

Sensory processing in autism across exteroceptive and interoceptive domains

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Abstract

Autism is a neurodevelopmental condition currently defined and diagnosed by the presence of lifelong difficulties in the domains of social interaction, social communication and social imagination, as well as restricted or stereotyped interests or behaviors. While early conceptualizations of autism incorporated sensory differences, they have been relatively neglected in proceeding years.

Recognition of sensory differences in formal diagnostic criteria is now starting to be reintroduced. To date, sensory research suggests that both external and internal signal perception diverges in autistic individuals, but has been largely segregated between interoceptive and exteroceptive domains, impeding the construction of a general framework for understanding how perceptual experiences may differ for autistic individuals. We review recent findings detailing exteroceptive and interoceptive processing in autism and discuss their neurobiological basis. Based on this synthesis, we suggest that future work should be sensitive to individual differences to determine if divergent patterns of sensory processing are observed within individuals, rather than looking for global changes at a group level. Determining whether divergent patterns of exteroceptive and interoceptive sensory processing may contribute to prototypical social and cognitive characteristics of autism may drive new directions in our conceptualization of autism.

Keywords: Autism, sensory processing, exteroception, interoception, Bayesian modelling

Public Significance Statement

Autism is traditionally characterized by the presence of cognitive and social difficulties and differences. However, recent research lends support to early observations and autistic anecdotal accounts that sensory perception may also be atypical. Here, we review findings showing that autistic individuals perceive both the environment and their bodies differently. We argue that this divergent perception may account for many of the difficulties and differences experienced by autistic individuals, but also form part of their unique strengths.

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Autism Spectrum Disorder (henceforth, 'autism') is a complex neurodevelopmental condition, clinically defined and diagnosed by the presence of lifelong difficulties with social interaction and communication as well as restricted and repetitive behaviors (DSM-5; American Psychiatric Association, 2013). Autism is now also commonly conceptualized as a form of neurodivergence i.e. 'a specific neurological state' (Beardon, 2017: 13) or 'disposition' (Milton, 2014) that is 'different, not less' (Fletcher-Watson & Happé, 2019: 23). In this paper we review a wide range of studies, many of which have been reported on in terms belonging to the former perspective (e.g. 'deficits', 'impairments', 'disorder'. etc.). We have made an effort to strike the balance between accurate reporting on findings and the use of non-pathologizing language.

In recent years, research interest has turned towards the sensorimotor and perceptual differences associated with autism (Robertson & Baron-Cohen, 2017), and the ways in which these differences may have cascading effects on higher order behavioral, communicative, and social skills. Sensory processing may be divided into two primary types; exteroception responds to external cues, while interoception is the sensing of signals originating from within the body. Although there is a growing body of research indicating that for autistic individuals, aspects of both interoceptive and exteroceptive processing may be atypical, these two research fields have rarely been combined.

The atypical sensory perception of autistic individuals was included in the earliest conceptualizations of the condition (Kanner, 1943). Throughout the rest of the 20th century, theories exploring how sensory perception might give rise to differences in behavior and sense of self in autistic individuals (Bergman & Escalona, 1947; Eveloff, 1960; Hermelin & O'Connor, 1970) were put forth, but a focus on the social difficulties associated with autism dominated. The formal inclusion of sensory-perceptual differences as part of an autism diagnosis occurred only in 2013, when the fifth edition of the [Diagnostic and Statistical Manual of Mental Disorders](#) (DSM-5; [American Psychiatric Association, 2013](#)) incorporated "hyper-or-hypo-reactivity to sensory input or unusual interests in sensory aspects of the environment" as a type of restricted and repetitive behavior.

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Interoception is defined as the “process by which the nervous system senses, interprets, and integrates signals originating from within the body, providing a moment-by-moment mapping of the body’s internal landscape across conscious and unconscious levels” (Khalsa et al., 2018). Two main interoceptive pathways relaying visceral signals from afferent fibers in the body to the brain have been identified. Motivational signals (e.g. hunger and satiety) originate from different types of visceroreceptors, such as chemoreceptors or baroreceptors and travel mostly along cranial nerves (e.g. the vagus nerve) to the nucleus of the solitary tract (Critchley & Harrison, 2013). Visceral signals related to tissue damage, originating from thermoreceptors and nociceptors (e.g., C-fibers; Craig, 2003), enter the spinal cord via lamina 1 neurons and are further projected along the spinothalamic tract. Signals from both pathways are further relayed to the thalamus, amygdala, hypothalamus, anterior cingulate cortex, and insula (Critchley et al., 2004). Posterior insula (PI) has been identified as the primary interoceptive cortex representing the objective physiological state of the body, while anterior insