models predicting formal math performance for TDs were nearly identical ($\hat{\beta}_{\log(\mathrm{w}_{dots})} = -0.11$; $\hat{\beta}_{\log(\mathrm{w}_{digits})} = -0.11$); however, building similar models for children with an ASD, the standardized β coefficients for these two predictors exhibited a greater difference ($\hat{\beta}_{\log(\mathrm{w}_{dots})} = -0.27$; $\hat{\beta}_{\log(\mathrm{w}_{digits})} = -0.37$). Similarly, when estimating Pearson partial correlation coefficients for each of these predictors and formal math achievement, there is a greater observed difference in correlations for individuals with an ASD than for TDs (TD: $r_{\log(\mathrm{w}_{dots})} = -0.29$, $r_{\log(\mathrm{w}_{digits})} = -0.38$; ASD: $r_{\log(\mathrm{w}_{dots})} = -0.36$, $r_{\log(\mathrm{w}_{digits})} = -0.50$). While these differences are not extreme, they might provide a possible explanation for the observed pattern of differences between groups in predicting formal math achievement.

Neural Correlates of Numerical Cognition

Number Sense. The ability to perceive the quantity parameter of a stimulus (i.e.,

number sense) has been explored at length in neurophysiological research, as well,

establishing candidate neural substrates in a frontoparietal network similarly in humans

and other primates (Ansari & Dhital, 2006; Cantlon et al., 2006; Nieder & Merten, 2007;

Nieder & Miller, 2004; Okuyama et al., 2015; Sawamura et al., 2009). The central

functional region with which activation is most consistently correlated in number sense

tasks is the horizontal segment of the intraparietal sulcus (IPS) in the posterior parietal

region of association cortex bilaterally separating the superior and inferior parietal

lobules (e.g., Dehaene et al., 2004; Dormal et al., 2012; Eger et al., 2003; Izard et al.,

2008; Piazza et al., 2004).

Neurophysiological research in primates has identified a class of neurons, so-

called "number neurons", that are uniquely tuned to the numerosity of a stimulus. It is the

computational parameters of this neuronal population that give rise to the perceptual

category of quantity (Hubbard et al., 2005; Piazza et al., 2004). In other words,

subpopulations of number neurons fire in response to many stimulus quantities, however,

they fire maximally for a preferred stimulus quantity (Nieder, 2016). The distribution of

these firing profiles is logarithmically compressed, obeying the Weber-Fechner law

(Dehaene, 2003; Nieder & Miller, 2003; *cf.* Billock & Tsou, 2011), which states that

linear increments in stimulus discriminability are proportional to logarithmic increments

in stimulus magnitude ($P = k \log(I)$; Fechner, 1860). Specifically, the normalized

average responses to varying numerosity inputs follow a lognormal distribution (i.e., their

output rates assume a Gaussian distribution when their inputs are plotted on a logarithmic

scale, as predicted by the Weber-Fechner law). To wit, the rate at which these neurons fire decreases as the distance between the stimulus' numerosity and their preferred numerosity increases.

This computational profile is also strikingly consistent with behavioral findings for humans in the numerosity literature (Nieder, 2016). For example, this model predicts the well-documented differences between perception of very small quantities (i.e., 4 or fewer) and perception of larger quantities (i.e., 5 or greater), as small quantities have a natural limit to the potential overlap in their tuning curves resulting in faster detection and less imprecision. This model is also consistent with canonical phenomena of numerosity perception, such as the size effect (i.e., smaller number pairings are easier to discriminate than larger number pairings) and the distance effect (i.e., distant number pairings are easier to discriminate than nearer number pairings) (Pinel et al., 2007). In addition, in an fMRI study of TD 3- to 6-year-old children completing a numerical discrimination task, Kersey and Cantlon (2017) compared neural tuning curves to behavioral performance curves at the individual level. Although, the individual level is generally subject to a larger error term than group-level models, the authors found a strikingly high correlation between individual children's neural and behavioral tuning curves ($r = 0.93, p < 0.00001$).

This model is also supported by studies of number sense dysfunction. In humans, disruption of this system has been associated with dyscalculia. For example, individuals diagnosed with Turner syndrome, a chromosomal disorder that often manifests dyscalculia, often exhibit parietal atrophy in general as well as substantial alterations in the shape and size of the IPS in particular, including decreased maximal depth and

irregular branching patterns (Molko et al., 2003). Price et al. (2007) also observed that a sample of children diagnosed with developmental dyscalculia ($\bar{X}_{age} = 11.43$) exhibited significantly less intraparietal modulation in response to increasing distance between numerical stimuli than was observed in TD age-matched controls.

      Symbolic Number System. Representing quantities with symbols requires not only that number sense be sufficiently developed to provide a reliable referent, but also intact symbol recognition and a mechanism with which to map these symbols onto the quantity representations (Cantlon et al., 2009), a complex system integrating numerous cortical regions. While numerosity computations proceed via the dorsal stream through medial occipital cortex and the posterior superior parietal lobule (PSPL) toward the IPS (Knops, 2017; Santens et al., 2010), symbol recognition and categorization proceed toward ventral occipitotemporal cortex (superior temporal gyrus [STG] for audition), which, in turn, directly activates the IPS (Dehaene, 2007; Santens et al., 2010). fMRI research has demonstrated an association between frontoparietal functional connectivity and matching number symbols to their non-symbolic referents (Emerson & Cantlon, 2012). Intracranial EEG has also implicated posterior inferotemporal cortex in number symbol recognition (Pinheiro-Chagas et al., 2018).

Excitatory/Inhibitory Imbalance in ASD

      Neurobiological models of ASD have been repeatedly characterized by broad disruption in the ratio of excitatory and inhibitory activity throughout the brain (Auerbach et al., 2011; Nelson & Valakh, 2015; Rubenstein & Merzenich, 2003; Xu et al., 2014). These alterations are consistent with the categorization of ASD as a pervasive developmental disorder and with key comorbidities, such as substantially increased rates

of epilepsy (Nelson & Valakh, 2015). Moreover, such alterations predict an array of behavioral findings evidenced in ASD, such as restricted and repetitive behaviors, decreased cognitive flexibility, and preservation or enhancement of low-level perception (Hines et al., 2008; Rosenberg et al., 2015; Silverman et al., 2015).

This form of neural dysregulation, known as excitatory/inhibitory (E/I) imbalance, appears likely to originate from multiple potential genetic alterations. For example, Hussman et al. (2011) used a genome-wide association study to identify a subset of ASD-risk genes, such as *GABBR2* and *GRIK2/4*, involved in encoding elements of GABAergic and glutamatergic receptors respectively. In addition, Nelson and Valakh (2015) also reviewed altered activity of numerous genes and gene products, such as *SHANK3*, *NRXN1*, neuroligins 1-4, and guanine deaminase, involved in synaptic formation and maturation as part of ASD pathologies.

Multiple transcriptional factors have also been noted as having a high likelihood of contributing to altered neurodevelopment in ASD. For example, Wang et al. (2009) report two genome-wide association studies that include among their genotyped and imputed markers the transcriptional factor *FEZF2*, which has been clearly evidenced to play a significant role in cortical gene expression subserving corticofugal network connections (see Kwan [2013] for a review). Similarly, Bowers and Konopka (2012) detail the potential impact of the *FOXP* family of cortical transcription factors on brain development, including altered language development. Estruch et al. (2018) expanded this further to identify the complex set of interactions between the *FOXP* family and five other cortical transcription factors relevant to ASD neurodevelopment processes.

These alterations impact early brain formation including neuronal proliferation, migration, and connectivity from embryonic development onward. Such early conditions can easily result in the disruption of E/I ratios in upstream regions, the output of which drives the appropriate tuning of downstream regions. Consequently, maturation of these downstream regions, such as limbic areas and association cortex, becomes a function of imbalanced inputs (Nelson & Valakh, 2015).

Exacerbating this problem is the role of homeostatic regulators, a family of mechanisms whose function is to prevent extreme states of network activation (Bourgeron, 2015). Multiple homeostatic regulators are likely to be compromised in ASD (Krey & Dolmetsch, 2007; Mabb et al., 2011; Pizzarelli & Cherubini, 2011; Yang et al., 2014; Xu et al., 2018). For example, release of brain-derived neurotrophic factor (BDNF) from postsynaptic neurons appears to facilitate enhancement of presynaptic activity as a mechanism of circuit homeostasis (Jakawich et al., 2010). Both BDNF and its encoding gene exhibit altered expression in many individuals with an ASD, leading to the supposition that it plays a substantial role in ASD pathogenesis (Cheng et al., 2009; Nishimura et al., 2007).

As a result, downstream regions are likely to experience upregulated excitability consistent with epileptiform activity and broad neuronal tuning curves (Bourgeron, 2015; Chistiakova et al., 2015; Nelson & Valakh, 2015; Pachitariu et al., 2016). In other words, homeostatic regulators should function to compensate for reduced excitatory outputs from upstream regions by upregulating downstream circuit excitability to an adaptive level. However, compromised regulators in the ASD brain overcorrect, resulting in overexcitability of downstream targets (Nelson & Valakh, 2015). This suggests a

distinctive E/I profile for individuals with an ASD, with a tendency toward excessive inhibition (i.e., signal overfitting) in upstream regions and excessive excitation (i.e., signal underfitting) in downstream regions, resulting in signal propagation that is poorly suited to signal abstraction in the higher-order receptive fields of association cortex.[5]

Upstream Visuospatial Processing. An E/I imbalance account is consistent with findings that individuals with an ASD show enhanced performance for low-level versus high-level visuospatial tasks (Allen & Chambers, 2011; Jobs et al., 2018; Kim & Cameron, 2016; Mitchell & Ropar, 2004; Muth et al., 2014; O'Riordan & Plaisted, 2001; Shah & Frith, 1993). Individuals with an ASD or above-average ASD traits have often been shown to exhibit high ability for decomposition and disembedding tasks in which attention to details of a stimulus facilitate task performance (Almeida et al., 2010; Shah & Frith, 1993; Stewart et al., 2009). Similarly, individuals with these traits are quicker than TD controls on single- and conjunctive-target visual search tasks (Mottron et al., 2003; O'Riordan et al., 2001; O'Riordan & Plaisted, 2001).

However, when the visuospatial task requires higher-level processing, no enhancement is found, and deficits may appear. Van der Hallen et al. (2019) reviewed 48 studies on global motion thresholds as a measure of high-level visual processing used to compare global perception in TD individuals and individuals with an ASD. Across paradigms (i.e., biological motion, coherent motion) and controlling for key covariates (e.g., age and IQ), individuals with an ASD were estimated to exhibit slightly higher

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[5] Overfitting here refers to the neural dynamics that lead to attempting to incorporate every idiosyncrasy of a stimulus presentation into the neural representation, while underfitting refers to the failure to identify a clear trend in the stimulus presentation (Bakouie et al., 2009; Van de Cruys et al., 2014). This is similar to the usage of such terms in statistics and machine learning (Hastie et al., 2016; Kuhn & Johnson, 2013).

global motion thresholds (Hedges' g $= -.30$).[6] Studies on face processing suggest a similar result; as higher-level perceptual task demands are increased, visuospatial enhancements decline (Behrmann et al. 2006; Gross, 2005).

The seemingly inconsistent findings across these visuospatial tasks are explained by an E/I imbalance account which predicts overfitting in upstream regions (e.g., striate cortex, early extrastriate cortex) but overexcitability in downstream regions (Bertone et al., 2003; Spencer et al., 2000). Perturbation of γ-band synchronization along the dorsal visual stream has been repeatedly noted in children with an ASD (Milne et al., 2009; Stroganova et al., 2012; Sun et al., 2012), suggesting low binding of stimulus features consistent with high-specificity, low-invariance processing. In other words, what often manifests behaviorally as a low-level task advantage may actually be the same neural dysregulation that results in later deficits.

Number Sense. Behavioral findings of visuospatial enhancements combined with evidence that number sense is scaffolded onto visuospatial ability led Hiniker et al. (2016) to predict that individuals with an ASD would outperform their TD peers on a number sense task. This prediction, however, does not take into account the compounding effects of E/I imbalance for downstream processes, such as number sense. In other words, neural dysregulation may lead to less inhibition of neighboring number-specific subpopulations resulting in broader tuning curves and less precise perception of quantity for individuals with an ASD. Given that individuals with an ASD exhibit reduced perceptual ability and broadened tuning curves for other tasks requiring downstream visual processing, such as complex motion (Bertone et al. 2005) and face

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[6] Importantly, Kendall's rank correlation coefficient confirmed no publication bias in the studies included ($\tau = .006, p = .89$).

processing (Dawson et al., 2010), this account is plausible. Consequently, an E/I imbalance account of ASD may elucidate some of the unexpected findings of ASD numerical cognition research.

Although little direct investigation of IPS functioning in ASD exists, the results of Hiniker et al. (2016) and Aagten-Murphy et al. (2015) are consistent with the idea that dysregulated E/I ratio may be affecting these individuals' ability to precisely perceive quantity. Both research teams found clear deficits in visual number sense discrimination tasks for individuals with an ASD, suggesting marked impairments in processing that occurs in highly integrated, downstream visuospatial processing, a category that includes the IPS.

Symbolic Number and Formal Mathematics. Although regions of the brain involved in symbolic processing may be affected by the same pervasive issue of E/I imbalance as number sense, the acquisition of the symbolic number system has an advantage that the acquisition of number sense does not have: stimulus standardization. Symbolic number stimuli have a standardized connection to their corresponding quantity with an explicit, relatively consistent, and highly repetitious method of presentation. At the neural level, this provides a lower-variance training set (i.e., reduced stimulus dimensionality) than that which is presented to the IPS for quantity abstraction, such that tuning properties in regions dedicated to object/symbol recognition may be more easily shaped (Riesenhuber & Poggio, 2000; Iuculano et al., 2014). This is further consistent with findings of deficits in the recognition of moving, but not static, stimuli in ASD (Dawson et al., 2005; Perrett et al., 1992; Schultz et al., 2000) as the former includes increased dimensionality requiring higher levels of computational abstraction. Based on

these principles, the E/I imbalance account of ASD suggests that affected individuals

should recognize, and thus make use of, the quantity represented by a number symbol

more easily than its equivalent amodal quantity property from a non-symbolic

representation.

Hyper-systemizing

In addition to task performance, ASD preferences may also be consistent with an

E/I imbalance account. The proclivity of individuals with an ASD to abstract rigid rules

is referred to by Baron-Cohen et al. (2009) as hyper-systemizing. Baron-Cohen et al.

(2009) describe systemizing as a cognitive style that identifies replicable, reliable rules in

order to understand how a system works. Although, according to Baron-Cohen &

Lombardo (2017), all individuals systemize to some degree, individuals diagnosed with

an ASD are more likely to hyper-systemize than others. For example, in earlier literature

Frith (1972) found that when children with an ASD sequence stimuli, they do so using

regularly repeating patterns to derive rigid rules (e.g., A-B, A-B, A-B). Using a measure

of their own design, the *Systemizing Quotient* (*SQ*, Baron-Cohen et al., 2003) found that

individuals with an ASD tended to score significantly higher on the *SQ* than did matched

controls.

Although Baron-Cohen et al. (2003) postulate that individuals with an ASD

systemize due to a preference and talent for recognizing rigid rules in order to make

predictable sense of the world, this conception has some limitations. For example,

neuroeconomics generally argues that all learners prefer high predictability, all else being

equal (Braeutigam, 2005; Grupe & Nitschke, 2013); a hyper-systemizing view would

need to account for why individuals with an ASD exhibit a higher preference than do TD

individuals. This problem is not resolved by Baron-Cohen et al.'s (2009) conception of hyper-systemizing as a tendency to utilize higher than average attention to detail to create these rules. Specifically, this account is unable to explain why individuals with an ASD, if they are in fact predisposed to becoming an "expert in recognizing repeating patterns" (Baron-Cohen et al., 2009, p. 1377), often perform more poorly than TD individuals on tasks with implicit rules that involve repeating patterns, including understanding facial expressions, determining social rules, and set-shifting on the Wisconsin Card Sorting Test (WCST) (Baron-Cohen et al., 2009; Clark, 2008; Ozonoff, 1995; Landry & Al-Taie, 2015; Sato et al., 2012).

A Signal Detection Theory Account of the *SQ*

A more consistent and parsimonious account grants that both neurotypicals and individuals with an ASD have the same preference for predictability, but that individuals with an ASD experience more difficulty building predictable models of the world due to neural dysregulation. According to signal detection theory, the ability to detect meaningful information (i.e., signal) in the midst of background interference (i.e., noise) is predicated on both external and internal factors (McNicol, 2005; Stanislaw & Todorov, 1999). This means that both neurotypical and neuroatypical individuals always experience both external and internal contributions to the total ratio of stimulus signal-to-noise (Dombrowski et al., 2011; McGrath et al., 2011). A stimulus is always presented with a given amount of noise relative to its signal amplitude (i.e., calling out a friend's name across a room full of loud conversations). These contributions to total SNR are external to the perceiver. However, the individual perceiving the intended signal also has internal sources of noise that contribute to SNR (Czanner et al., 2015). Because neural

processing requires appropriately balanced neuronal dynamics in local circuits as well as faithful signal propagation from region to region, every person's brain is susceptible to internal noise.

E/I imbalance severity affects this degree of internal noise. Specifically, individuals with an ASD are proposed to exhibit a profile of upstream overfitting and downstream underfitting compared to neurotypicals (Nelson & Valakh, 2015). Although both preference and performance for both TDs and individuals with an ASD should be higher for high SNR tasks than low SNR tasks, the experienced task SNR would be different for TDs than for individuals with an ASD due to neural dysregulation. Upstream tasks would have a higher SNR for individuals with an ASD than for TDs. This is consistent with findings concerning performance on low-level perception tasks (e.g., Embedded Figures) (Jolliffe & Baron-Cohen, 2006; Shah & Frith, 1983). Downstream tasks would have a lower SNR for individuals with an ASD than for TDs. This is consistent with findings concerning complex perception tasks (e.g., global motion) and tasks that require learners with an ASD to abstract implied rules (e.g., facial recognition, theory of mind) (Dakin & Frith, 2005; Van der Hallen et al., 2019). Downstream tasks that have undergone sufficient signal enhancement would be expected to have a similar SNR for both TDs and individuals with an ASD. This is consistent with findings that individuals with an ASD perform as well as TDs on variations of the Wisconsin Card Sorting Task (WCST) when the set rule is made explicit (see Liandry & Al-Taie [2016] for a thorough meta-analysis) as well as findings that include evidence of intact memory involving standardized representations (i.e., rote facts versus episodes; Shalom, 2003; Toichi & Kamio, 2002) and math ability in adulthood (Baron-Cohen, 2007).

It is, therefore, proposed that a more parsimonious account of the *SQ* is that, rather than measuring the tendency to systemize, it measures preference for tasks that individuals with an E/I imbalance would experience as having a high SNR: tasks that have been explicitly systemized. In other words, it is proposed that the *SQ* is not measuring either a preference for rule-based tasks or an inclination to abstract rigid rules. Rather, it is proposed that the reason individuals with an ASD tend to score higher on the *SQ* than TD individuals is because neural dysregulation makes the process of abstracting rules from complex tasks more difficult than it is for neurotypicals, resulting in a preference for tasks for which the rules have already been made explicit. Consequently, the current study argues in favor of the use of the *SQ* as a proxy for E/I imbalance severity, leading to predictions that (1) scores on the *SQ* predict performance on tasks consistent with an E/I imbalance account, and 2) scores on the SQ show greater predictive power for these tasks than do scores on the *AQ*. As the *AQ* has been demonstrated to broadly measure ASD traits across the general population, (Baron-Cohen et al., 2001), there is reason to believe that the *AQ* is a convenient measure of ASD-related symptom pervasiveness. However, the current study proposed that the *AQ* would not be as sensitive as the *SQ* at capturing the underlying effects of E/I imbalance severity.[7] Therefore, it would be expected for there to be some overlap of variance between the *SQ* and the *AQ*, but that scores on the *SQ* would better predict performance on unenhanced downstream tasks than would scores on the *AQ*.

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[7] While the *SQ* would also be susceptible to some of the same limitations as the *AQ*, and is not proposed to be a perfectly unidimensional measure, the current study is arguing that the construction of the SQ resulted in greater internal consistency, and consequently, is more sensitive to E/I imbalance severity.

Experiment 1

Overview

Experiment 1 examined the performance of adults with a wide range of *AQ* and *SQ* scores on measures of numerical cognition, including number sense, symbolic number, and formal math. This study proposed that, although the *SQ* has been argued by Baron-Cohen et al. (2009) to be a measure of preference to systemize, a more accurate conception of the *SQ* is as a measure of preference for tasks that have been explicitly systemized. It is argued that this preference increases as E/I imbalance increases due to the ameliorating effects of signal enhancement, a relationship that the *AQ* would not be sensitive enough to capture well. If, as Baron-Cohen et al. (2009) has proposed, *SQ* is a measure of tendency toward or talent for determining rigid rules, performance should increase as *SQ* increases for all numerical cognition tasks. That is, even though the number sense task is not standardized, individuals higher on the *SQ* range would be expected to perform better than individuals lower on the *SQ* range due to an increasing inclination to systemize the task. If, however, *SQ* is a suitable proxy for E/I imbalance severity, performance on the number sense task should decrease as *SQ* increases.

This study also predicted that, while potential math ability may be the same across *SQ*, high-*SQ* individuals would be more likely to pursue math as a high SNR domain, and consequently show higher math achievement in adulthood, similar to previous findings (Baron-Cohen et al., 2001; Baron-Cohen et al., 2007).

In addition, consistent with the findings of Hiniker et al. (2016), this study proposed that due to decreasing number sense acuity, but not symbolic number acuity, as *SQ* increases, symbolic number mediates the relationship between number sense and

formal math for individuals in the higher *SQ* range. While Hiniker et al. (2016) found

symbolic number acuity to be more predictive of formal math achievement than number

sense for both the ASD and TD groups, the difference was more pronounced for

individuals with an ASD. It may be that for TDs, number sense and symbolic number

acuity are more interchangeably employed in formal math, while for individuals with an

ASD low number sense acuity encourages a stronger employment of the symbolic

number system. This study examined these relationships across the spectrum of ASD

traits in adults.

Predicted Outcomes

The present study tested the following predictions:

1. There is a significant partial positive correlation between *AQ* and *SQ*.

2. As *SQ*, but not *AQ*, increases, number sense acuity decreases.

3. Symbolic number acuity is intact across the range of *AQ* and *SQ*.

4. As *SQ*, but not *AQ*, increases, formal math performance increases.

5. Symbolic number acuity mediates the relationship between number sense

   performance and formal math performance for individuals in the higher *SQ*

   range, but not for individuals in the lower *SQ* range.

Participants

This study ultimately sought to collect data from sixty-eight participants.[8]

Following the collection of data for fifty-eight participants, the COVID-19 public health

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[8] Projected sample size was established to facilitate multiple linear regression analyses permitting model comparisons to evaluate R^2 increase ($\alpha = .05; 1 - \beta = .80$). Given the relatively limited data on the substantial heterogeneity of ASD and the consequent diversity of results in visuospatial and numerical processing literature, we have selected a relatively conservative, moderate effect size ($f^2 = .15$). Using

crisis led to a university-wide suspension of in-person research activities. This required cancellation of multiple data collection sessions and subsequent online administration of data collection sessions. Because online administration necessarily required alterations to stimulus delivery and response recording, changes in methods for specific measures are noted in the Methods section below. Power analyses were recomputed to facilitate the additional statistical control of the data collection method (i.e., in-person versus online). Inclusion of data collection method as a covariate made no difference to the any of the findings included in the results for this experiment.

The sample consists of seventy-four individuals between the ages of 18 and 43 (see Data Cleaning below). Participants were recruited through the SONA Research Participation program and FindParticipants.com. An email with information about the study was also distributed through the USU Disability Resource Center to individuals diagnosed with an ASD. Individuals were given an initial questionnaire to filter for preliminary exclusion criteria, including comorbidity with another pervasive developmental disorder sharing notable overlapping deficits with ASD (e.g., Williams Syndrome), current or prior neurological disease or brain trauma, and substantial sensorimotor impairment or physical abnormality, following St. John et al. (2018). Exception was made for a comorbid diagnosis of Fragile X Syndrome, due to its high candidacy as a leading monogenic ASD cause (Budimirovic et al., 2017). Such cases were not expected in this sample, nor did any occur. Because of the high-level of comorbidity and possible misdiagnosis of ADHD alongside ASD (especially in high-functioning ASD; Van Elst et al., 2013), participants with ADHD were not excluded.

G*Power 3.1.9, we calculated a minimum sample size of 68 to facilitate analyses and subsequently adjusted for possible attrition.

Procedures

All participants completed informed consent forms prior to any testing. Following a participant's completion of the informed consent form and the demographic questionnaire (including exclusion criteria), eligible participants completed a single, ninety-minute session for the remaining assessments. For in-person participants, data collection took place at the Multisensory Cognition Lab (MCL) at Utah State University. The *Wechsler Abbreviated Scale of Intelligence, Second Edition* (*WASI-II*; Wechsler, 1999) and *Wechsler Individual Achievement Test, Third Edition* (*WIAT-III*, 2009) were administered via hard copy versions. Numerosity discrimination trial protocols were administered using pre-programmed presentations on a desktop computer.

Following COVID-19 restrictions, remaining participants were provided an automatically generated link to complete informed consent and demographic questionnaire. Participants signed up for a time to complete a Zoom session with a researcher who administered the *WASI-II* and *WIAT-III* using digital versions of the same stimuli used for in-person testing. After completing these assessments, participants were provided a link to a Qualtrics data collection pipeline that administered the *AQ* and *SQ* and finally redirected participants to download and complete numerosity discrimination tasks via E-Prime Go (Psychology Software Tools, Pittsburgh, PA). All participants were compensated for their time with their choice of course credit or monetary incentive.

Methods

The study was a quasi-experimental design carried out through the Multisensory Cognition Lab (MCL) at Utah State University (USU). Following Hiniker et al. (2016), this study measured number sense acuity and symbolic number ability using forced-

choice quantity comparison tasks, as well as a population-normed measure of formal math ability. Additionally, ASD traits were measured to investigate their explanatory value for numerical cognition profiles. General cognitive abilities were assessed via a normed assessment to statistically control for domain-general effects. Trait analyses were chosen over diagnostic groupings to more fully characterize the potential interactions of variables, improve the overall power of analyses, permit exploration of nonlinear relationships, and understand the role of such traits in general, not only in the special case of clinically significant cutoffs.

Materials.

Neuropsychological Measures. The *WASI-II* was used to control for Full-Scale IQ (FSIQ). While IQ varies substantially in ASD (Autism and Developmental Disabilities Monitoring Network, 2014), individuals considered to be "high-functioning" have an IQ of 75 or above. Consequently, individuals with a FSIQ below 75 were excluded from the present study. Given the assessment load placed upon participants in this study, the FSIQ-2 form of the test was chosen over the comprehensive form. Importantly, the test-retest reliability of the FSIQ-2 form of the *WASI-II* has been well established, and has a very high correlation to the FSIQ-4 form (McCrimmon & Smith, 2013).

The *WIAT-III* contains Numerical Operations and Mathematical Reasoning subtests that can be used to give a composite Math score as an index of formal math ability. Composite scores for the *WIAT-III* are also very stable and tend to have high discriminability for educational groups (McCrimmon & Climie, 2011).

The *AQ* is a fifty-item, forced-choice questionnaire, designed as a brief measure of ASD traits across the spectrum, including diagnosable ASD and the general

population. The *AQ's* psychometric properties have been thoroughly established across

diverse samples (Baron-Cohen et al., 2001; Broadbent et al., 2013; Hoekstra et al., 2008;

Hurst et al., 2007). While it is not recommended to serve as a unilateral diagnostic tool, it

is particularly useful for characterizing the range of ASD traits across clinical and non-

clinical populations (Baron-Cohen et al., 2001; Hurst et al., 2007).

The *SQ* is a sixty-item, forced-choice questionnaire, designed to measure a

cognitive style that identifies replicable, reliable rules in order to understand how a

system works. The test has exhibited strong reliability and validity in clinical and non-

clinical adults across multiple cultural contexts (Groen et al., 2015; Ling et al., 2009;

Wright & Skagerberg, 2012). Moreover, *SQ* scores positively correlate with ASD traits as

measured on the *AQ* (Baron-Cohen et al., 2003), permitting analyses that parse distinct

and interactive contributions of ASD traits across the population.

Numerosity Discrimination Tasks. Participants completed two rounds of two-

alternative forced choice tasks,[9] which permit the derivation of a psychometric value to

index numerical discriminability (*cf.* Fechner, 2012) by individual and condition (Figure

1). In the number sense task, participants were simultaneously presented with two

adjacent arrays consisting of different numbers of dots for a 1500 stimulus period. They

were then asked to quickly determine which array had the greater number of dots and

responded with a button press indicating their choice within a 1000 ms test period. All

number pairs between 2 and 9 conforming to commonly used ratios (i.e., 1:2, 2:3, 3:4,

4:5, 5:6, 6:7, 7:8, 8:9) were presented four times each, for a total of fifty-two pairings.

Following standard practice, various parameters were controlled between arrays (i.e.,

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[9] The author owes special thanks to Drs. Hiniker, Rosenberg-Lee, and Menon for kindly sharing their stimulus sets and programs for use in this study. In so doing, this study is far more capable of replicating important components of Hiniker et al.'s (2016) original research protocol, permitting more stable extension of that protocol to explore other variables of interest.

total surface area, average dot size) and counterbalanced across trials (i.e., left/right

position of larger numerosity) to preclude participants' use of supplementary indicators

of quantity (Halberda et al., 2008; Hiniker et al., 2016; Wagener et al., 2018).

In the symbolic number acuity task, participants were presented with the same

stimuli and procedure as in the number sense task, except that the stimuli were symbolic

representations of the tested numerosities (e.g., Arabic numerals).

Figure 1

Diagram of Forced-Choice Numerosity Discrimination Tasks
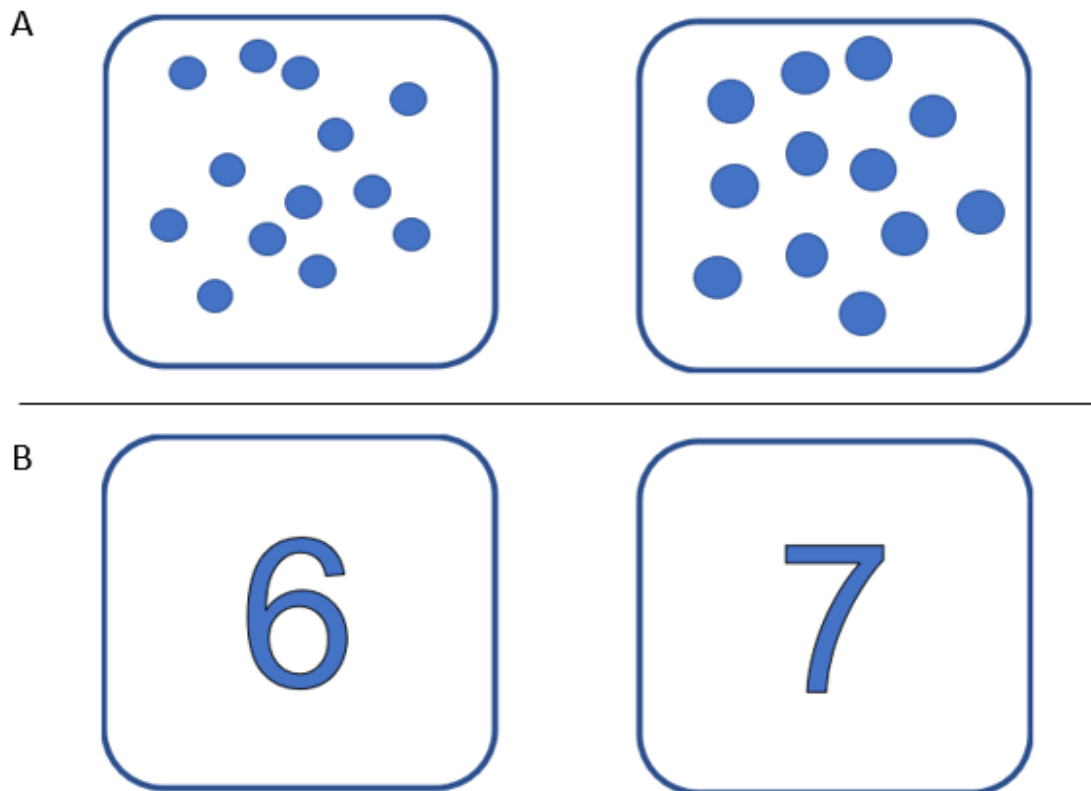
Note. Stimuli are presented as either a side-by-side array of dots (A) or side-by-side
Arabic digits reflecting the same numerosity pairings (B).

Analyses

     Data Cleaning. Of seventy-four total participants, data for six were subject to listwise deletion. Three were removed due to technical errors that led to large sections of missing data, precluding stable imputation. Three were removed due to extremely abnormal scores (beyond ±3 SDs) on quantity discrimination tasks, consistent with likely task disengagement. Due to the response time limitation of numerosity discrimination tasks, trials with no response were coded as an incorrect with the maximum allowable reaction time. Because some response variables followed non-normal distributions, diagnostic analyses were conducted on regression models to identify cases of significant leverage, distance, and influence. When any model assumption was not met, bootstrapped coefficients were instead estimated using the *car* package (Fox & Weisberg, 2019). In cases where bootstrapped estimates differ from those produced by the regression model, the difference is made explicit in the text.

     Calculation of Numerosity Weber Ratios (w). Following the established practice of previous work on numerical discrimination (Aagten-Murphy et al., 2015; Hiniker et al., 2016; Price et al., 2012), the present study used the Weber ratio (w) to index the least noticeable difference of numerical magnitude for each participant. Thus, every participant has two values of w, one for dot arrays and one for Arabic digits. Every value of w falls between 0 and 1, with 0 indicating flawless discriminability and 1 indicating purely chance performance.

     The method used in this study to estimate w was first detailed by Pica et al. (2004), in which they model each participant's observed error on a given task against a series of hypothetical w values to determine which value provides the best fit. This

method makes use of the relationship between the number pairings n₁ and n₂, both of

which are normal random variables. The difference of these variables' distributions gives

the distribution of $\mathcal{N}(|n_1 - n_2|, w^2[n_1^2 + n_2^2])$, the tails of which correspond to a

predicted error rate when w, n_1, and n_2 are given. With n_1, n_2 pairs fixed for this study,

w is permitted to vary such that the following algorithm produces a list of comparative fit

statistics for hypothetical values of w to characterize a participant's score for each task

type:

1. Identify every n_1, n_2 pair used in the experiment.

2. For every n_1, n_2 pair, estimate the error rate of the aforementioned Gaussian

    distribution according to the following equation, permitting w to vary between

    0 and 1 in 0.01 increments.

$$E(error) = \frac{1}{2} erfc \left(\frac{|n_1 - n_2|}{\sqrt{2}\, w\, \sqrt{n_1^2 + n_2^2}} \right) \tag{1}$$

    Note: Equation 1 is a simplification of Pica et al.'s (2004) original formula

    given in Halberda and Feigenson (2008). The latter version was chosen for

    interpretability.

3. For every n_1, n_2 pair, determine the observed error rate from experimental

    data.

4. For every n_1, n_2 pair, compute the difference between the sum of squares for

    the observed error rates and the sum of squares for the predicted error rates.

5. For a given participant, select the value of w that produces the smallest

    difference in step 4 (i.e., the w of best fit).

Based on this process, each participant is fitted with a Weber ratio for each task that best represents their observed error rate and can be used to compare number discrimination across conditions.

Results

      Descriptive Statistics. The final sample for analysis consisted of sixty-eight adult participants ($n_{female} = 40$). Overall, the sample represented individuals with above-average FSIQ ($\bar{X} = 109.9, s = 9.0$). The sample's AQ scores ($\bar{X} = 18.9, s = 9.1$) mirror that of the general population (Baron-Cohen et al., 2001). The same relationship holds for SQ ($\bar{X} = 25.1, s = 11.3$; Baron-Cohen et al., 2003). While diagnostic status was not recorded in this experiment, trait scores did also extend into the range characteristic of individuals with an ASD (SQ: $\bar{X} = 35.7, s = 15.3$ [Baron-Cohen et al., 2003]; AQ: $\bar{X} = 35.8, s = 6.5$ [Baron-Cohen et al., 2001]).[10] There were significant differences in SQ scores between males and females, consistent with prior research (Baron-Cohen et al., 2001; Baron-Cohen et al., 2003), emphasizing the importance of biological sex as a covariate in the subsequent models (Table 1).

      Relationship Between AQ and SQ. Previous research suggests a significant correlation between AQ and SQ (Baron-Cohen et al., 2003). Given the focus of this study on demonstrating the particular predictive value of SQ on numerical cognition performance above and beyond that predicted by AQ, it was important to establish if this

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[10] Baron-Cohen et al. (2003) report SQ scores and Baron-Cohen et al. (2001) report AQ scores for individuals with high-functioning ASD or Asperger's Syndrome and TD controls. The present sample includes 9 responses (13.2%) that would constitute unusually high ASD trait scores for an individual with an ASD ($SQ > 49.7$; $AQ > 28.7$). However, it warrants clear note that neither of these tools are intended to be used as a core diagnostic tool. While a lack of diagnostic status information precludes certain groupwise inferences, there is cause for confidence that the present sample allows a substantial characterization of the majority of the SQ/AQ ranges.

Table 1

Summary Statistics by Biological Sex

	Female	Male	t	p
	n=40	n=28		
Age	19.2 (1.5)	21.3 (5.6)	-2.28	0.026
IQ	109.0 (8.7)	111.2 (9.4)	-0.98	0.329
AQ	17.3 (8.4)	21.1 (9.7)	-1.72	0.091
SQ	21.6 (9.9)	30.1 (11.3)	-3.32	0.001

relationship was observed in the present sample. As expected, AQ and SQ exhibited a

moderate positive correlation ($r(66) = .46, p < .001$).

Number Sense Acuity. The present study predicted that as SQ, but not AQ,

increases, number sense acuity decreases. Beginning with a baseline model of covariates

(age, sex, and FSIQ) predicting number sense, another model was fit including AQ and

SQ as additional predictors. There were no significant effects of any covariates in either

model. These nested models were directly compared to determine the best fitting model

as a significant change in adjusted R^2. The model including AQ and SQ exhibited a better

fit ($R^2_{adj} = 0.04$) than the baseline model ($R^2_{adj} = -0.02$; Table 2), with the direct

comparison producing a marginally significant statistic ($F(2) = 3.07, p = 0.053$). In the

better fitting model, SQ exhibited a significant effect on number sense ($\beta_{SQ} =$

$0.0146, p = 0.018$) while controlling for the effect of AQ (Figure 2); however, the

reverse was not the case ($\beta_{AQ} = -0.003, p = 0.736$; Figure 3). This confirms the

predicted finding that as SQ, but not AQ, increases, number sense decreases.

Table 2

Comparative Models Predicting Number Sense Acuity

	Baseline Model	Full Model
Intercept	−2.7441 (0.8215) **	−2.8476 (0.8004) ***
Age	0.0185 (0.0158)	0.0094 (0.0173)
Sex	0.0225 (0.1236)	−0.0744 (0.1260)
FSIQ	0.0030 (0.0066)	0.0030 (0.0064)
AQ		−0.0026 (0.0076)
SQ		0.0146 (0.0060) *
R²	0.0271	0.1149
Adj. R²	−0.0185	0.0435
Num. obs.	68	68

Note. ***p < 0.001; **p < 0.01; *p < 0.05

Symbolic Number Acuity. The present study predicted that symbolic number acuity would be intact across the range of AQ and SQ. A baseline model was built regressing symbolic number acuity on age, sex, and FSIQ. A subsequent model fit with the addition of AQ and SQ was compared to the baseline. Again, none of the covariates in either model exhibited a significant effect on symbolic number acuity. Moreover, the model including AQ and SQ did not exhibit a better fit ($R^2_{adj} = -0.031$) than the baseline model ($R^2_{adj} = -0.014$; Table 3), with the direct comparison demonstrating no significant difference ($F(2) = 0.4876, p = 0.616$). Investigating the model including AQ and SQ, it is evident that changes in neither predictor lead to changes in symbolic number acuity ($\beta_{AQ} = 0.0004, p = 0.387$; $\beta_{SQ} = -0.0002, p = 0.465$), as predicted.

Figure 2

Effect of SQ on Number Sense Acuity
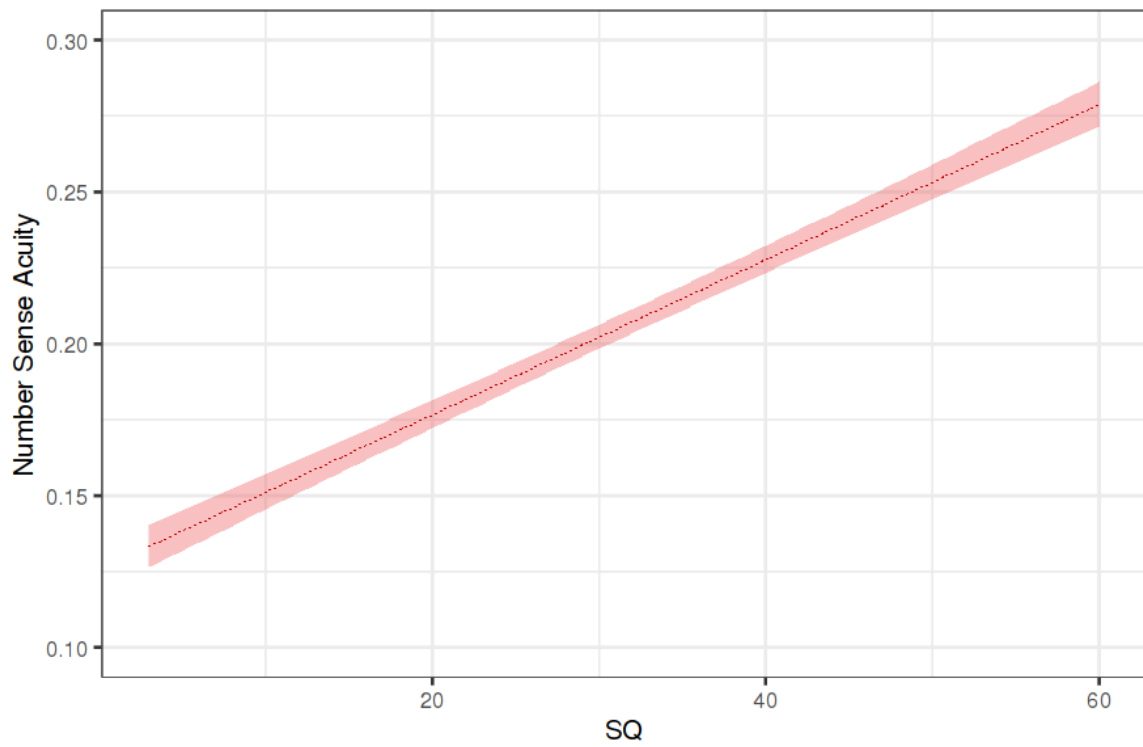
Note. SQ significantly predicts number sense acuity when controlling for *AQ*. Errors bars represent ±1 SEM.

Figure 3

Effect of AQ on Number Sense Acuity
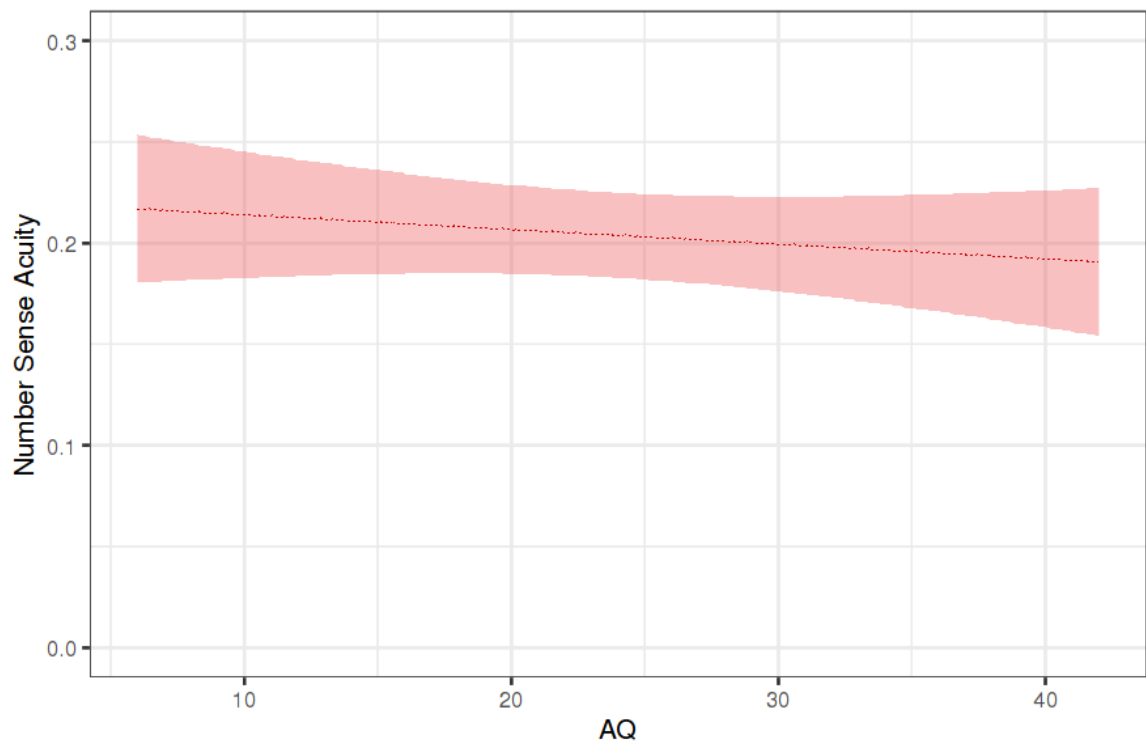
Note. *AQ* has no significant effect on number sense acuity when controlling for *SQ*.

Errors bars represent ±1 SEM.

Table 3

Comparative Models Predicting Symbolic Number Acuity

	Baseline Model	Full Model
Intercept	−0.8441 (0.0483) ***	−0.8391 (0.0489) ***
Age	0.0003 (0.0009)	0.0001 (0.0011)
Sex	−0.0058 (0.0073)	−0.0044 (0.0077)
FSIQ	−0.0004 (0.0004)	−0.0004 (0.0004)
AQ		0.0004 (0.0005)
SQ		−0.0003 (0.0004)
R^2	0.0315	0.0465
Adj. R^2	−0.0139	−0.0304
Num. obs.	68	68

Note. ***p < 0.001; **p < 0.01; *p < 0.05

Formal Math Achievement. The present study predicted that as SQ, but not AQ, increases, formal math performance increases. Baseline and comparison models were built regressing Math Composite scores on the same predictors of interest. In the baseline model, age and FSIQ both predicted statistically significant increases in Math Composite scores on the *WIAT-III* ($\beta_{age} = 0.8209, p = 0.029$; $\beta_{FSIQ} = -0.0002, p = 0.006$), while biological sex did not ($\beta_{sex:male} = -4.8006, p = 0.0998$). A subsequent model fit with the addition of AQ and SQ was compared to the baseline model. The model including AQ and SQ did not exhibit a better fit ($R^2_{adj} = 0.095$) than the baseline model ($R^2_{adj} = 0.1181$; Table 4), with the direct comparison demonstrating no significant difference ($F(2) = 0.1633, p = 0.8497$). Investigating the model including AQ and SQ, it is evident that changes in neither predictor lead to changes in formal math achievement

$(\beta_{AQ} = 0.1057, p = 0.570; \beta_{SQ} = -0.0301, p = 0.838)$, consistent with the notion that

math performance would not decrease as *SQ* increased, but against the prediction that

formal math achievement would increase as *SQ* increased.

Mediation Analysis. The present study predicted that symbolic number acuity

mediates the relationship between number sense performance and formal math

performance for individuals in the higher *SQ* range, but not for individuals in the lower

SQ range. To investigate this possible mediation relationship, the sample was median-

dichotomized along the *SQ* variable. Mediation analyses with 1,000 iterations of a

bootstrapped resampling procedure were performed separately for both subgroups,

controlling for covariates (including *AQ*). Neither subgroup exhibited a significant total

Table 4

Comparative Models Predicting Formal Math Achievement

	Baseline Model	Full Model
Intercept	46.6759 (19.1129) *	47.7549 (19.4733) *
Age	0.8209 (0.3672)	0.7299 (0.4207)
Sex	−4.8006 (2.8749)	−4.7389 (3.0646)
FSIQ	0.4323 (0.1530) **	0.4276 (0.1552) **
AQ		0.1057 (0.1850)
SQ		−0.0301 (0.1467)
R²	0.1576	0.1620
Adj. R²	0.1181	0.0945
Num. obs.	68	68

Note. ***p < 0.001; **p < 0.01; *p < 0.05

effect of number sense on formal math achievement (Low-SQ subgroup: $t(30) = -0.39, p = 0.70$; High-SQ subgroup: $t(30) = 0.73, p = 0.47$). Consequently, no significant indirect effect through symbolic number acuity was observed (Low-SQ subgroup: 95% $CI[-6.85, 7.32]$; High-SQ subgroup: 95% $CI[-1.98, 3.05]$), against prediction and inconsistent with the finding in Hiniker et al. (2016). This pattern was then confirmed in the entire sample (total effect: $t(64) = 0.14, p = 0.89$; 95% $CI[-2.13, 0.89]$).

Discussion

As expected, the current study found a moderate positive correlation between AQ and SQ scores across a sample of adults in a university setting. This finding is consistent with previous findings that both the AQ and the SQ measure ASD traits without complete overlap. The current study proposed that, while the AQ is a better measure of broad ASD traits, the SQ is a better measure of a singular trait: the preference for explicitly systemized domains, and that this preference is particularly consistent with a neural dysregulation account of ASD. This claim is supported by the finding that the SQ predicts performance on an unenhanced downstream task (number sense) while the AQ does not. It is worth noting, however, limitations concerning indirect measurement of neural correlates. Although the current study attempted to make responsible predictions consistent with known neurophysiological correlates, as with all exclusively behavioral research the present study can only propose neurophysiologically plausible explanations underlying observed relationships. Future research is needed, however, to directly measure neural correlates alongside the phenomena observed here (see related imaging approaches in Flevaris & Murray, 2015; Karten & Hirsch, 2015; Takarae et al. 2014).

The finding of a negative correlation between *SQ* and number sense performance also supports the claim that the *SQ* does not properly measure a tendency to abstract rigid rules. A hyper-systemizing account of the *SQ* would predict that as *SQ* scores increase, performance on tasks with abstractable rules would increase. However, the current study found that as *SQ* scores increased, number sense acuity (a task with abstractable rules) decreased. The current study argues that this finding is more in line with the notion that rule abstraction for complex tasks is more difficult for individuals high in ASD traits, as predicted by an E/I imbalance account.

Also as predicted, the current study found intact symbolic number acuity across levels of both *AQ* and *SQ*. Although symbolic number recognition is a downstream task that would be affected by neural dysregulation, the SNR for this task would be sufficiently enhanced via stimulus standardization. Consequently, trait measures of ASD would not be expected to predict task performance. It was also found, as expected, that formal math performance did not change across *AQ*. These findings together support the notion that individuals who are high in ASD traits do not have a deficit in formal math *per se* or in acquiring a symbolic number system, but may instead struggle with number sense acuity in a fashion consistent with the effects of an E/I imbalance on the IPS. It may be the case that such individuals would benefit from either more supportive resources to help them persist in this domain despite acquisition delays or from earlier instruction in the more predictable symbolic number system. Future studies could also examine whether number sense instruction that intentionally provides explicit rules and high levels of repetition could facilitate the earlier acquisition of sufficient number sense

acuity, which would allow for a timelier acquisition of the symbolic number system and, consequently, formal math.

Against prediction, *SQ* did not predict formal math performance. This prediction was based on the idea that, while potential math ability may be the same across the score range of ASD traits, individuals with higher trait scores would be more likely to pursue math as a standardized domain (compared to non-standardized domains) due to the potential amelioration of low SNR. This preference was expected to result in greater math achievement by adulthood compared to TDs. However, this prediction failed to take into account that while TD individuals may show more evenly distributed interest across domains with varying degrees of standardization due to lower variance in experienced task SNR, they are also a larger proportion of the population. Consequently, absolute, rather than proportional, differences in formal math achievement would likely not be related to *SQ*.

The current study predicted that symbolic number acuity would mediate the relationship between number sense and formal math for individuals in the higher *SQ* range, but not for individuals in the lower *SQ* range. This prediction was based on mediation analyses run by Hiniker et al. (2016) that found that symbolic number acuity was the dominant predictive factor of formal math performance for children with an ASD but not for TD children. This suggested the possibility that for TDs, number sense and symbolic number acuity are more interchangeably employed in formal math, such that they assume a partially redundant predictor configuration. However, individuals with an ASD may be less able to successfully employ number sense due to decreased acuity, and thus, rely more heavily on their symbolic number acuity when engaging formal math.

The current study, however, found no predictive relationship between number sense and formal math achievement for either subgroup or for the sample as a whole; consequently, there is no mediation to observe. It may be the case that by adulthood neither TDs nor individuals with an ASD are likely to depend on number sense to a significant degree when engaging formal math. While estimating quantity might be helpful, the current sample especially consists of individuals who necessarily are required to have achieved a level of formal math proficiency commensurate with their educational attainment, for which estimation-based strategies are unlikely to play the primarily role. This may make any remaining role of number sense very difficult to detect. It may also be difficult to assess whether or not adults across the range of ASD trait scores are likely to depend on the symbolic number system to engage formal math due to the level of task difficulty employed here, as suggested by the ceiling effect for symbolic number found in the current study.

In addition, both the present study and the work of Hiniker et al. (2016) are snapshots of number sense, symbolic number acuity, and formal math achievement at a single time frame. Consequently, there are likely elements of developmental and learning processes in mathematical cognition that would be more successfully modeled by longitudinal research (e.g., growth curve modeling, linear mixed-effect modeling for multiple time points). Thus, while mediation analyses might be able to suggest something of the relative impacts of multiple predictors on formal math achievement, future research would also benefit from a focus on longitudinal designs that measure each ability during periods when there is substantial variability among participants and scores are not yet approaching an upper limit of performance. If it is substantiated that over time

TDs tend to depend relatively equally on both number sense and the symbolic number system, early presentation of symbolic number may not make much difference to formal math acquisition for this group. If, however, it is substantiated that over time children with an ASD tend to depend more on the symbolic number system, timely formal math acquisition may be facilitated by earlier presentation of this preferred system.

Experiment 2

Overview

To further examine whether an E/I imbalance account is consistent with the relationship between ASD traits and numerical cognition performance, experiment 2 explored whether utilizing a multimodal presentation of number sense stimuli would improve number sense performance due to its proposed effects on perceptual SNRs. As number sense is an unenhanced downstream task, it was expected that enhancing the target signal by adding a second signal modality should improve number sense performance across the range of ASD traits (as measured by the *AQ* and the *SQ*). The current study also postulated that as scores on the *SQ* increase, the acuity of quantity perception decreases in a fashion that would be consistent with increasing neural dysregulation. However, multisensory gains were expected to largely ameliorate unisensory performance losses related to increasing *SQ*. In other words, if the difference in number sense performance between TDs and individuals with an ASD is due to E/I imbalance-related decreases in SNR, enhancing the stimulus SNR should bring performance toward TD levels.

Due to the nature of the stimuli used for number sense tasks, this study also provided the opportunity to explore the effects of high-level stimulus feature manipulation on multisensory integration (MSI). Although the MSI literature has demonstrated that decreasing the SNR of low-level stimulus features results in greater MSI recruitment, the effects of manipulating the SNR of high-level stimulus features have been less explored. The current study predicted that, as with low-level stimulus features, manipulation of high-level stimulus features would result in changes in MSI recruitment, such that stimulus SNR is negatively correlated with MSI gains.

The design of this study also allowed for further examination of the effects of E/I imbalance on MSI recruitment. Many neurophysiological and behavioral studies have demonstrated MSI abnormalities for individuals with an ASD; however, whether these are differences in integration itself or the result of differences in the signals projecting to this region is unclear. The current study proposed that due to the somewhat downstream location of MSI, it would also be susceptible to the effects of an E/I imbalance (Populin, 2005; Razak & Pallas, 2006). Consequently, the current study predicted that as *SQ*, but not *AQ*, increases, variance of MSI gains increases.

This study also explored possible nonlinear relationships between stimulus SNR and MSI recruitment. While MSI literature has focused on characterizing the difference between unisensory and multisensory performance across the concomitant levels of stimulus SNR, referred to as MSI gains, the trade-off between MSI improvement and decreasing stimulus SNR has been less explored. This study proposed that there is a peak level of stimulus SNR past which the benefit of adding a second stimulus modality is outweighed by the effects of continued increases in stimulus noise. In other words, it was

predicted that the relationship between SNR costs and MSI benefits is best modeled as a quadratic relationship.

Multisensory Integration

Based on signal detection theory, decreasing the SNR of a stimulus leads to decreased unimodal signal detection (e.g., Edward & Badcock, 1995; Koppen et al., 2009; Macmillan & Creelman, 2004; McNicol, 2005; Wixted, 2007). However, these losses can be recovered by introducing the same signal in a second modality (Parraga, 2015; Vroomen & De Gelder, 2000), referred to in the psychology and neuroscience literature as multisensory integration.[11] Enhancement of a less detectable signal can be achieved by either strengthening the signal or reducing the noise surrounding the signal. One of the key methods for achieving both goals at once is to introduce a supplemental stimulus (s_2) whose noise is orthogonal to the original stimulus (s_1). Doing so results in amplification of the overlapping elements of each of the stimuli and suppression of the non-overlapping elements (Macmillan & Creelman, 2004; McNicol, 2005).

Many studies have shown that adding a concurrent presentation of a stimulus in a second modality can significantly improve performance on a variety of perceptual tasks, including visual motion coherence (Kim et al. 2008), the pip-and-pop visual search (Van der Burg et al., 2008), and voice recognition training (Von Kriegstein & Giraud, 2006; see also de Dieuleveult et al., 2017 and Koelewijn et al., 2010 for general reviews). For example, in an investigation of the role of multisensory presentations on the detection of stimuli impacting pilot effectiveness in aerial combat maneuvering, Nelson et al. (1998)

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[11] Multisensory integration is a method of improving signal detectability comparable to the signal detection theory term signal recovery.

found that the inclusion of localized auditory information associated with a simple visual stimulus (an aircraft silhouette) significantly improved detection rates and search strategies. Similarly, Noesselt et al. (2008) found significant enhancement in response rates and accuracy for a brief visual event (identifying which of two visual stimuli briefly disappears from the screen) when the event was accompanied by a concurrent auditory cue.

Inverse Effectiveness. Studies have demonstrated that an important principle of MSI for determining the optimal degree of recruitment is that of inverse effectiveness (Holmes, 2007; Holmes, 2009; Stevenson et al., 2012). According to this principle, the lower the SNR of unisensory signals, the greater the need to implement a signal recovery process and, therefore, the greater the MSI recruitment (Meijer et al., 2018; Stein & Meredith, 1993). Behaviorally, this principle can be observed as multisensory-condition gains that correlate with decreased unisensory signal strength (Holmes, 2009).

However, decreasing SNR does not necessarily lead to increased performance overall in multisensory paradigms. Rather, MSI often serves to attenuate losses of performance due to decreased SNR by providing a supplementary tool for remediating performance beyond that which would be predicted by increased vigilance (due to higher overall levels of energy in sensory processing regions) or statistical facilitation (i.e., the well-defined race model of Gielen et al., 1983). Although MSI studies typically characterize the difference in scores between the unisensory condition and the multisensory condition, referred to as MSI gains, the current study also used number sense stimuli as an opportunity to examine the point at which the benefits of adding a second modality are outweighed by decreases in unisensory reliability. The current study

proposed that MSI benefits would exhibit a peak level past which increasing stimulus noise attenuates MSI benefits and which can be identified as the extremum of a quadratic model.

Neural Correlates of Multisensory Integration. The superior colliculus (SC) is arguably the most thoroughly investigated neural region with respect to MSI, with numerous studies demonstrating sensitivity of neuronal subpopulations to cross-modal conditions (Anastasio et al., 2000; Anastasio & Patton, 2003; Bell et al., 2003; Meredith & Stein, 1986; Perrault et al., 2005; Wallace & Stein, 1997). For example, Burnett et al. (2004) found that lesioning of the SC in cats produced durative deficits in multisensory orientation to the contralesional hemifield despite recovery of unisensory orientation behavior.

While much remains to be discovered about the processes subserving MSI, substantial research provides at least a partial account of this process (for reviews, see Cornelio et al., 2021; Koelewijn et al., 2010; Stein & Stanford, 2008). For both TDs and individuals with an ASD, input signals project from multiple regions of cortex, each involved in unimodal processing to the SC (Siemann et al., 2017; Stein & Rowland, 2011; Stein et al., 2014; Stein & Rowland, 2020). For example, the SC receives information from Brodmann's areas 41 and 42 in the lateral temporal lobes (dedicated specifically to auditory processing and implicated in cortical deafness [Polster & Rose, 1998]) and from Brodmann's areas 17 through 19 (dedicated broadly to visual perception and implicated in cortical blindness [Aldrich et al., 1987; Huff et al., 2020]).

Neural correlates of inverse effectiveness are also well established (Ghose et al., 2014; Sabes, 2011; Stein & Stanford, 2008; Van Opstal, 2016). For example, as the

magnitude of unimodal signals from the aforementioned projections decreases, SC activation increases in a fashion consistent with compensatory functions of inverse effectiveness that attenuate performance losses (Ohshiro et al., 2011; Stein et al., 2020).

Divisive Normalization. Another principle that would be expected to effect MSI is divisive normalization. Divisive normalization is a canonical computational mechanism that has been evidenced in numerous brain regions (e.g., V1, hippocampus, medial superior temporal area, lateral intraparietal cortex) in a variety of species. It is defined as a neural operation by which the total excitatory input to a neuron is driven by the sum of afferent projections and attenuated by both the neuronal subpopulation's own firing limit (i.e., semisaturation constant) and the collective excitatory activity of the neighboring neuronal environment (Bhatia et al., 2019; Busse et al., 2009; Ohshiro et al., 2017; Olsen et al., 2010; Sato et al., 2016). This operation describes limits on neurons' total sensitivity to stimulus magnitude (producing a form of gain control) such that there is a peak input past which the slope of output amplification decreases significantly (i.e., the output of its derivative function is negative).

Although the literature on inverse effectiveness has almost exclusively investigated linear relationships between stimulus reliability and MSI gains, given this canonical principle of saturation corresponding to diminishing returns of increases in stimulus intensity, it would be reasonable to investigate a possible nonlinear relationship between MSI gains related to stimulus reliability, such as a logarithmic growth function. The current study explored whether multilevel mixed-effects modeling may be able to detect a logarithmic relationship between stimulus SNR and MSI gains consistent with the computational constraints of divisive normalization.

Multisensory Integration and Number Sense. In addition to visual motion, visual search, and voice recognition tasks, studies have also found that number sense performance for TD individuals improves with the addition of another modality (Jordan & Baker, 2011; Kanitscheider et al., 2015; Lechelt, 1975; Philippi et al., 2008). For example, Philippi et al. (2008) investigated whether multisensory presentation of sequential numerosity stimuli improved participants' numerosity estimates. Across the included pulse quantities (2 to 10) and interstimulus intervals (20 to 320 ms), multisensory estimates were observed to be more accurate than estimates from any unisensory condition (visual, auditory, or tactile), with the most accurate estimates observed in the trimodal condition.

Similarly, Kanitscheider et al. (2015) compared error rates from unisensory and multisensory numerosity estimation tasks in participants ages 18 to 62, finding that judgements based on multisensory information concerning relative numerosity were consistently more precise than unisensory decisions from either modality. Jordan and Baker (2011) investigated whether intersensory redundancy improved numerosity judgements in 3- to 5-year-old children. Participants observed a sequential numerosity stimulus in visual, auditory, and synchronized multisensory conditions followed by a forced-choice presentation from which the child was to identify the numerosity that matched the probe. The authors observed a significant increase in children's accuracy in the multisensory condition over both unisensory conditions.

Multisensory Integration and ASD. Behavioral studies have demonstrated that adding another stimulus modality can also improve task performance for individuals with an ASD (see Feldman et al., 2018 for a review), as well as evidence that the principle of

inverse effectiveness also applies to MSI for individuals with an ASD (Iarocci, G., &

McDonald, 2006; Stevenson et al., 2017). For example, Stevenson et al. (2017) found

that both ASD and TD children exhibited higher MSI gains for phoneme recognition in

lower SNR conditions. Stevenson et al. (2018) evaluated the sociolinguistic processing

abilities of thirty-eight individuals with an ASD (ages 7 to 16) and thirty-eight age- and

IQ-matched controls using a speech-in-noise paradigm that tested participants' ability to

correctly identify tri-phonemic, monosyllabic nouns in three different conditions (i.e.,

visual, auditory, and audiovisual). A main effect of modality on speech perception was

observed, such that participants exhibited significantly higher accuracy in the

multisensory condition than in unisensory conditions ($p < 0.001$), without an interaction

between diagnostic status and modality ($p = 0.20$), suggesting gains for participants

irrespective of diagnosis. Previous studies have also found lower MSI gains for

individuals with an ASD on tasks with low-level stimulus feature manipulation (see

Feldman et al., 2018 for review). However, it is unknown whether these differences are

the result of alterations in processing at the MSI or sensory level, and whether this would

be true for tasks with high-level stimulus feature manipulation.

     Multisensory Integration and E/I Imbalance. These findings are also consistent

with an E/I imbalance account of ASD. How individuals with an ASD integrate multiple

sensory modalities is necessarily affected by how unimodal sensory signals are

propagated. As has been discussed above (see Upstream Visuospatial Processing),

individuals with an ASD show differences in visuospatial processing that are consistent

with an E/I Imbalance account which predicts perceptual overfitting. Studies have also

demonstrated that individuals with an ASD tend to exhibit significant alterations in

audition, apart from hearing impairment,[12] that are similar to their differences in visuospatial processing (see Ouimet et al., 2012 for a review). For example, regions of primary auditory cortex exhibit increased local connectivity alongside decreased interconnectivity with distal projections (Just et al., 2004). Perturbation of γ-band synchronization has also been repeatedly noted in children with an ASD in audition (Edgar et al., 2015; Gandal et al., 2010; Jochaut et al., 2016; Simon & Wallace, 2016), again consistent with low stimulus-feature binding. Gandal et al. (2010) found in parallel human and mouse studies of ASD that affected subjects demonstrated a reduced γ phase-locking factor (correlated with neuroligin-3 expression in mice) alongside delayed M100 evoked responses in superior temporal gyrus (*cf.* Bruneau et al., 1999). Such findings coincide with auditory behavioral results that parallel previously detailed visuospatial processing in ASD. Specifically, many affected individuals exhibit enhanced low-dimensional auditory abilities, such as pitch discrimination, concurrent with deficits in high-dimensional abilities, such as speech-in-noise (Bonnel et al., 2003; Heaton, 2003; Ouimet et al., 2012; O'Connor, 2012).

It is also reasonable to expect that high-level perceptual alterations in ASD would impact MSI function. In addition to inputs from primary sensory cortex, the SC also receives inputs from multiple regions of association cortex, (Lynch et al., 1985; May, 2006; Stein & Meredith, 1993; Yu et al., 2016), though these have been less thoroughly investigated. For example, Yu et al. (2016) demonstrated that altering activation of the anterior ectosylvian sulcus and the rostral lateral suprasylvian sulcus in cats significantly

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[12] Hearing impairment, specifically peripheral hearing loss (PHL), is a common exclusion criterion in research on audition in ASD, given that there is much ongoing debate as to a possibly increased prevalence rate of PHL among individuals with an ASD.

altered cross-modal integration of visual and auditory inputs. Lynch et al. (1985) have also specifically identified projections in macaques from the inferior bank of the IPS to the interior layers of the SC. As a region of association cortex that communicates bidirectionally with the SC (Clower et al., 2001; Anderson et al., 2008), the IPS is also expected to impact MSI. Consequently, any imbalance to this region might further complicate the degree to which MSI would improve performance on IPS-dependent tasks.

Some research also indicates irregular activation within the SC for individuals with an ASD (Jure, 2019; Kleinhans et al., 2011). For example, Kleinhans et al. (2011) measured BOLD signal corresponding to the SC in adults with an ASD ($\bar{X} = 23.57$) compared to TD controls ($\bar{X} = 23.32$) during a rapid facial processing task. The ASD group exhibited significantly lower activation in the SC compared to the TD group.[13]

This relates as well to another feature of SC research that may have some bearing on the present studies. Previous research on cortical and subcortical activation during a variety of tasks relevant to ASD function has established altered functional connectivity in pathways involving the SC (Jure, 2019; Kleinhans et al., 2008; Hadjikkhani et al., 2017). For example, Kleinhans et al. (2008) found significantly reduced connectivity between the fusiform gyrus and the SC in ASD participants in a study of face-related socio-emotional processing. Jure (2019) also notes that multiple networks activated by the SC, including large-scale white matter tracts such as the bilateral uncinate and superior longitudinal fasciculi, have exhibited hypoconnectivity in ASD. This further

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[13] While this addresses a different feature of sensory integration that facilitates saccadic behavior, its focus on SC activation makes it relevant to the focus of the present study.

supports a picture of ASD etiology in which MSI itself may be disrupted, potentially altering its contribution to signal enhancement in affected individuals.

Located in the posterior midbrain, the SC occupies a position upstream of many regions to which it projects, but also receives projections from primary visual, auditory and tactile regions of cortex (King, 2004; Paula-Barbosa & Sousa-Pinto, 1973). Consequently, irregular activation might suggest primary dysregulation due to compensation for altered activity in lower layers of the signal propagation pipeline (e.g., Nelson & Valakh 2015), dysregulation due simply to the ongoing receipt of poorly fit signal inputs, or both. Such forms of dysregulation could, in theory, result in decreased overall MSI contributions with increased variability in the case of an altered suppressive field gain term (Rosenberg et al., 2015) given the role divisive normalization has been proposed to play in SC function as well (Basso & Wurtz, 1997; Ohshiro et al., 2011).

In other words, the signal inputs received by the SC from primary auditory cortex and primary visual cortex are expected to be overfit compared to TDs, while the signal input received by the SC from the IPS would be underfit compared to TDs. In addition, the current study argues that, as a somewhat downstream region, the SC itself would also be affected by signal disruption leading to both decreased MSI benefits and greater variability in MSI gains for individuals with an ASD.

Multisensory Integration, Number Sense and ASD. Although studies have found MSI benefits for individuals with an ASD on a variety of tasks (e.g., speech in noise tasks, temporal perception tasks) (Stevenson et al., 2014, Feldman et al., 2018), the effects of MSI have not been explored across ASD traits for number sense. In addition, the effect of manipulating high-level stimulus features on MSI across ASD traits has been

less explored. Studies which have examined the manipulation of high-level stimulus features have been limited by issues of confounding stimulus complexity and/or collinearity (e.g., Stevenson et al., 2017). Number sense, however, may permit a closer examination of how high-level stimulus features impact MSI recruitment. The computational profile of number-sensitive neurons presented a unique opportunity to explore the effects of high-level feature dimensionality on MSI. These neurons represent number as a perceptual category without respect to stimulus modality. Consequently, there is lesser likelihood of a confound in MSI gains from high-level feature manipulation due to a specific strong unisensory modality bias in numerosity processing. Moreover, features that do tend to covary can be experimentally controlled more easily than in other tasks that have been used to examine high-level SNR in MSI (e.g., phoneme versus whole-word recognition in Stevenson et al., 2017). Moreover, number neurons exhibit overlapping tuning functions that conform to the psychophysical Weber-Fechner law. This feature of number neurons permits precise measurement connected to firmly established experimental paradigms.

Predicted Outcomes

The present study tested the following predictions:

1. Multisensory number sense performance is higher than unisensory number sense performance across all levels of *AQ* and *SQ*.

2. As *SQ*, but not *AQ*, increases, variance of MSI gains across ratio bins increases.

3. There is a peak level of MSI benefit past which additional high-level stimulus feature noise reduces MSI benefits. In other words, MSI benefit is best predicted by a quadratic relationship with high-level stimulus feature noise.

Participants

The present study ultimately sought to collect data suitable for analyses from sixty-eight participants (separate from those recruited for experiment 1).[14] The full sample consists of seventy-seven individuals between the ages of 18 and 49 (see Data Cleaning below). Recruitment and filtering for preliminary exclusion criteria proceeded in the same fashion as in experiment 1.

Procedures

Due to the COVID-19 public health crisis that led to a university-wide suspension of in-person research activities, all data collection for this experiment was completed remotely. All participants completed informed consent forms prior to any testing. Following a participant's completion of the informed consent form and the demographic questionnaire (including exclusion criteria), eligible participants completed a single, ninety-minute session for the remaining assessments. Participants were provided a link to a Qualtrics data collection pipeline that administered the *AQ*, *SQ* and the *Shortened Raven Standard Progressive Matrices* (*S-RSPM*; Van der Elst et al., 2013). Finally, participants were redirected to complete the numerosity discrimination tasks through the

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[14] Projected sample size was established to facilitate multiple linear regression analyses, including multilevel analysis, permitting model comparisons to evaluate R^2 increase ($\alpha = .05$; $1 - \beta = .80$). Given many of the same limitations in background evidence as addressed in experiment one, a moderate effect size was again selected ($f^2 = .15$). Using G*Power 3.1.9, a minimum sample size of 68 was calculated to facilitate analyses and subsequently adjusted for possible attrition.

Pavlovia repository and launch platform (www.pavlovia.org). All participants were compensated for their time with their choice of course credit or monetary incentive.

Methods

The current study was a quasi-experimental design. This study measured unisensory and multisensory number sense acuity using a sequential-stimulus, simultaneous-choice design. ASD traits were again measured to investigate their explanatory value for numerical cognition profiles and contributions to MSI gains. General cognitive abilities were assessed via a normed assessment to statistically control for domain-general effects.

Materials.

Standardized Measures. The *S-RSPM* is a standardized tool for non-verbal measurement of IQ. Reliability and validity of the *S-RSPM* have been established (Raven, 2006; Strauss et al., 2006; Van der Elst et al., 2013). As in experiment one, the *AQ* and *SQ* were used to measure general and specific ASD-related traits.[15]

Numerosity Discrimination Tasks. Numerosity discrimination tasks were coded in the PsychoPy3 builder program (Peirce et al., 2019). Each trial stimulus consisted of a set of sequentially presented elements indicating a numerosity between 10 and 50 (Jordan, et al.2008; *cf.* Jordan & Baker, 2011 with children). Auditory (A) trials consisted of pulse trains of clicks presented centrally at uniform magnitude. Visual (V) trials

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[15] While the *S-RSPM* was selected for experiment largely due to logistical constraints, it does allow investigation of the degree to which such a non-verbal measure of IQ may differ in its relationship to the variables investigated here when compared to the *WASI-II*, which includes both Matrix Reasoning and Vocabulary. In cases where the two experiments analyses overlapped, the measure of IQ did not change the pattern of results (see "Number Sense Performance and *SQ*" below). This may suggest a particular usefulness of the *S-RSPM* when investigating number sense in children with high ASD traits, especially in cases where verbal ability is significantly impaired.

consisted of achromatic pulse trains of black circles with variable size and position on a white background. Audiovisual (AV) trials consisted of similar visual stimuli synchronized with auditory pulse trains (Figure 4).

Multiple controls were included to preclude counting strategies and use of numerosity-covarying features (e.g., total stimulus duration). Within each trial in all conditions, interpulse intervals varied randomly from 20-680 ms and stimulus duration ($\bar{X} = 3000$ ms) was permitted to vary up to 35% for each trial (*cf.* Brunton et al., 2013) to attenuate temporal information in numerosity estimation. MATLAB (2020) was used to compute randomized vectors of pulse timings under a sum constraint to the total stimulus duration. Visual elements were also permitted to vary in area across trials by up to 35% (*cf.* Jordan & Baker, 2011; Jordan et al., 2008). To attenuate the potential impact of sensory adaptation between trials (e.g., the numerosity of trial n skews perception of trial $n + 1$), an intertrial interval of 1000-2000 ms was included (Bruneau et al., 2003; Doyon et al., 2020).

After each trial, two visual, dot array choice stimuli were presented simultaneously in side-by-side, 10 x 10 cm panels, only one of which contained the previously presented numerosity (Jordan & Baker, 2011). Participants were then be asked to determine which array matched the numerosity of the sequentially presented stimulus, indicating their choice with a right-left button press within a 1000 ms test period. To permit greater performance variance, ratio bins in experiment two included all possible ratios ($n = 26$) between included numerosities, giving trial ratios ranging from .2 (e.g., 10 compared to 50) to .9 (e.g., 45 compared to 50).

Figure 4

Diagram of Sequential Stimulus, Forced-Choice Numerosity Discrimination Tasks
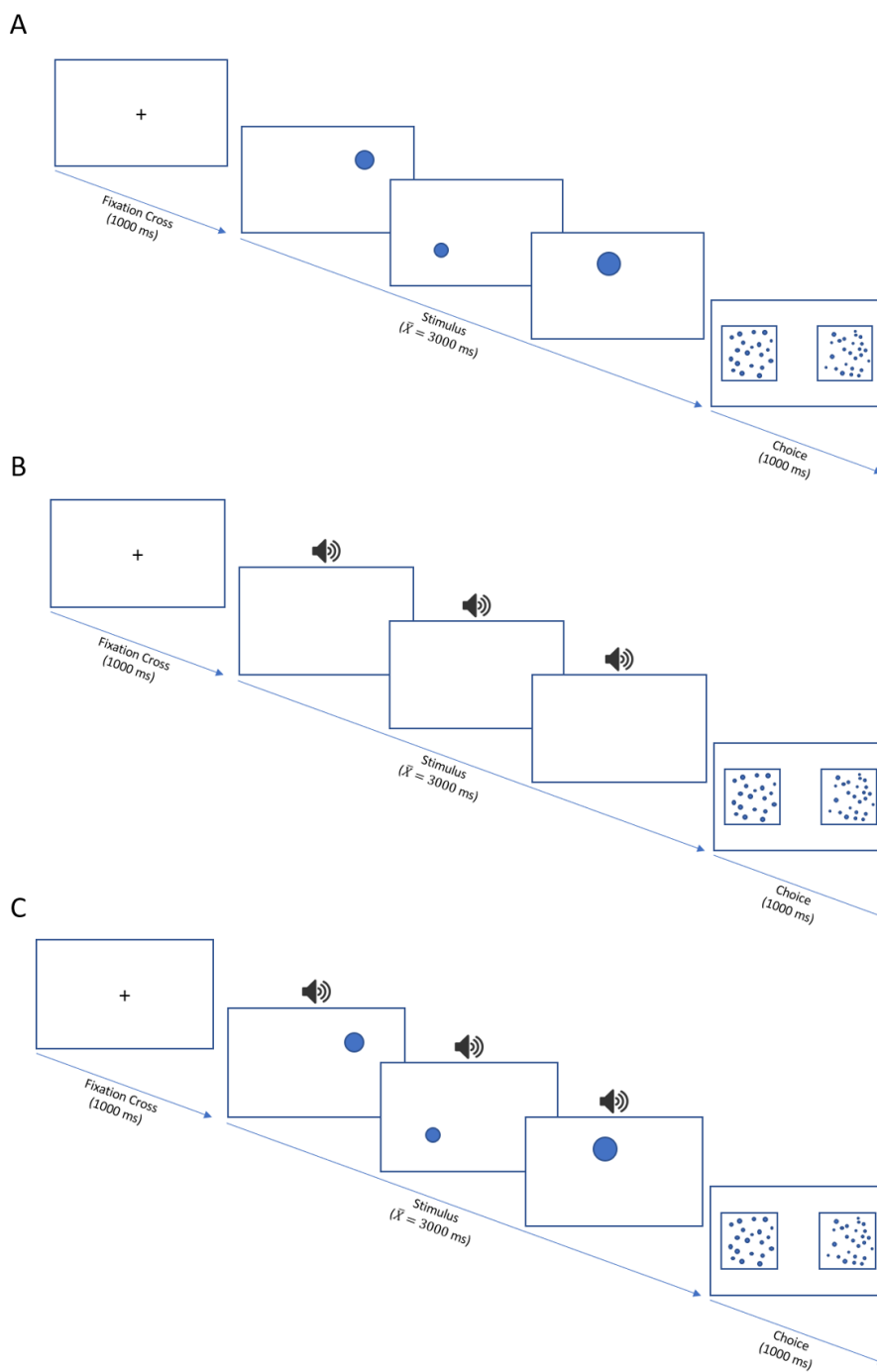
Note. Stimuli a presented as a series of randomly positioned dots (A), a train of auditory clicks (B), or a synchronized train of both (C).

Analyses

      Data Cleaning. Of seventy-seven total participants, data for nine were subject to listwise deletion. Five were removed due to exceptionally low time-on-task measures ($<$ 4 SDs), suggesting likely task disengagement. Four were similarly removed for failing attention checks during data collection. Due to the response time limitation of numerosity discrimination tasks, trials with no response were coded as incorrect with the maximum allowable reaction time. Because some response variables followed non-normal distributions, diagnostic analyses were conducted on regression models to identify cases of significant leverage, distance, and influence. When any model assumption was not met, bootstrapped coefficients were instead estimated using the *car* package (Fox & Weisberg, 2019).[16] For variables that followed a non-normal distribution, Box-Cox transformed values were used when possible. Optimal λ values were generated using the *forecast* package (Hyndman & Khandakar, 2008). When data transformations were insufficient to addressed unmet assumptions, assumption-free testing was used. All data were processed and analyzed in R (R Core Team, 2019).

      Calculation of Numerosity Weber Ratios (w). Calculation of each subject's w scores proceeded in the same fashion as for experiment 1. Separate w scores were computed for the each of the unimodal and the multimodal conditions. MSI performance gains were computed as the difference between the most reliable unisensory signal (given as the lowest of the two conditions' w scores) and the multisensory signal (Stein & Rowland, 2011).

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[16] In cases where bootstrapped estimates differ from those produced by the regression model, the difference is made explicit in the text.

Results

      Descriptive Statistics. The final sample for analysis consisted of sixty-eight adult participants ($n_{female} = 45$). Overall, the sample represented individuals with above-average S-RSPM scores ($\bar{X} = 17.015, s = 7.023$). The sample's AQ ($\bar{X} = 16.765, s = 8.056$) mirrors that of the general population (Baron-Cohen et al., 2001). The same relationship holds for SQ ($\bar{X} = 23.515, s = 11.971$; Baron-Cohen et al., 2003). Diagnostic status was also recorded in this experiment. Six individuals in the sample disclosed having been diagnosed with an ASD ($n_{female} = 2$), and the sample's trait scores did also extend into the range characteristic of individuals with an ASD (SQ: $\bar{X} = 35.7, s = 15.3$ [Baron-Cohen et al., 2003]; AQ: $\bar{X} = 35.8, s = 6.5$ [Baron-Cohen et al., 2001]).[17] There were significant differences in SQ scores between males and females according to Welch's t-test ($t(45.362) = -2.1988, p = 0.033$; Table 5), consistent with prior research (Baron-Cohen et al., 2001; Baron-Cohen et al., 2003), emphasizing the value of biological sex as a covariate in the subsequent models.

      Relationship Between AQ and SQ. As with the previous experiment, this experiment explored the relative contributions of SQ on numerical cognition performance above and beyond that predicted by AQ. Consequently, it was important to confirm the expected partial positive correlation between these two variables for the sample used in experiment two. Similar to the previous experiment, AQ and SQ exhibited a moderate positive correlation ($r(66) = 0.406, p = .0006$).

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[17] The present sample includes 8 responses (11.8%) that would constitute unusually high ASD trait scores for an individual with an ASD (SQ > 49.7; AQ > 28.7). As noted in experiment 1, neither of these tools are intended to be used as a core diagnostic tool.

Table 5

Summary Statistics by Biological Sex

	Female	Male	t	p
	n=45	n=23		
Age	21.289 (5.311)	22.174 (2.622)	-0.75	0.455
IQ	17.600 (6.405)	15.870 (8.131)	0.96	0.340
AQ	16.133 (7.294)	16.565 (7.896)	-0.22	0.823
SQ	21.333 (11.707)	27.826 (11.468)	-2.18	0.033

Number Sense Performance and SQ. The current study also examined the

relationship between ASD traits and number sense acuity under both the unimodal

conditions and the multimodal condition. The model-building process for assessing best

model fit proceeded in the same fashion as in experiment 1. Controlled covariates of age,

sex, and IQ were not significant in any of the tested models. For the visual, auditory, and

multisensory conditions, models including AQ and SQ exhibited a statistically

significantly better fit than the covariates-only model (Visual: $F(2) = 3.40, p = 0.040$;

Auditory: $F(2) = 23.188, p < 0.001$; Multisensory: $F(2) = 3.20, p = 0.048$). In all

conditions, SQ exhibited a significant effect on number sense (Visual: $\beta_{SQ} = 0.0023, p = 0.019$;

0.019; Auditory: $\beta_{SQ} = 0.0053, p < 0.001$; Multisensory: $\beta_{SQ} = 0.0017, p = 0.018$)

while controlling for the effect of AQ, while the reverse was not true (Visual: $\beta_{AQ} = -0.0001, p = 0.941$; Auditory: $\beta_{AQ} = 0.002, p = 0.171$; Multisensory: $\beta_{AQ} = -0.0003, p = 0.746$). These results confirmed the expected finding (consistent with

Table 6

Comparative Models Predicting Number Sense Acuity Across Conditions

	Visual Condition	Auditory Condition	Multisensory Condition
Intercept	0.1591 (0.0622) *	0.0821 (0.0625)	0.0979 (0.0470) *
Age	−0.0012 (0.0022)	0.0029 (0.0022)	−0.0001 (0.0017)
Sex	0.0193 (0.0221)	0.0062 (0.0222)	0.0157 (0.0167)
IQ [a]	0.0001 (0.0015)	−0.0017 (0.0015)	−0.0002 (0.0011)
AQ	0.0024 (0.0010) *	0.0051 (0.0010) ***	0.0018 (0.0008) *
SQ	−0.0002 (0.0016)	0.0022 (0.0016)	−0.0003 (0.0012)
R^2	0.1447	0.4556	0.1334
Adj. R^2	0.0757	0.4117	0.0635
Num. obs.	68	68	68

[a] Given the scoring of the *S-RSPM*, scores are reported in a scale-dependent fashion, in contrast to the use of the *WASI-II* in experiment 1.

Note. ∗∗∗p < 0.001; ∗∗p < 0.01; ∗p < 0.05.

experiment 1) that, both unimodally and multimodally, as *SQ*, but not *AQ*, increases, number sense decreases (Table 6).

SQ-Dependent Losses Ameliorated by Multisensory Integration. The current study postulated that if number sense performance differences between individuals with low *SQ* and individuals with high *SQ* are the result of the effects of neural dysregulation, enhancing the stimulus signal should largely ameliorate those differences. To address this prediction, a model was fit predicting accuracy by *SQ* and stimulus condition with two levels, multisensory and highest unisensory. Significant effects were evident for both *SQ* ($\beta = -0.001, p = 0.012$) and condition ($\beta = 0.0757, p < .001$). Computing across the

range of measured SQ scores in the present sample (5 to 57) using these coefficients, it is evident that the gains of the multisensory condition are sufficient to ameliorate losses due to increasing SQ (Table 7).

Multisensory Gain Across Levels of AQ and SQ. The current study predicted that number sense performance in the multisensory condition would be higher than number sense performance in the unisensory condition across all levels of AQ and SQ. A one-sample t-test was used to confirm that the multisensory gain across the sample to the test value of zero ($t(67) = 9.9088, p < 0.0001$). This confirms that the sample-wide MSI gain is positive (Figure 5). Next, another model was fit to the baseline model of covariates (age, sex, and IQ) including AQ and SQ as additional predictors to determine whether either variable predicted a change in multisensory gain (Table 8). There were no significant effects of any covariates in either model. A direct comparison of the two models revealed that the addition of AQ and SQ did not improve model fit ($F(2) =$

Table 7

Models Testing Effect of MSI on SQ-Dependent Number Sense Losses

	SQ Only	SQ and Condition
Intercept	0.8737 (0.0120) ***	0.8359 (0.0105)
SQ	−0.0009 (0.0005) *	−0.0009 (0.0004) *
Condition		0.0757 (0.0086) ***
R^2	0.0299	0.3880
Adj. R^2	0.0226	0.3788
Num. obs.	68	68

Note. ∗∗∗p < 0.001; ∗∗p < 0.01; ∗p < 0.05.

Figure 5

Multisensory Gain for Entire Sample
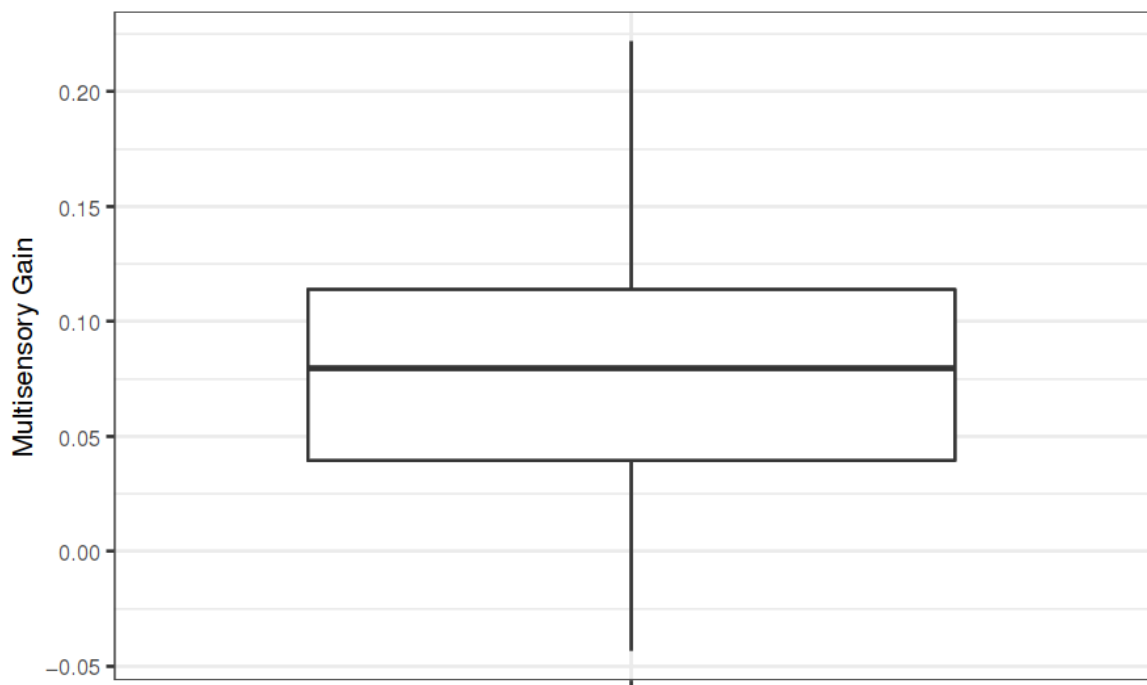
Note. Sample-wide mean multisensory gain is significantly greater than zero.

Table 8

Comparative Models of Multisensory Main Across Levels of AQ *and* SQ.

	Baseline Model	Full Model
Intercept	0.0715 (0.0285) *	0.0485 (0.0329)
Age	−0.0009 (0.0013)	−0.0006 (0.0013)
Sex	0.0102 (0.0124)	0.0061 (0.0130)
IQ	0.0019 (0.0059)	0.0004 (0.0061)
AQ		0.0005 (0.0009)
SQ		0.0005 (0.0006)
R^2	0.0175	0.0478
Adj. R^2	−0.0285	−0.0290
Num. obs.	68	68

Note. ∗∗∗p < 0.001; ∗∗p < 0.01; ∗p < 0.05.

$1.079, p = 0.346$). Investigating the model including AQ and SQ, it is evident that

changes in neither predictor lead to changes in number sense acuity ($\beta_{AQ} = 0.0006, p =$

0.477; $\beta_{SQ} = 0.0005, p = 0.381$). There is clear evidence for multisensory gain in the

sample as a whole, and slopes of tested coefficients support the idea that multisensory

gain occurs at statistically indistinguishable levels across the ranges of AQ and SQ scores.

SQ and Variance of MSI Gains Across Ratio Bins. The current study predicted

that as SQ, but not AQ, increases, variance of MSI gains across all ratio bins increases. To

address this prediction, variance scores were first computed for each subject as the mean

of the squared deviations of the MSI gain for a given ratio bin from the mean MSI gain

for the subject across bins, given as

$$Var(MSI) = \frac{\sum(\Delta MSI_{i,j} - \overline{\Delta MSI_i})^2}{\# \ bins} \tag{2}$$

for a given subject i and ratio bin j. As ratio bins were equally represented in the experiment, no weighting was employed.

An initial model was built regressing subject's MSI variance scores on age, sex, and IQ. A subsequent model fit with the addition of *AQ* and *SQ* was again compared to the baseline model. None of the controlled covariates in either model exhibited a significant effect on number sense acuity. The model including *AQ* and *SQ* did exhibit a better fit than the baseline model and indicated a significant effect of *SQ* on MSI gain variance ($\beta_{SQ} = 0.0006, p = 0.045$); however, subsequent evaluation of model diagnostics suggested that these models did not meet multiple model assumptions. Specifically, diagnostics suggested that the response variable is significantly skewed (assumption of normality of errors) and the variance of the model residuals is not constant across the range of at least one predictor (assumption of homoscedasticity of errors). Consequently, bootstrapped coefficients were estimated using the *car* package (Fox & Weisberg, 2019). The bootstrapped confidence interval around the coefficient for *SQ* (Table 9) did not suggest a significant effect of *SQ* on MSI gain variance, against the prediction of the present study. Thus, there is not sufficient evidence to support the notion that increases in *SQ* are associated with increased variance in MSI gains.

Peak MSI Benefit Across Ratio Bins. The current study predicted that participants would exhibit a peak level of MSI benefit past which additional high-level stimulus noise reduces net MSI benefits. To address this prediction, regression equations were fit predicting multisensory performance and maximum unisensory performance according to ratio bin while controlling for covariates. The maximum unisensory performance for each subject was taken as a baseline from which to compare the

Table 9

*Bootstrapped Estimates Testing the Effect of* SQ *on MSI Variance*

	2.5%	97.5%
Intercept	-0.0095	0.0517
Age	-0.0015	0.0009
Sex	-0.0122	0.0158
IQ	-0.0043	0.0066
SQ	-0.0001	0.0009

Note. ∗∗∗p < 0.001; ∗∗p < 0.01; ∗p < 0.05.

continued benefit of MSI against performance losses due to increasing ratio bin. The

regression equation for the multisensory condition was set equal to the maximum

unisensory performance to solve for the highest level of ratio bin past which MSI benefits

were no longer sufficient to maintain a level of performance at or above the maximum

unisensory performance, giving a peak ratio bin of .607 (Figure 6).

To confirm this extremum for ratio bin, models were fit comparing linear and

quadratic terms for ratio bin on the deviation scores of MSI performance from baseline

performance (Table 10). The quadratic model produced a better model fit ($R^2_{adj} =$

0.0157) than the baseline model ($R^2_{adj} = 0.0141$) and produced the same peak ratio bin

value of .607. These results are consistent with the current study's proposal that there is a

peak past which additional high-level stimulus noise reduces net MSI benefits.

Logarithmic Growth Curve for MSI Recruitment. The current study also

explored whether a multilevel analysis may be able to detect a logarithmic relationship

between stimulus SNR and MSI gains in a fashion consistent with the computational

Figure 6

Peak MSI Benefit Across Ratio Bins
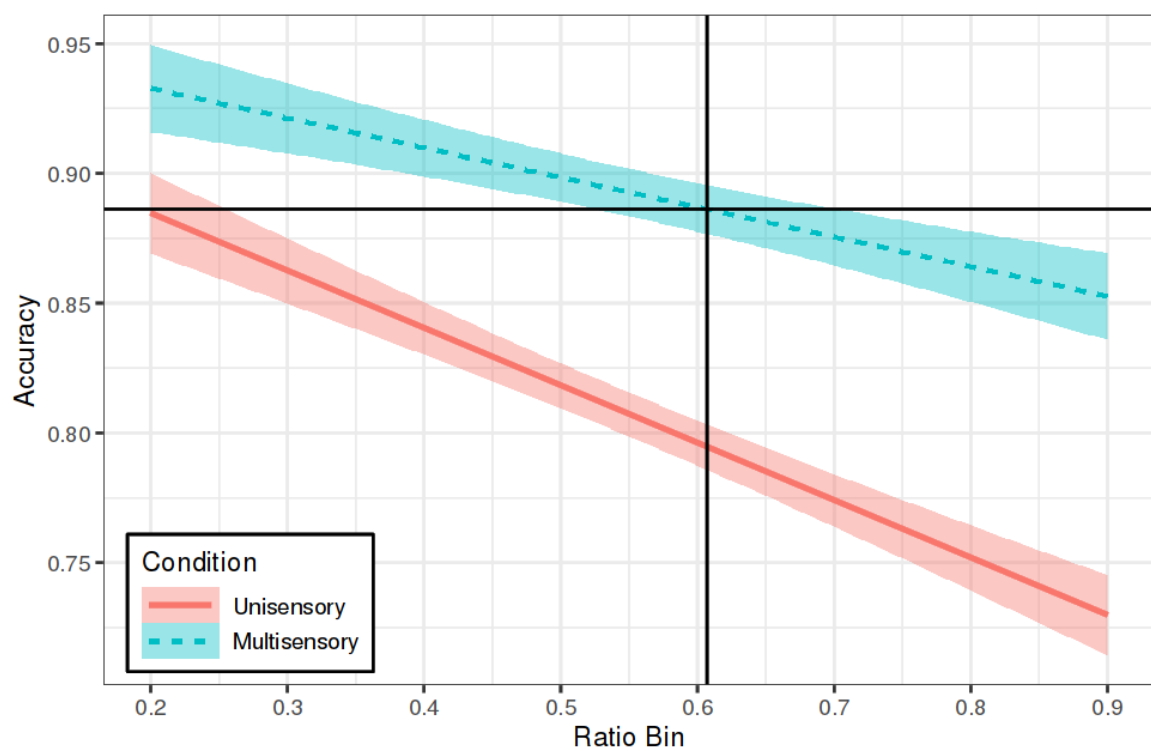
Note. Up to a certain point, MSI provides a net benefit relative to maximum unisensory performance. Past this peak value, additional stimulus noise reduces MSI benefits, Errors bars represent ±1 SEM.

Table 10

Comparative Models Testing Peak Level of MSI Benefit

	Baseline Model	Full Model
Intercept	0.1072 (0.0230) ***	0.1155 (0.0220) ***
Age	−0.0004 (0.0008)	−0.0004 (0.0008)
Sex	0.0145 (0.0078)	0.0145 (0.0078)
IQ	0.0005 (0.0005)	0.0005 (0.0005)
AQ	−0.0006 (0.0005)	−0.0006 (0.0005)
SQ	−0.0002 (0.0003)	−0.0002 (0.0003)
Ratio Bin	0.0391 (0.0148) **	
Ratio Bin^2		0.0371 (0.0132) **
R^2	0.0250	0.0266
Adj. R^2	0.0141	0.0157
Num. obs.	544	544

Note. ***p < 0.001; **p < 0.01; *p < 0.05.

constraints of divisive normalization. Models were fit following the design of Hox et al.

(2018). An initial empty model fitting only random intercepts was fit as a reference for

subsequent model comparisons. The level-one predictor (ratio bin) was added as a fixed

effect and expectedly produced significantly better fit according to a loglikelihood test

($\chi(1) = 170.01, p < .001$). Level-two fixed variables, including covariates, were then

added in a series of comparative models and each was tested against the level-one model.

The best fitting fixed-effect model when compared to the level-one model ($\chi(1) =$

$13.062, p = .0003$) was of the form $w_{MSI} = 1 + (1 + subject) + bin + sq$. At this

point, ratio was also included as a random term to allow varying slopes for each subject.

Again, a loglikelihood test revealed improved fit over the fixed-effects only model

($\chi(1) = 115.26, p < .001$). Adding a subsequent cross-level interaction between *SQ* and

ratio bin did not improve model fit.

     With a best fitting multilevel linear model available, it was possible to test the

prediction of a logarithmic function for MSI recruitment across ratio bins by refitting the

same model with a variation on the ratio bin term. The linear model was refit with a

Table 11

MLM: Comparative Models for MSI Gains

	Baseline Model	Full Model
Intercept	0.0819 (0.0134) ***	−0.0493 (0.0128) ***
SQ	0.0007 (0.0004)	0.0007 (0.0004)
Ratio Bin	0.1540 (0.0180) ***	
Log(Ratio Bin)		0.1510 (0.0184) ***
AIC	−1497.0237	−1571.6237
BIC	−1466.9311	−1541.5310
Log Likelihood	755.5118	792.8118
Num. obs.	544	544
Num. groups: subject	68	68
Var: subject (Intercept)	0.0033	0.0054
Var: subject I(log10(ratio))		0.0145
Cov: subject (Intercept) I(log10(ratio))		0.0081
Var: Residual	0.0021	0.0026
Var: subject ratio		0.0180
Cov: subject (Intercept) ratio		−0.0063

*Note.* ∗∗∗p < 0.001; ∗∗p < 0.01; ∗p < 0.05.

logarithmic predictive term for ratio bin and compared. Because these models are not nested, they could not be compared via loglikelihood tests. Consequently, the Akaike information criterion (AIC) was compared instead (Hox et al., 2018). The logarithmic model provided an improved model fit over the linear model (Table 11), suggesting that the best fit to the present data is consistent with a plateau of MSI recruitment at the upper end of the high-level stimulus noise range (Figure 7). Because AIC does not permit a formal goodness of fit test, a conservative interpretation is warranted. However, the results are, at the very least, consistent with the predictions made based on work suggesting a key role of divisive normalization in MSI.

Discussion

Experiment 1 demonstrated, as predicted, that as *SQ* increased number sense performance decreased. Experiment 2 not only replicated this finding, but demonstrated the same relationship across different modalities (vison and audition), as well as under a multisensory condition. The findings of experiment 2 further substantiate the claim that scores on the *SQ* reflect the subjective experience of number sense SNR such that, as *SQ* increases the experienced SNR for unenhanced number sense decreases. This claim is further substantiated by the finding that when the number sense signal was enhanced via multimodal presentation, losses occasioned by increasing *SQ* were ameliorated. The current study also found, as predicted, that number sense performance in the multisensory condition was higher than number sense performance in the unisensory condition for adults across ASD traits. This finding is consistent with previous findings of

Figure 7

Effect of High−Level Stimulus Noise and SQ on Multisensory Gain
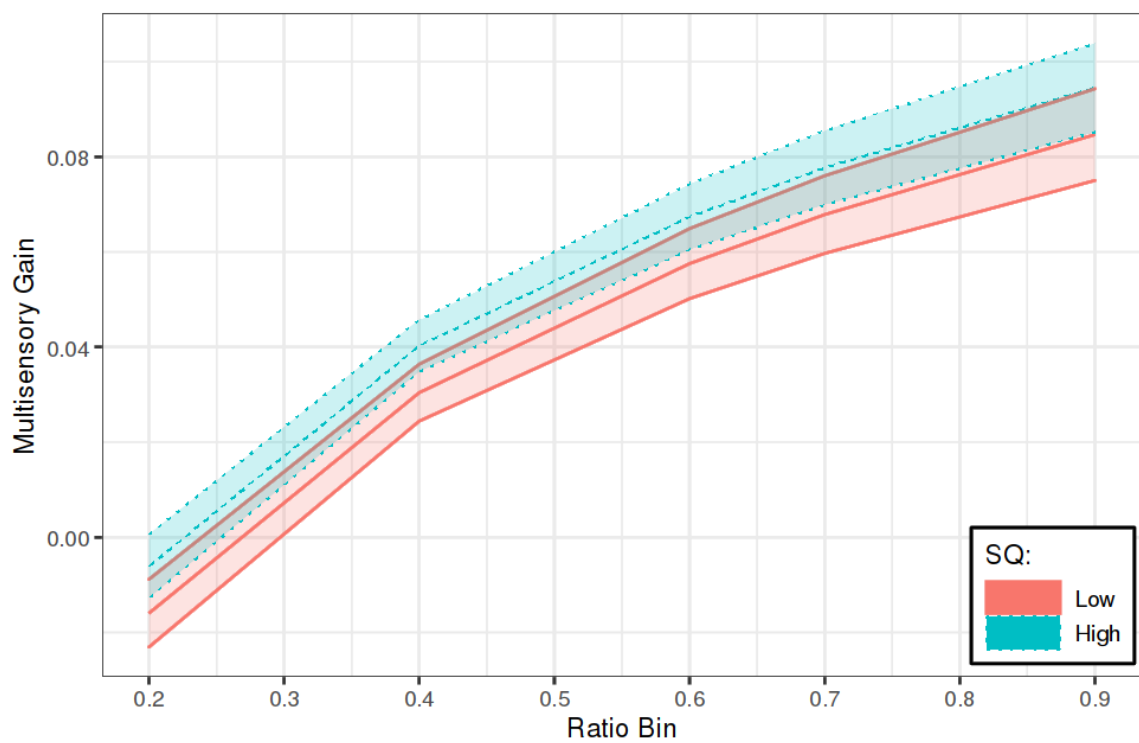
Note. MSI gains appear to approach a plateau as signal-to-noise ratio decreases for high-level stimulus noise. Error bars represent ±1 SEM.

MSI gains for both TDs and ASDs, on a variety of perception tasks (Feldman et al., 2018). While this finding adds to the literature on MSI gains for number sense for TDs, this finding represents the first experimental support for MSI gains for number sense performance across levels of ASD traits.

These findings also suggest that MSI may be an ideal candidate for number sense interventions in childhood. Although some studies have indicated less stability in MSI during childhood for individuals with an ASD (Brandwein et al., 2013), studies have also indicated that MSI training can affect earlier stabilization, especially when the intervention address the effects of attention on MSI (Magnée et al., 2011; Stefanou et al., 2020). In other words, future studies could examine whether an MSI number sense training paradigm would potentially improve both MSI and number sense acuity for high ASD-trait individuals.

Against prediction, the current study did not find differences in the variance of MSI gains across *SQ*. The current study also expected to find that a multimodal presentation would largely, but not entirely, ameliorate losses due to *SQ.* Somewhat against prediction, the current study found that these losses were entirely ameliorated for this sample. One possible interpretation may be that for both predictions the current study overestimated the degree of the effects of neural dysregulation on the SC. The current study expected that, as a moderately downstream region, the SC would be subject to the effects of an E/I imbalance resulting in both dysregulated (i.e., increasingly variable) integration of multiple sensory inputs and mean effects of noise on number sense performance (i.e., incomplete amelioration). These findings may suggest, however, that while the output of the SC is likely affected by overfit messages from primary sensory

cortex and underfit messages from association cortex, its position in compromised signal propagation pathways may not be so poor as to produce large effects of neural dysregulation.

Although MSI studies typically focus on the difference between unisensory performance and multisensory performance (i.e., MSI gains) the trade-off between MSI gain and stimulus SNR losses has been less explored. The current study found, as predicted, that a quadratic predictor fit ideally to highlight the peak ratio bin for MSI gains and stimulus SNR losses. In other words, there is a point of stimulus SNR degradation past which any benefit from integrating another signal modality is outweighed by the cost of low stimulus SNR. This pattern was specifically found in the current study for a paradigm that manipulated high-level stimulus features; however, based on the principle of inverse effectiveness, it is expected that this same trend would be observed for manipulation of low-level stimulus features. Future studies would be needed to verify whether this pattern is also found for the manipulation of low-level stimulus features. As the current study has demonstrated that a number sense paradigm is useful for manipulating high-level stimulus features independent of low-level stimulus features, future studies could also use this paradigm to examine whether this quadratic relationship holds when both levels of stimulus features are manipulated.

General Discussion

The current study investigated numerical cognition in adults across ASD traits. Although previous findings examining math performance for individuals with a high-functioning ASD have been highly variable, a closer look at the literature suggests a

pattern of childhood deficit followed by proficiency in adulthood. The current study has argued that this trajectory is consistent with the development of numerical cognition and an E/I imbalance account of ASD. Based on this account, learners with high ASD-trait scores would show impaired number sense acuity due to the compounding effects of neural dysregulation. The proposed consequence would be a delay in the acquisition of sufficient abstract representation of quantity on which to map number symbols. As the effects of neural dysregulation are proposed to be ameliorated by sufficient signal enhancement, performance on symbolic number and formal math (tasks enhanced via standardization) are proposed to be largely the same between TDs and individual with an ASD once number sense delays are accounted for. Consistent with this account, experiments 1 and 2 found a relationship between number sense performance and an ASD-related trait (i.e., as scores on the *SQ* increase number sense performance decreases) for visual, auditory, and multimodal conditions, as well as intact symbolic number and formal math performance across ASD traits.

These findings, however, have some limitations. First, although the current study found a pattern of ASD-related deficits for number sense but intact symbolic number and formal math, this was found for adults and did not directly examine the developmental trajectory. It is recommended that longitudinal studies more directly examine the acquisition of numerical cognition over time across ASD traits. If the account of the current study is correct, it is expected that the majority of young children who are high in ASD traits will show lower number sense acuity than low ASD-trait peers, but that individual-level analyses would reveal improvement in numerical cognition over time that results in remediation for tasks with enhanced SNR.

Second, the findings of the current study are also limited by the education level of the sample used. As the majority of the sample consisted of university students, it may not reflect the math achievement levels of the general population. It is possible that a more inclusive sample would show *SQ*-related differences in symbolic number and formal math performance even in adulthood. It is recommended that future studies examine numerical cognition across ASD traits across a broader sample of adults to better understand whether formal math performance for this population continues to be problematic in adulthood.

Finally, it warrants reiterating that while these studies were informed by established literature regarding individuals diagnosed with an ASD, the focus here has been on traits associated with ASD across a broader population. Consequently, implications specifically for individuals with clinically significant presentations should be taken with caution. It is recommended that future studies, when possible, investigate these variables in the context of both diagnostic status and trait scores to clarify the relationships between them.

The current study also proposed that if the number sense deficits for this population are due to neural dysregulation, sufficient signal enhancement should ameliorate related losses. Using an MSI paradigm, the current study found that increasing the SNR of the number sense stimuli by adding a second stimulus modality ameliorated losses related to an ASD trait (*SQ*). The current study also demonstrated for the first time across ASD trait scores that MSI can improve performance on a number sense task. This finding not only highlights the possible benefits of MSI as a number sense intervention, but supports the idea that, in general, enhancing signal strength for number sense could

improve number sense acuity. It is recommended that future studies examine which methods of enhancement would be most beneficial for children high in ASD traits, including those diagnosed with an ASD. Although experiment 2 has demonstrated that MSI is a promising candidate, the results of experiment 1 also suggest that signal enhancement via standardization may be effective. For example, standardization may involve repeated exposure to nonsymbolic stimuli where a geometric feature (e.g., the orientation of items in a numerosity set) is held constant while other features (e.g., rotation of the set, total surface area of the set) are allowed to vary. This may reduce stimulus noise and allow students the opportunity to begin to abstract the numerosity rule before adding more complexity back into the stimulus.

The current study also used experiment 2 as an opportunity to explore questions concerning both MSI and neural dysregulation. First, while many MSI studies have reported linear growth terms for MSI gains, the current study explored whether closer examination would reveal a logarithmic growth term due to the principle of divisive normalization. In other words, as the integration system reaches its upper processing limit, the growth rate in MSI gains would be characterized by diminishing returns due to saturation. The current study found, as expected, that as number sense ratio bin increased, the growth in MSI gains diminished logarithmically. As this was found for a paradigm manipulating high-level stimulus features, it is recommended that future studies explore whether the principle of divisive normalization would have the same effect on MSI gains when low-level stimulus features are manipulated. Future studies could also explore whether the principle of divisive normalization would predict that perceptual accuracy would show a quadratic term when stimulus SNR levels were pushed to both very high

and very low levels. In other words, it would be expected that performance improvement would diminish as task difficulty moved from easy to too easy, and performance degradation would diminish as task difficulty moved from hard to too hard, resulting in a non-linear term.

Second, the current study used experiment 2 to explore the trade-off between performance improvement as a result of MSI and performance loss due to decreased stimulus SNR. The current study proposed that there is a peak level of stimulus SNR past which the benefit of adding a second stimulus modality is outweighed by the effects of low stimulus SNR. Regression analyses revealed that by using a quadratic term for stimulus SNR, the relationship between SNR performance costs and MSI benefits could be fit with peak ratio bin given at the function's global extremum. As this was found for a paradigm manipulating high-level stimulus features, it is recommended that future studies explore whether a quadradic term is found when low-level stimulus features are manipulated. Moreover, as previously stated, future research would benefit from directly measuring neural correlates corresponding to numerosity processing (especially the IPS) alongside the phenomena observed in the present studies to more precisely parameterize the relationship between high-level stimulus SNR and neural activation (cf. Flevaris & Murray, 2015; Karten & Hirsch, 2015; Takarae et al. 2014).

In conclusion, the findings of the current study support the notion that individuals who are high in ASD traits do not have a deficit in formal math *per se*, or a deficit in acquiring a symbolic number system, but rather struggle with number sense acuity in a fashion consistent with an E/I imbalance. In addition, the current study found support for the idea that *SQ*-related deficits in number sense performance can be ameliorated via the

enhancement of stimulus signal strength. These findings suggest that there may be ways to improve the early number sense acuity of learners who are high in ASD traits and, consequently, how they engage formal math. These findings may be able to inform valuable interventions for a population falling behind in a domain where they may have the potential to excel.

References

Aagten-Murphy, D., Attucci, C., Daniel, N., Klaric, E., Burr, D., & Pellicano, E. (2015). Numerical estimation in children with autism. *Autism Research*, *8*(6), 668-681.

Aldrich, M. S., Alessi, A. G., Beck, R. W., & Gilman, S. (1987). Cortical blindness: etiology, diagnosis, and prognosis. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, *21*(2), 149-158.

Allen, M. L., & Chambers, A. (2011). Implicit and explicit understanding of ambiguous figures by adolescents with autism spectrum disorder. *Autism*, *15*(4), 457-472.

Almeida, R. A., Dickinson, J. E., Maybery, M. T., Badcock, J. C., & Badcock, D. R. (2010). A new step towards understanding Embedded Figures Test performance in the autism spectrum: The radial frequency search task. *Neuropsychologia*, *48*(2), 374-381.

Anastasio, T. J., & Patton, P. E. (2003). A two-stage unsupervised learning algorithm reproduces multisensory enhancement in a neural network model of the corticotectal system. *Journal of Neuroscience*, *23*(17), 6713-6727.

Anastasio, T. J., Patton, P. E., & Belkacem-Boussaid, K. (2000). Using Bayes' rule to model multisensory enhancement in the superior colliculus. *Neural Computation*, *12*(5), 1165-1187.

Anderson, E. J., Husain, M., & Sumner, P. (2008). Human intraparietal sulcus (IPS) and competition between exogenous and endogenous saccade plans. *Neuroimage*, *40*(2), 838-851.

Anghileri, J. (2000). *Teaching number sense*. A&C Black.

Ansari, D., & Dhital, B. (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: an event-related functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, *18*(11), 1820-1828.

Ashcraft, M. H., & Krause, J. A. (2007). Working memory, math performance, and math anxiety. *Psychonomic Bulletin & Review*, *14*(2), 243-248.

Auerbach, B. D., Osterweil, E. K., & Bear, M. F. (2011). Mutations causing syndromic autism define an axis of synaptic pathophysiology. *Nature*, *480*(7375), 63-68.

Autism and Developmental Disabilities Monitoring Network Surveillance Year 2010 Principal Investigators. (2014). Prevalence of autism spectrum disorder among children aged 8 years—Autism and developmental disabilities monitoring network, 11 sites, United States, 2010. *Morbidity and Mortality Weekly Report: Surveillance Summaries*, *63*(2), 1-21.

Bae, Y. S., Chiang, H. M., & Hickson, L. (2015). Mathematical word problem solving ability of children with autism spectrum disorder and their typically developing peers. *Journal of Autism and Developmental Disorders*, *45*(7), 2200-2208.

Bakouie, F., Zendehrouh, S., & Gharibzadeh, S. (2009). Does a kind of over-fitting occur in the brain of autistic patients? *The Journal of Neuropsychiatry and Clinical Neurosciences*, *21*(3), 343-343.

Barnett, J. E. H., & Cleary, S. (2015). Review of evidence-based mathematics interventions for students with autism spectrum disorders. *Education and Training in Autism and Developmental Disabilities*, 172-185.

Baron-Cohen, S., Murphy, L., Chakrabarti, B., Craig, I., Mallya, U., Lakatošová, S., Rehnstrom, K., Peltonen, L., Wheelwright, S., Allison, C., Fisher, S., & Warrier, V. (2014). A genome wide association study of mathematical ability reveals an association at chromosome 3q29, a locus associated with autism and learning difficulties: a preliminary study. *PloS One*, *9*(5), e96374.

Baron-Cohen, S., & Belmonte, M. K. (2005). Autism: A window onto the development of the social and the analytic brain. *Annual Review of Neuroscience*, *28*, 109-126.

Baron-Cohen, S., & Lombardo, M. V. (2017). Autism and talent: The cognitive and neural basis of systemizing. *Dialogues in Clinical Neuroscience*, *19*(4), 345.

Baron-Cohen, S., Ashwin, E., Ashwin, C., Tavassoli, T., & Chakrabarti, B. (2009). Talent in autism: Hyper-systemizing, hyper-attention to detail and sensory hypersensitivity. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 364(1522), 1377-1383.

Baron-Cohen, S., Richler, J., Bisarya, D., Gurunathan, N., & Wheelwright, S. (2003). The systemizing quotient: An investigation of adults with Asperger syndrome or high–functioning autism, and normal sex differences. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *358*(1430), 361-374.

Baron-Cohen, S., Wheelwright, S., Burtenshaw, A., & Hobson, E. (2007). Mathematical talent is linked to autism. *Human Nature*, *18*(2), 125–131.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism spectrum quotient (AQ): Evidence from Asperger syndrome/high functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, *31*, 5–17.

Basso, M. A., & Wurtz, R. H. (1997). Modulation of neuronal activity by target uncertainty. *Nature*, *389*(6646), 66-69.

Behrmann, M., Avidan, G., Leonard, G. L., Kimchi, R., Luna, B., Humphreys, K., & Minshew, N. (2006). Configural processing in autism and its relationship to face processing. *Neuropsychologia*, *44*(1), 110-129.

Bell, A. H., Corneil, B. D., Munoz, D. P., & Meredith, M. A. (2003). Engagement of visual fixation suppresses sensory responsiveness and multisensory integration in the primate superior colliculus. *European Journal of Neuroscience*, *18*(10), 2867-2873.

Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2003). Motion perception in autism: A "complex" issue. *Journal of Cognitive Neuroscience*, *15*(2), 218-225.

Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2005). Enhanced and diminished visuo-spatial information processing in autism depends on stimulus complexity. *Brain*, *128*(10), 2430-2441.

Bhatia, A., Moza, S., & Bhalla, U. S. (2019). Precise excitation-inhibition balance controls gain and timing in the hippocampus. *Elife*, *8*, e43415.

Billock, V. A., & Tsou, B. H. (2011). To honor Fechner and obey Stevens: Relationships between psychophysical and neural nonlinearities. *Psychological Bulletin*, *137*(1), 1.

Bonnel, A., Mottron, L., Peretz, I., Trudel, M., Gallun, E., & Bonnel, A. M. (2003). Enhanced pitch sensitivity in individuals with autism: a signal detection analysis. *Journal of Cognitive Neuroscience*, *15*(2), 226-235.

Bourgeron, T. (2015). From the genetic architecture to synaptic plasticity in autism

    spectrum disorder. *Nature Reviews Neuroscience*, *16*(9), 551-563.

Bowers, J. M., & Konopka, G. (2012). The role of the FOXP family of transcription

    factors in ASD. *Disease Markers*, *33*(5), 251-260.

Braeutigam, S. (2005). Neuroeconomics—From neural systems to economic

    behaviour. *Brain Research Bulletin*, *67*(5), 355-360.

Brandwein, A. B., Foxe, J. J., Butler, J. S., Russo, N. N., Altschuler, T. S., Gomes, H., &

    Molholm, S. (2013). The development of multisensory integration in high-

    functioning autism: high-density electrical mapping and psychophysical measures

    reveal impairments in the processing of audiovisual inputs. *Cerebral

    Cortex*, *23*(6), 1329-1341.

Broadbent, J., Galic, I., & Stokes, M. A. (2013). Validation of autism spectrum quotient

    adult version in an Australian sample. *Autism Research and Treatment*, *2013*.

Bruneau, N., Roux, S., Adrien, J. L., & Barthélémy, C. (1999). Auditory associative

    cortex dysfunction in children with autism: Evidence from late auditory evoked

    potentials (N1 wave–T complex). *Clinical Neurophysiology*, *110*(11), 1927-1934.

Bruneau, N., Bonnet-Brilhault, F., Gomot, M., Adrien, J. L., & Barthélémy, C. (2003).

    Cortical auditory processing and communication in children with autism:

    Electrophysiological/behavioral relations. *International Journal of

    Psychophysiology*, *51*(1), 17-25.

Brunton, B. W., Botvinick, M. M., & Brody, C. D. (2013). Rats and humans can

    optimally accumulate evidence for decision-making. *Science*, *340*(6128), 95-98.

Budimirovic, D. B., Protic, D., & Toma, A. E. (2017). Fragile X syndrome: Leading the way as the most common monogenic form of autism spectrum disorder and the most translated among neurodevelopmental disorders in clinical trials. *Journal of Clinical Genetics and Genomics*, *1*(1).

Bullen, J. C., Lerro, L. S., Zajic, M., McIntyre, N., & Mundy, P. (2020). A developmental study of mathematics in children with autism spectrum disorder, symptoms of attention deficit hyperactivity disorder, or typical development. *Journal of Autism and Developmental Disorders*, *50*(12), 4463-4476.

Burnett, L. R., Stein, B. E., Chaponis, D., & Wallace, M. T. (2004). Superior colliculus lesions preferentially disrupt multisensory orientation. *Neuroscience*, *124*(3), 535-547.

Busse, L., Wade, A. R., & Carandini, M. (2009). Representation of concurrent stimuli by population activity in visual cortex. *Neuron*, *64*(6), 931-942.

Butterworth, B. (1999). *What counts: How every brain is hardwired for math*. Free Press.

Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biology*, *4*(5), e125.

Cantlon, J. F., Platt, M. L., & Brannon, E. M. (2009). Beyond the number domain. *Trends in Cognitive Sciences*, *13*(2), 83-91.

Chen, L., Abrams, D. A., Rosenberg-Lee, M., Iuculano, T., Wakeman, H. N., Prathap, S., ... & Menon, V. (2019). Quantitative analysis of heterogeneity in academic achievement of children with autism. *Clinical Psychological Science*, *7*(2), 362-380.

Cheng, Y., Chou, K. H., Chen, I. Y., Fan, Y. T., Decety, J., & Lin, C. P. (2010). Atypical development of white matter microstructure in adolescents with autism spectrum disorders. *Neuroimage*, *50*(3), 873-882.

Chistiakova, M., Bannon, N. M., Chen, J. Y., Bazhenov, M., & Volgushev, M. (2015). Homeostatic role of heterosynaptic plasticity: Models and experiments. *Frontiers in Computational Neuroscience*, *9*, 89.

Clark, T. F., Winkielman, P., & McIntosh, D. N. (2008). Autism and the extraction of emotion from briefly presented facial expressions: Stumbling at the first step of empathy. *Emotion*, *8*(6), 803.

Clower, D. M., West, R. A., Lynch, J. C., & Strick, P. L. (2001). The inferior parietal lobule is the target of output from the superior colliculus, hippocampus, and cerebellum. *Journal of Neuroscience*, *21*(16), 6283-6291.

Czanner, G., Sarma, S. V., Ba, D., Eden, U. T., Wu, W., Eskandar, E., Lim, H., Temereanca, S., Suzuki, W., & Brown, E. N. (2015). Measuring the signal-to-noise ratio of a neuron. *Proceedings of the National Academy of Sciences*, *112*(23), 7141-7146.

Dakin, S., & Frith, U. (2005). Vagaries of visual perception in autism. *Neuron*, *48*(3), 497-507.

Dawson, G., Webb, S. J., & McPartland, J. (2005). Understanding the nature of face processing impairment in autism: Insights from behavioral and electrophysiological studies. *Developmental Neuropsychology*, *27*(3), 403-424.

Desoete, A., Ceulemans, A., De Weerdt, F., & Pieters, S. (2012). Can we predict mathematical learning disabilities from symbolic and non-symbolic comparison

tasks in kindergarten? Findings from a longitudinal study. *British Journal of Educational Psychology*, *82*(1), 64-81.

De Vos, T. (1992). *Tempo Test Rekenen*. Nijmegen, The Netherlands: Berkhout.

Dehaene, S. (2001). Précis of the number sense. *Mind & Language*, *16*(1), 16-36.

Dehaene, S. (2007). Symbols and quantities in parietal cortex: Elements of a mathematical theory of number representation and manipulation. *Sensorimotor Foundations of Higher Cognition*, *22*, 527-574.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*(3-6), 487-506.

Dehaene, S., Molko, N., Cohen, L., & Wilson, A. J. (2004). Arithmetic and the brain. *Current Opinion in Neurobiology*, *14*(2), 218-224.

Dehaene, S. (2011). *The number sense: How the mind creates mathematics*. OUP USA.

de Dieuleveult, A. L., Siemonsma, P. C., van Erp, J. B., & Brouwer, A. M. (2017). Effects of aging in multisensory integration: a systematic review. *Frontiers in Aging Neuroscience*, *9*, 80.

Dombrowski, S. C., Gischlar, K. L., Mrazik, M., & Greer, F. W. (2011). Feral Children. In *Assessing and Treating Low Incidence/High Severity Psychological Disorders of Childhood* (pp. 81-93). Springer, New York, NY.

Dormal, V., Andres, M., & Pesenti, M. (2012). Contribution of the right intraparietal sulcus to numerosity and length processing: An fMRI-guided TMS study. *Cortex*, *48*(5), 623-629.

Doyon, J., Mahoney, A. D., Golding, C., Shomstein, S., & Rosenblau, G. (2020, May 2–5). *Potential biomarker for ASD: Reduced pupil responses to repeated*

multisensory stimuli in young children with autism [Conference presentation].

CNS 2020 Convention, Virtual Meeting, United States.

Dumontheil, I., & Klingberg, T. (2011). Brain activity during a visuospatial working

memory task predicts arithmetical performance 2 years later. *Cerebral*

Cortex, *22*(5), 1078-1085.

Edgar, J. C., Khan, S. Y., Blaskey, L., Chow, V. Y., Rey, M., Gaetz, W., Cannon, K. M.,

Monroe, J. F., Cornew, L., Qasmieh, S., Liu, S., Welsh, J. P., Levy, S. E., &

Roberts, T. P. L. (2015). Neuromagnetic oscillations predict evoked-response

latency delays and core language deficits in autism spectrum disorders. *Journal of*

Autism and Developmental Disorders, *45*(2), 395-405.

Edwards, M., & Badcock, D. R. (1995). Global motion perception: No interaction

between the first-and second-order motion pathways. *Vision Research*, *35*(18),

2589-2602.

Eger, E., Sterzer, P., Russ, M. O., Giraud, A. L., & Kleinschmidt, A. (2003). A

supramodal number representation in human intraparietal cortex. *Neuron*, *37*(4),

719-726.

Emerson, R. W., & Cantlon, J. F. (2012). Early math achievement and functional

connectivity in the fronto-parietal network. *Developmental Cognitive*

Neuroscience, *2*, S139-S151.

Estruch, S. B., Graham, S. A., Quevedo, M., Vino, A., Dekkers, D. H., Deriziotis, P.,

Sollis, E., Demmers, J., Poot, R., & Fisher, S. E. (2018). Proteomic analysis of

FOXP proteins reveals interactions between cortical transcription factors

associated with neurodevelopmental disorders. *Human Molecular Genetics*, *27*(7), 1212-1227.

Fechner, G. T. (1860). *Elemente der psychophysik* (Vol. 2). Breitkopf & Härtel.

Fechner, G. T. (2012). *Elemente der psychophysik*. Рипол Классик.

Feldman, J. I., Dunham, K., Cassidy, M., Wallace, M. T., Liu, Y., & Woynaroski, T. G. (2018). Audiovisual multisensory integration in individuals with autism spectrum disorder: A systematic review and meta-analysis. *Neuroscience & Biobehavioral Reviews*, *95*, 220-234.

Fischer, B., Gebhardt, C., & Hartnegg, K. (2008). Subitizing and Visual Counting in Children with Problems in Acquiring Basic Arithmetic Skills. *Optometry & Vision Development*, *39*(1).

Flevaris, A. V., & Murray, S. O. (2015). Orientation-specific surround suppression in the primary visual cortex varies as a function of autistic tendency. *Frontiers in Human Neuroscience*, *8*, 1017.

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., ... & Murdoch, D. (2012). Package 'car'. *Vienna: R Foundation for Statistical Computing*, 16.

Frith, U. (1972). Cognitive mechanisms in autism: Experiments with color and tone sequence production. *Journal of Autism and Childhood Schizophrenia*, *2*(2), 160-173.

Gagnon, L., Mottron, L., Bherer, L., & Joanette, Y. (2004). Quantification judgement in high functioning autism: Superior or different? *Journal of Autism and Developmental Disorders*, *34*(6), 679-689.

Gandal, M. J., Edgar, J. C., Ehrlichman, R. S., Mehta, M., Roberts, T. P., & Siegel, S. J. (2010). Validating γ oscillations and delayed auditory responses as translational biomarkers of autism. *Biological Psychiatry*, *68*(12), 1100-1106.

Gevarter, C., Bryant, D. P., Bryant, B., Watkins, L., Zamora, C., & Sammarco, N. (2016). Mathematics interventions for individuals with autism spectrum disorder: A systematic review. *Review Journal of Autism and Developmental Disorders*, *3*(3), 224-238.

Ghose, D., Maier, A., Nidiffer, A., & Wallace, M. T. (2014). Multisensory response modulation in the superficial layers of the superior colliculus. *Journal of Neuroscience*, *34*(12), 4332-4344.

Gielen, S. C., Schmidt, R. A., & Van Den Heuvel, P. J. (1983). On the nature of intersensory facilitation of reaction time. *Perception & Psychophysics*, *34*(2), 161-168.

Ginsburg, H. P., & Baroody, A. J. (2003). *TEMA-3: Test of Early Mathematics Ability– Third Edition*.

Groen, Y., Fuermaier, A. B. M., Den Heijer, A. E., Tucha, O., & Althaus, M. (2015). The empathy and systemizing quotient: The psychometric properties of the Dutch version and a review of the cross-cultural stability. *Journal of Autism and Developmental Disorders*, *45*(9), 2848-2864.

Gross, T. F. (2005). Global–local precedence in the perception of facial age and emotional expression by children with autism and other developmental disabilities. *Journal of Autism and Developmental Disorders*, *35*(6), 773-785.

Grupe, D. W., & Nitschke, J. B. (2013). Uncertainty and anticipation in anxiety: An integrated neurobiological and psychological perspective. *Nature Reviews Neuroscience*, *14*(7), 488-501.

Hadjikhani, N., Johnels, J. Å., Zürcher, N. R., Lassalle, A., Guillon, Q., Hippolyte, L., Billstedt, E., Ward, N., Lemonnier, E., & Gillberg, C. (2017). Look me in the eyes: constraining gaze in the eye-region provokes abnormally high subcortical activation in autism. *Scientific Reports*, *7*(1), 1-7.

Halberda, J., & Feigenson, L. (2008). Developmental change in the acuity of the "number sense": The approximate number system in 3-, 4-, 5-, and 6-year-olds and adults. *Developmental Psychology*, *44*(5), 1457.

Halberda, J., Mazzocco, M. M., & Feigenson, L. (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, *455*(7213), 665-668.

Hastie, T., Tibshirani, R., & Friedman, J. (2016). *The elements of statistical learning: Data mining, inference, and prediction* (2nd ed.). Springer Science & Business Media.

Heaton, P. (2003). Pitch memory, labelling and disembedding in autism. *Journal of Child Psychology and Psychiatry*, *44*(4), 543-551.

Hines, R. M., Wu, L., Hines, D. J., Steenland, H., Mansour, S., Dahlhaus, R., Singaraja, R. R., Cao, X., Sammler, E., Hormuzdi, S. G., Zhuo, M., & El-Husseini, A. (2008). Synaptic imbalance, stereotypies, and impaired social interactions in mice with altered neuroligin 2 expression. *Journal of Neuroscience*, *28*(24), 6055-6067.

Hiniker, A., Rosenberg-Lee, M., & Menon, V. (2016). Distinctive role of symbolic number sense in mediating the mathematical abilities of children with autism. *Journal of Autism and Developmental Disorders*, *46*(4), 1268–1281.

Hoekstra, R. A., Bartels, M., Cath, D. C., & Boomsma, D. I. (2008). Factor structure, reliability and criterion validity of the Autism-Spectrum Quotient (AQ): A study in Dutch population and patient groups. *Journal of Autism and Developmental Disorders*, *38*(8), 1555-1566.

Holmes, N. P. (2007). The law of inverse effectiveness in neurons and behaviour: multisensory integration versus normal variability. *Neuropsychologia*, *45*(14), 3340-3345.

Holmes, N. P. (2007). The law of inverse effectiveness in neurons and behaviour: Multisensory integration versus normal variability. *Neuropsychologia*, *45*(14), 3340-3345.

Hornung, C., Schiltz, C., Brunner, M., & Martin, R. (2014). Predicting first-grade mathematics achievement: The contributions of domain-general cognitive abilities, nonverbal number sense, and early number competence. *Frontiers in Psychology*, *5*, 272.

Hox, J. J., Moerbeek, M., & Van de Schoot, R. (2017). *Multilevel analysis: Techniques and applications*. Routledge.

Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, *6*(6), 435–448.

Huff, T., Mahabadi, N., & Tadi, P. (2020). Neuroanatomy, visual cortex. *StatPearls [Internet]*.

Hurst, R. M., Mitchell, J. T., Kimbrel, N. A., Kwapil, T. K., & Nelson-Gray, R. O. (2007). Examination of the reliability and factor structure of the Autism Spectrum Quotient (AQ) in a non-clinical sample. *Personality and Individual Differences*, *43*(7), 1938-1949.

Hussman, J. P., Chung, R. H., Griswold, A. J., Jaworski, J. M., Salyakina, D., Ma, D., ... & Cuccaro, M. L. (2011). A noise-reduction GWAS analysis implicates altered regulation of neurite outgrowth and guidance in autism. *Molecular Autism*, *2*(1), 1-16.

Hyndman, R. J., & Khandakar, Y. (2008). Automatic time series forecasting: the forecast package for R. *Journal of Statistical Software*, *27*(1), 1-22.

Iarocci, G., & McDonald, J. (2006). Sensory integration and the perceptual experience of persons with autism. *Journal of Autism and Developmental Disorders*, *36*(1), 77-90.

Iuculano, T., Rosenberg-Lee, M., Supekar, K., Lynch, C. J., Khouzam, A., Phillips, J., Uddin, L. Q., & Menon, V. (2014). Brain organization underlying superior mathematical abilities in children with autism. *Biological Psychiatry*, *75*(3), 223–230.

Izard, V., Dehaene-Lambertz, G., & Dehaene, S. (2008). Distinct cerebral pathways for object identity and number in human infants. *PLoS Biology*, *6*(2), e11.

Izard, V., Sann, C., Spelke, E.S., & Streri, A. (2009). Newborn infants perceive abstract numbers. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 10382–10385.

Jakawich, S. K., Nasser, H. B., Strong, M. J., McCartney, A. J., Perez, A. S., Rakesh, N., ... & Sutton, M. A. (2010). Local presynaptic activity gates homeostatic changes in presynaptic function driven by dendritic BDNF synthesis. *Neuron*, *68*(6), 1143-1158.

Jarrold, C., & Russell, J. (1997). Counting abilities in autism: Possible implications for central coherence theory. *Journal of Autism and Developmental Disorders*, *27*(1), 25-37.

Jobs, E. N., Falck-Ytter, T., & Bölte, S. (2018). Local and global visual processing in 3-year-olds with and without autism. *Journal of Autism and Developmental Disorders*, *48*(6), 2249-2257.

Jochaut, D., Lehongre, K., Saitovitch, A., Devauchelle, A.-D., Olasagasti, I., Chabane, N., et al. (2015). Atypical coordination of cortical oscillations in response to speech in autism. *Frontiers in Human Neuroscience, 9*, 171.

Jolliffe, T., & Baron-Cohen, S. (1997). Are people with autism and Asperger syndrome faster than normal on the Embedded Figures Test? *Journal of Child Psychology and Psychiatry*, *38*(5), 527-534.

Jordan, N. C., Kaplan, D., Locuniak, M. N., & Ramineni, C. (2007). Predicting first-grade math achievement from developmental number sense trajectories. *Learning Disabilities Research & Practice*, *22*(1), 36-46.

Jordan, K. E., & Baker, J. (2011). Multisensory information boosts numerical matching abilities in young children. *Developmental Science*, *14*(2), 205-213.

Jordan, K. E., Baker, J., & Mitroff, S. R. (2008). The sensitive geek: Enhanced matching of numerosity in videogamers. Unpublished manuscript.

Jordan, N. C., Glutting, J., & Ramineni, C. (2010). The importance of number sense to mathematics achievement in first and third grades. *Learning and Individual Differences*, *20*(2), 82-88.

Jordan, N. C., Glutting, J., Ramineni, C., & Watkins, M. W. (2010). Validating a number sense screening tool for use in kindergarten and first grade: Prediction of mathematics proficiency in third grade. *School Psychology Review*, *39*(2), 181-195.

Jure, R. (2019). Autism pathogenesis: The superior colliculus. *Frontiers in Neuroscience*, *12*, 1029.

Just, M. A., Cherkassky, V. L., Keller, T. A., & Minshew, N. J. (2004). Cortical activation and synchronization during sentence comprehension in high-functioning autism: Evidence of underconnectivity. *Brain*, *127*(8), 1811-1821.

Kanitscheider, I., Brown, A., Pouget, A., & Churchland, A. K. (2015). Multisensory decisions provide support for probabilistic number representations. *Journal of Neurophysiology*, *113*(10), 3490-3498.

Karten, A., & Hirsch, J. (2015). Brief report: anomalous neural deactivations and functional connectivity during receptive language in autism spectrum disorder: A functional MRI study. *Journal of Autism and Developmental Disorders*, *45*(6), 1905-1914.

Kersey, A. J., & Cantlon, J. F. (2017). Neural tuning to numerosity relates to perceptual tuning in 3–6-year-old children. *Journal of Neuroscience*, *37*(3), 512-522.

Kim, H., & Cameron, C. E. (2016). Implications of visuospatial skills and executive functions for learning mathematics: Evidence from children with autism and Williams syndrome. *AERA Open*, *2*(4), 2332858416675124.

Kim, R. S., Seitz, A. R., & Shams, L. (2008). Benefits of stimulus congruency for multisensory facilitation of visual learning. *PLoS One*, *3*(1), e1532.

King, A. J. (2004). The superior colliculus. *Current Biology*, *14*(9), R335-R338.

King, S. A., Lemons, C. J., & Davidson, K. A. (2016). Math interventions for students with autism spectrum disorder: A best-evidence synthesis. *Exceptional Children*, *82*(4), 443-462.

Kleinhans, N. M., Richards, T., Sterling, L., Stegbauer, K. C., Mahurin, R., Johnson, L. C., Greenson, J., Dawson, G., & Aylward, E. (2008). Abnormal functional connectivity in autism spectrum disorders during face processing. *Brain*, *131*(4), 1000-1012.

Kleinhans, N. M., Richards, T., Johnson, L. C., Weaver, K. E., Greenson, J., Dawson, G., & Aylward, E. (2011). fMRI evidence of neural abnormalities in the subcortical face processing system in ASD. *Neuroimage*, *54*(1), 697-704.

Knops, A. (2017). Probing the neural correlates of number processing. *The Neuroscientist*, *23*(3), 264-274.

Koelewijn, T., Bronkhorst, A., & Theeuwes, J. (2010). Attention and the multiple stages of multisensory integration: A review of audiovisual studies. *Acta Psychologica*, *134*(3), 372-384.

Koppen, C., Levitan, C. A., & Spence, C. (2009). A signal detection study of the Colavita visual dominance effect. *Experimental Brain Research*, *196*(3), 353-360.

Krey, J. F., & Dolmetsch, R. E. (2007). Molecular mechanisms of autism: a possible role for Ca2+ signaling. *Current Opinion in Neurobiology*, *17*(1), 112-119.

Kuhn, M., & Johnson, K. (2013). *Applied predictive modeling* (Vol. 26). New York: Springer.

Kwan, K. Y. (2013). Transcriptional dysregulation of neocortical circuit assembly in ASD. *International Review of Neurobiology*, *113*, 167-205.

Landry, O., & Al-Taie, S. (2016). A meta-analysis of the Wisconsin Card Sort Task in autism. *Journal of Autism and Developmental Disorders*, *46*(4), 1220-1235.

Lechelt, E. C. (1975). Temporal numerosity discrimination: Intermodal comparisons revisited. *British Journal of Psychology*, *66*(1), 101-108.

Libertus, M. E., Feigenson, L., & Halberda, J. (2011). Preschool acuity of the approximate number system correlates with school math ability. *Developmental Science*, *14*(6), 1292-1300.

Ling, J., Burton, T. C., Salt, J. L., & Muncer, S. J. (2009). Psychometric analysis of the systemizing quotient (SQ) scale. *British Journal of Psychology*, *100*(3), 539-552.

Lynch, J. C., Graybiel, A. M., & Lobeck, L. J. (1985). The differential projection of two cytoarchitectonic subregions of the inferior parietal lobule of macaque upon the deep layers of the superior colliculus. *Journal of Comparative Neurology*, *235*(2), 241-254.

Mabb, A. M., Judson, M. C., Zylka, M. J., & Philpot, B. D. (2011). Angelman syndrome: insights into genomic imprinting and neurodevelopmental phenotypes. *Trends in Neurosciences*, *34*(6), 293-303.

Macmillan, N. A., & Creelman, C. D. (2004). *Detection theory: A user's guide*. Psychology Press.

Magnée, M. J., de Gelder, B., van Engeland, H., & Kemner, C. (2011). Multisensory integration and attention in autism spectrum disorder: Evidence from event-related potentials. *PLoS One*, *6*(8), e24196.

MATLAB. (2020). *version 9.8.0 (R2020a)*. Natick, Massachusetts: The MathWorks Inc.

May, P. J. (2006). The mammalian superior colliculus: Laminar structure and connections. *Progress in Brain Research*, *151*, 321-378.

Mazzocco, M. M., Feigenson, L., & Halberda, J. (2011). Preschoolers' precision of the approximate number system predicts later school mathematics performance. *PLoS One*, *6*(9), e23749.

McCrimmon, A. W., & Climie, E. A. (2011). Test Review: Wechsler Individual Achievement Test—Third Edition. San Antonio, TX: NCS Pearson, 2009. *Canadian Journal of School Psychology*, *26*(2), 148-156.

McCrimmon, A. W., & Smith, A. D. (2013). Review of the Wechsler Abbreviated Scale of Intelligence, (WASI-II). *Journal of Psychoeducational Assessment, 31*(3), 337-341.

McGrath, J. J., Hannan, A. J., & Gibson, G. (2011). Decanalization, brain development and risk of schizophrenia. *Translational Psychiatry*, *1*(6), e14-e14.

McNicol, D. (2005). *A primer of signal detection theory*. Psychology Press.

Meijer, G. T., Pie, J. L., Dolman, T. L., Pennartz, C., & Lansink, C. S. (2018). Audiovisual integration enhances stimulus detection performance in mice. *Frontiers in Behavioral Neuroscience*, *12*, 231.

Meredith, M. A., & Stein, B. E. (1986). Visual, auditory, and somatosensory convergence on cells in superior colliculus results in multisensory integration. *Journal of Neurophysiology*, *56*(3), 640-662.

Milne, E., Scope, A., Pascalis, O., Buckley, D., & Makeig, S. (2009). Independent component analysis reveals atypical electroencephalographic activity during visual perception in individuals with autism. *Biological Psychiatry*, *65*(1), 22-30.

Mitchell, P. & Ropar, D. (2004) Visuo-spatial abilities in autism: A review. *Infant and Child Development*, *13*, 185–198.

Molko, N., Cachia, A., Rivière, D., Mangin, J. F., Bruandet, M., Le Bihan, D., Cohen, L., & Dehaene, S. (2003). Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. *Neuron*, *40*(4), 847-858.

Mottron, L., Burack, J. A., Iarocci, G., Belleville, S., & Enns, J. T. (2003). Locally oriented perception with intact global processing among adolescents with high-functioning autism: Evidence from multiple paradigms. *Journal of Child Psychology and Psychiatry*, *44*(6), 904-913.

Muth, A., Hönekopp, J., & Falter, C. M. (2014). Visuo-spatial performance in autism: A meta-analysis. *Journal of Autism and Developmental Disorders*, *44*(12), 3245-3263.

Nelson, W. T., Hettinger, L. J., Cunningham, J. A., Brickman, B. J., Haas, M. W., & McKinley, R. L. (1998). Effects of localized auditory information on visual target

detection performance using a helmet-mounted display. *Human Factors*, *40*(3), 452-460.

Nelson, S. B., & Valakh, V. (2015). Excitatory/inhibitory balance and circuit homeostasis in autism spectrum disorders. *Neuron*, *87*(4), 684-698.

Nieder, A. (2016). The neuronal code for number. *Nature Reviews Neuroscience*, *17*(6), 366.

Nieder, A., & Merten, K. (2007). A labeled-line code for small and large numerosities in the monkey prefrontal cortex. *Journal of Neuroscience*, *27*(22), 5986-5993.

Nieder, A., & Miller, E. K. (2003). Coding of cognitive magnitude: Compressed scaling of numerical information in the primate prefrontal cortex. *Neuron*, *37*(1), 149-157.

Nieder, A., & Miller, E. K. (2004). A parieto-frontal network for visual numerical information in the monkey. *Proceedings of the National Academy of Sciences*, *101*(19), 7457-7462.

Nishimura, K., Nakamura, K., Anitha, A., Yamada, K., Tsujii, M., Iwayama, Y., Hattori, E., Toyota, T., Takei, N., Miyachi, T., Iwata, Y., Suzuki, K., Matsuzaki, H., Kawai, M., Sekine, Y., Tsuchiya, K., Sugihara, G., Suda, S., Ouchi, Y., Sugiyama, T., Yoshikawa, T., & Mori, N. (2007). Genetic analyses of the brain-derived neurotrophic factor (BDNF) gene in autism. *Biochemical and Biophysical Research Communications*, *356*(1), 200-206.

Noesselt, T., Bergmann, D., Hake, M., Heinze, H. J., & Fendrich, R. (2008). Sound increases the saliency of visual events. *Brain Research*, *1220*, 157-163.

O'Connor, K. (2012). Auditory processing in autism spectrum disorder: A review. *Neuroscience & Biobehavioral Reviews*, *36*(2), 836-854.

O'Hearn, K., Franconeri, S., Wright, C., Minshew, N., & Luna, B. (2013). The development of individuation in autism. *Journal of Experimental Psychology: Human Perception and Performance*, *39*(2), 494.

Ohshiro, T., Angelaki, D. E., & DeAngelis, G. C. (2011). A normalization model of multisensory integration. *Nature Neuroscience*, *14*(6), 775-782.

Ohshiro, T., Angelaki, D. E., & DeAngelis, G. C. (2017). A neural signature of divisive normalization at the level of multisensory integration in primate cortex. *Neuron*, *95*(2), 399-411.

Okuyama, S., Kuki, T., & Mushiake, H. (2015). Representation of the numerosity 'zero' in the parietal cortex of the monkey. *Scientific Reports*, *5*(1), 1-9.

Olsen, S. R., Bhandawat, V., & Wilson, R. I. (2010). Divisive normalization in olfactory population codes. *Neuron*, *66*(2), 287-299.

O'Riordan, M. A., Plaisted, K. C., Driver, J., & Baron-Cohen, S. (2001). Superior visual search in autism. *Journal of Experimental Psychology: Human Perception and Performance*, *27*(3), 719.

O'Riordan, M., & Plaisted, K. (2001). Enhanced discrimination in autism. *The Quarterly Journal of Experimental Psychology: Section A*, *54*(4), 961-979.

Oswald, T. M., Beck, J. S., Iosif, A. M., McCauley, J. B., Gilhooly, L. J., Matter, J. C., & Solomon, M. (2016). Clinical and cognitive characteristics associated with mathematics problem solving in adolescents with autism spectrum disorder. *Autism Research*, *9*(4), 480-490.

Ouimet, T., Foster, N. E., Tryfon, A., & Hyde, K. L. (2012). Auditory-musical processing in autism spectrum disorders: A review of behavioral and brain imaging studies. *Annals of the New York Academy of Sciences*, *1252*(1), 325-331.

Ozonoff, S. (1995). Reliability and validity of the Wisconsin card sorting test in studies of autism. *Neuropsychology*, *9*(4), 491.

Parraga, C. A. (2015). Perceptual psychophysics. *Biologically-inspired computer vision: Fundamentals and applications*, 81-108.

Paula-Barbosa, M. M., & Sousa-Pinto, A. (1973). Auditory cortical projections to the superior colliculus in the cat. *Brain Research*, *50*(1), 47-61.

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., & Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods*, *51*(1), 195-203.

Penner-Wilger, M., Fast, L., LaFevre, J. A., Smith-Chant, B. L., Skwarchuck, S. L., Kamawar, D., & Bisanz, J. (2007). The foundations of numeracy: Subitizing, finger gnosia, and fine motor ability. In *Proceedings of the Annual Meeting of the Cognitive Science Society*, *29*(29), 1385-1390.

Perrault Jr, T. J., Vaughan, J. W., Stein, B. E., & Wallace, M. T. (2005). Superior colliculus neurons use distinct operational modes in the integration of multisensory stimuli. *Journal of Neurophysiology*, *93*(5), 2575-2586.

Perrett, D. I., Hietanen, J. K., Oram, M. W., & Benson, P. J. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical transactions of the royal society of London. Series B: Biological Sciences*, *335*(1273), 23-30.

Philippi, T. G., van Erp, J. B., & Werkhoven, P. J. (2008). Multisensory temporal
    numerosity judgment. *Brain Research*, *1242*, 116-125.

Piazza, M., Izard, V., Pinel, P., Le Bihan, D., & Dehaene, S. (2004). Tuning curves for
    approximate numerosity in the human intraparietal sulcus. *Neuron*, *44*(3), 547-
    555.

Pica, P., Lemer, C., Izard, V., & Dehaene, S. (2004). Exact and approximate arithmetic in
    an Amazonian indigene group. *Science*, *306*(5695), 499-503.

Pinel, P., Dehaene, S., Riviere, D., & LeBihan, D. (2001). Modulation of parietal
    activation by semantic distance in a number comparison task. *Neuroimage*, *14*(5),
    1013-1026.

Pinheiro-Chagas, P., Daitch, A., Parvizi, J., & Dehaene, S. (2018). Brain mechanisms of
    arithmetic: A crucial role for ventral temporal cortex. *Journal of Cognitive
    Neuroscience*, *30*(12), 1757-1772.

Pizzarelli, R., & Cherubini, E. (2011). Alterations of GABAergic signaling in autism
    spectrum disorders. *Neural Plasticity*, *2011*.

Polster, M. R., & Rose, S. B. (1998). Disorders of auditory processing: Evidence for
    modularity in audition. *Cortex*, *34*(1), 47-65.

Populin, L. C. (2005). Anesthetics change the excitation/inhibition balance that governs
    sensory processing in the cat superior colliculus. *Journal of Neuroscience*, *25*(25),
    5903-5914.

Price, G. R., Holloway, I., Räsänen, P., Vesterinen, M., & Ansari, D. (2007). Impaired
    parietal magnitude processing in developmental dyscalculia. *Current
    Biology*, *17*(24), R1042-R1043.

Price, G. R., Palmer, D., Battista, C., & Ansari, D. (2012). Nonsymbolic numerical

  magnitude comparison: Reliability and validity of different task variants and

  outcome measures, and their relationship to arithmetic achievement in

  adults. *Acta Psychologica*, *140*(1), 50-57.

Raghubar, K. P., Barnes, M. A., & Hecht, S. A. (2010). Working memory and

  mathematics: A review of developmental, individual difference, and cognitive

  approaches. *Learning and Individual Differences*, *20*(2), 110-122.

Rathé, S., Torbeyns, J., De Smedt, B., & Verschaffel, L. (2019). Spontaneous focusing on

  Arabic number symbols and its association with early mathematical

  competencies. *Early Childhood Research Quarterly*, *48*, 111-121.

Raven, J. C. (2006). *Raven Standard Progressive Matrices: Handleiding*. [Raven

  Standard Progressive Matrices: Manual]. San Antonio, TX: Harcourt Assessment.

Razak, K. A., & Pallas, S. L. (2006). Dark rearing reveals the mechanism underlying

  stimulus size tuning of superior colliculus neurons. *Visual Neuroscience*, *23*(5),

  741-748.

Riesenhuber, M., & Poggio, T. (2000). Models of object recognition. *Nature

  Neuroscience*, *3*(11), 1199-1204.

Rosenberg, A., Patterson, J. S., & Angelaki, D. E. (2015). A computational perspective

  on autism. *Proceedings of the National Academy of Sciences*, *112*(30), 9158-

  9165.

Rubenstein, J. L. R., & Merzenich, M. M. (2003). Model of autism: Increased ratio of

  excitation/inhibition in key neural systems. *Genes, Brain and Behavior*, *2*(5), 255-

  267.

Rust, J. (1996). *Wechsler objective numerical dimensions*. The Psychological

    Corporation. London: Harcourt Brace.

Sabes, P. N. (2011). Sensory integration for reaching: models of optimality in the context

    of behavior and the underlying neural circuits. *Progress in Brain Research*, *191*,

    195-209.

Sagar, A., Bishop, J. R., Tessman, D. C., Guter, S., Martin, C. L., & Cook, E. H. (2013).

    Co-occurrence of autism, childhood psychosis, and intellectual disability

    associated with a de novo 3q29 microdeletion. *American Journal of Medical

    Genetics Part A*, *161*(4), 845-849.

Santens, S., Roggeman, C., Fias, W., & Verguts, T. (2010). Number processing pathways

    in human parietal cortex. *Cerebral Cortex*, *20*(1), 77-88.

Sasanguie, D., Göbel, S. M., Moll, K., Smets, K., & Reynvoet, B. (2013). Approximate

    number sense, symbolic number processing, or number–space mappings: What

    underlies mathematics achievement? *Journal of Experimental Child

    Psychology*, *114*(3), 418-431.

Sato, T. K., Haider, B., Häusser, M., & Carandini, M. (2016). An excitatory basis for

    divisive normalization in visual cortex. *Nature Neuroscience*, *19*(4), 568-570.

Sato, W., Toichi, M., Uono, S., & Kochiyama, T. (2012). Impaired social brain network

    for processing dynamic facial expressions in autism spectrum disorders. *BMC

    Neuroscience*, *13*(1), 1-17.

Scalise, N. R., & Ramani, G. B. (2021). Symbolic Magnitude Understanding Predicts

    Preschoolers' Later Addition Skills. *Journal of Cognition and

    Development*, *22*(2), 185-202.

Schultz, R. T., Gauthier, I., Klin, A., Fulbright, R. K., Anderson, A. W., Volkmar, F., ...
& Gore, J. C. (2000). Abnormal ventral temporal cortical activity during face
discrimination among individuals with autism and Asperger syndrome. *Archives
of General Psychiatry*, *57*(4), 331-340.

Shah, A., & Frith, U. (1993). Why do autistic individuals show superior performance on
the block design task? *Journal of Child Psychology and Psychiatry*, *34*(8), 1351-
1364.

Shumway, J. F. (2011). *Number sense routines: Building numerical literacy every day in
grades K-3*. Stenhouse Publishers.

Siemann, J. K., Muller, C. L., Forsberg, C. G., Blakely, R. D., Veenstra-VanderWeele, J.,
& Wallace, M. T. (2017). An autism-associated serotonin transporter variant
disrupts multisensory processing. *Translational Psychiatry*, *7*(3), e1067-e1067.

Silverman, J. L., Pride, M. C., Hayes, J. E., Puhger, K. R., Butler-Struben, H. M., Baker,
S., & Crawley, J. N. (2015). GABA B receptor agonist R-baclofen reverses social
deficits and reduces repetitive behavior in two mouse models of autism.
Neuropsychopharmacology, *40*(9), 2228-2239.

Simon, D. M., & Wallace, M. T. (2016). Dysfunction of sensory oscillations in autism
spectrum disorder. *Neuroscience & Biobehavioral Reviews*, *68*, 848-861.

Spencer, J., O'Brien, J., Riggs, K., Braddick, O., Atkinson, J., & Wattam-Bell, J. (2000).
Motion processing in autism: Evidence for a dorsal stream
deficiency. *Neuroreport*, *11*(12), 2765-2767.

Stanislaw, H., & Todorov, N. (1999). Calculation of signal detection theory measures. *Behavior Research Methods, Instruments, & Computers*, *31*(1), 137-149.

Stefanou, M. E., Dundon, N. M., Bestelmeyer, P. E., Ioannou, C., Bender, S., Biscaldi, M., ... & Klein, C. (2020). Late attentional processes potentially compensate for early perceptual multisensory integration deficits in children with autism: Evidence from evoked potentials. *Scientific Reports*, *10*(1), 1-13.

St. John, T. S., Dawson, G., & Estes, A. (2018). Brief report: Executive function as a predictor of academic achievement in school-aged children with ASD. *Journal of Autism and Developmental Disorders*, *48*(1), 276-283.

Starkey, P., Spelke, E. S., & Gelman, R. (1990). Numerical abstraction by human infants. *Cognition*, *36*(2), 97-127.

Starr, A., Libertus, M. E., & Brannon, E. M. (2013). Number sense in infancy predicts mathematical abilities in childhood. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(45), 18116–18120.

Stein, B. E., & Meredith, M. A. (1993). *The merging of the senses*. The MIT Press.

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, *9*(4), 255-266.

Stein, B. E., & Rowland, B. A. (2011). Organization and plasticity in multisensory integration: early and late experience affects its governing principles. *Progress in Brain Research*, *191*, 145-163.

Stein, B. E., Stanford, T. R., & Rowland, B. A. (2014). Development of multisensory integration from the perspective of the individual neuron. *Nature Reviews Neuroscience*, *15*(8), 520-535.

Stein, B. E., & Rowland, B. A. (2020). Using superior colliculus principles of multisensory integration to reverse hemianopia. *Neuropsychologia*, *141*, 107413.

Stein, B. E., Stanford, T. R., & Rowland, B. A. (2020). Multisensory integration and the society for neuroscience: then and now. *Journal of Neuroscience*, *40*(1), 3-11.

Stevenson, R. A., Baum, S. H., Segers, M., Ferber, S., Barense, M. D., & Wallace, M. T. (2017). Multisensory speech perception in autism spectrum disorder: From phoneme to whole-word perception. *Autism Research*, *10*(7), 1280-1290.

Stevenson, R. A., Segers, M., Ncube, B. L., Black, K. R., Bebko, J. M., Ferber, S., & Barense, M. D. (2018). The cascading influence of multisensory processing on speech perception in autism. *Autism*, *22*(5), 609-624.

Stevenson, R. A., Bushmakin, M., Kim, S., Wallace, M. T., Puce, A., & James, T. W. (2012). Inverse effectiveness and multisensory interactions in visual event-related potentials with audiovisual speech. *Brain Topography*, *25*(3), 308-326.

Stevenson, R. A., Siemann, J. K., Woynaroski, T. G., Schneider, B. C., Eberly, H. E., Camarata, S. M., & Wallace, M. T. (2014). Evidence for diminished multisensory integration in autism spectrum disorders. *Journal of Autism and Developmental Disorders*, *44*(12), 3161-3167.

Stewart, M. E., Watson, J., Allcock, A. J., & Yaqoob, T. (2009). Autistic traits predict performance on the block design. *Autism*, *13*(2), 133-142.

Strauss, E., Sherman, E. M., & Spreen, O. (2006). *A compendium of neuropsychological tests: Administration, norms, and commentary*. American Chemical Society.

Stroganova, T. A., Orekhova, E. V., Prokofyev, A. O., Tsetlin, M. M., Gratchev, V. V., Morozov, A. A., & Obukhov, Y. V. (2012). High-frequency oscillatory response to illusory contour in typically developing boys and boys with autism spectrum disorders. *Cortex*, *48*(6), 701-717.

Sun, L., Grützner, C., Bölte, S., Wibral, M., Tozman, T., Schlitt, S., ... & Uhlhaas, P. J. (2012). Impaired gamma-band activity during perceptual organization in adults with autism spectrum disorders: evidence for dysfunctional network activity in frontal-posterior cortices. *Journal of Neuroscience*, *32*(28), 9563-9573.

Szucs, D., Devine, A., Soltesz, F., Nobes, A., & Gabriel, F. (2013). Developmental dyscalculia is related to visuo-spatial memory and inhibition impairment. *Cortex*, *49*(10), 2674-2688.

Takarae, Y., Luna, B., Minshew, N. J., & Sweeney, J. A. (2014). Visual motion processing and visual sensorimotor control in autism. *Journal of the International Neuropsychological Society*, *20*(1), 113-122.

Trick, L. M., & Pylyshyn, Z. W. (1994). Why are small and large numbers enumerated differently? A limited-capacity preattentive stage in vision. *Psychological Review*, *101*(1), 80.

Van de Cruys, S., Evers, K., Van der Hallen, R., Van Eylen, L., Boets, B., de-Wit, L., & Wagemans, J. (2014). Precise minds in uncertain worlds: Predictive coding in autism. *Psychological Review*, *121*(4), 649.

Van der Burg, E., Olivers, C. N., Bronkhorst, A. W., & Theeuwes, J. (2008). Pip and pop: Nonspatial auditory signals improve spatial visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *34*(5), 1053.

Van der Elst, W., Ouwehand, C., Van Rijn, P., Lee, N., Van Boxtel, M., & Jolles, J. (2013). The shortened raven standard progressive matrices: item response theory–based psychometric analyses and normative data. *Assessment*, *20*(1), 48-59.

Van der Hallen, R., Manning, C., Evers, K., & Wagemans, J. (2019). Global motion perception in autism spectrum disorder: a meta-analysis. *Journal of Autism and Developmental Disorders*, *49*(12), 4901-4918.

Van Elst, L. T., Pick, M., Biscaldi, M., Fangmeier, T., & Riedel, A. (2013). High-functioning autism spectrum disorder as a basic disorder in adult psychiatry and psychotherapy: Psychopathological presentation, clinical relevance and therapeutic concepts. *European Archives of Psychiatry and Clinical Neuroscience*, *263*(2), 189-196.

Van Opstal, J. (2016). *The auditory system and human sound-localization behavior*. Academic Press.

Von Aster, M. (2000). Developmental cognitive neuropsychology of number processing and calculation: varieties of developmental dyscalculia. *European Child & Adolescent Psychiatry*, *9*(2), S41-S57.

Von Kriegstein, K., & Giraud, A. L. (2006). Implicit multisensory associations influence voice recognition. *PLoS Biology*, *4*(10), e326.

Vroomen, J., & Gelder, B. D. (2000). Sound enhances visual perception: Cross-modal effects of auditory organization on vision. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(5), 1583.

Wagener, L., Loconsole, M., Ditz, H. M., & Nieder, A. (2018). Neurons in the endbrain of numerically naive crows spontaneously encode visual numerosity, *Current Biology*, *28*, 1-5.

Wallace, M. T., & Stein, B. E. (1997). Development of multisensory neurons and multisensory integration in cat superior colliculus. *Journal of Neuroscience*, *17*(7), 2429-2444.

Wang, K., Zhang, H., Ma, D., Bucan, M., Glessner, J. T., Abrahams, B. S., ... & Hakonarson, H. (2009). Common genetic variants on 5p14.1 associate with autism spectrum disorders. *Nature*, *459*(7246), 528-533.

Wang, J. J., Odic, D., Halberda, J., & Feigenson, L. (2016). Changing the precision of preschoolers' approximate number system representations changes their symbolic math performance. *Journal of Experimental Child Psychology*, *147*, 82-99.

Watson, A. B., & Pelli, D. G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113-120.

Wechsler, D. (1999). *Wechsler abbreviated scale of intelligence — Second edition*. New York, NY: The Psychological Corporation.

Wechsler, D. (2001). *Wechsler individual achievement test — Second edition*. San Antonio, TX: The Psychological Corporation.

Wechsler, D. (2009). *Wechsler individual achievement test — Third edition*. San Antonio, TX: The Psychological Corporation.

Wei, X., Jennifer, W. Y., Shattuck, P., McCracken, M., & Blackorby, J. (2013). Science, technology, engineering, and mathematics (STEM) participation among college students with an autism spectrum disorder. *Journal of Autism and Developmental Disorders*, *43*(7), 1539-1546.

Wei, X., Christiano, E. R., Yu, J. W., Wagner, M., & Spiker, D. (2015). Reading and math achievement profiles and longitudinal growth trajectories of children with an autism spectrum disorder. *Autism*, *19*(2), 200-210.

Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, *114*(1), 152.

Wright, D. B., & Skagerberg, E. M. (2012). Measuring empathizing and systemizing with a large US sample. *PloS One*, *7*(2), e31661.

Xu, G., Strathearn, L., Liu, B., & Bao, W. (2018). Prevalence of autism spectrum disorder among US children and adolescents, 2014-2016. *Journal of the American Medical Association*, *319*(1), 81-82.

Xu, X., Wells, A. B., O'Brien, D. R., Nehorai, A., & Dougherty, J. D. (2014). Cell type-specific expression analysis to identify putative cellular mechanisms for neurogenetic disorders. *Journal of Neuroscience*, *34*(4), 1420-1431.

Yang, X., Hou, D., Jiang, W., and Zhang, C. (2014). Intercellular protein-protein interactions at synapses. *Protein Cell*, *5*, 420–444.

Yu, L., Xu, J., Rowland, B. A., & Stein, B. E. (2016). Multisensory plasticity in superior colliculus neurons is mediated by association cortex. *Cerebral Cortex*, *26*(3), 1130-1137.

CURRICULUM VITAE
Benjamin Covington

EDUCATION

2021	Ph.D. in Neuroscience, Utah State University *Summa cum laude*
2014	Master of Divinity, Abilene Christian University *Summa cum laude*
2009	Bachelor of Arts, Biblical Text, Abilene Christian University *Magna cum laude*

PROFESSIONAL EXPERIENCE

GRADUATE INSTRUCTOR/TEACHING ASSISTANT, Utah State University (2017 – Present).
Develop and instruct undergraduate psychological statistics. Guest lecture for psychology and experimental design courses as needed. Oversee teaching assistants and student tutors when applicable. Maintain regular communication with students. Adjusted courses for altered delivery methods in a rapidly changing environment.

OPERATIONS AND POLICY ANALYST II, Oregon Department of Revenue (2015 – 2016).
Manage, query, and analyze taxpayer data to improve operational efficiency of the Processing Center. Write transparent code for automated analyses and reporting. Work with team leaders and managers to identify irregularities in the taxpayer data pipeline. Translate and interpret results for diverse stakeholders. Author protocols for data management and reporting.

OFFICE SPECIALIST II, Oregon Department of Revenue (2015).
Enter, clean, and query data to address inconsistencies in taxpayer returns. Review intersectional account data to determine correct liability applications with limited information.

GRADUATE ASSISTANT, Abilene Christian University (2010 – 2013).
Guest lecture as necessary. Review and grade coursework. Design recruitment materials.

INSTRUCTOR/TUTOR, The Princeton Review (2007 – 2013).
Teach courses and tutor individual students. Analyze student performance data and submit action plan recommendations.

PEER ADVISOR, Abilene Christian University (2010 – 2011).
Advise at-risk, probationary students. Evaluate and report student performance data. Maintain case notes for supervisor review. Work with students to create academic action plans.

PUBLICATIONS

Niccum, C., Brown, J., Covington, B., Gentry, E., Lollar, J., & White, J. (2009). Objects of worship: Wallace's case for proskynein. *Restoration quarterly*, *51*(2), 115-119.

Goldstein, A., Covington, B., Mahabadi, N., & Mesfin, F. (2017). Neuroanatomy, Corpus Callosum. In D. Peterson and C. Prewitt (Eds.) *StatPearls*. St. Petersburg, FL: StatPearls Publishing, LLC.

Moyer-Packenham, P. S., Lommatsch, C. W., Litster, K., Ashby, J., Bullock, E. K., Roxburgh, A. L., Shumway, J. F., Speed, E., Covington, B., Hartmann, C., Clarke-Midura, J., Skaria, J., Westenskow, A., MacDonald, B., Symanzik, J., & Jordan, K. (2019). How design features in digital math games support learning and mathematics connections. *Computers in Human Behavior*, *91*, 316-332.

Grider, M. H., Belcea, C. Q., Covington, B., & Sharma, S. (2019). Neuroanatomy, Nodes of Ranvier. In *StatPearls [Internet]*. StatPearls Publishing.

Covington, B., & Al Khalili, Y. (2020). Neuroanatomy, Nucleus Lateral Geniculate. In D. Peterson and C. Prewitt (Eds.) *StatPearls*. St. Petersburg, FL: StatPearls Publishing, LLC.

Bundock, K., Simonsmeier, V., Golson, M. E., Covington, B., & McClain, M. B. (2020). Promoting Academic Success. In *Interprofessional Care Coordination for Pediatric Autism Spectrum Disorder* (pp. 117-135). Springer, Cham.

Ha, J., McClain, M. B., Covington, B., & Golson, M. (2021) Brief report: A brief video intervention for increasing autism knowledge in a general population sample. *Journal of Autism and Developmental Disorders*. https://doi.org/10.1007/s10803-021-05341-w.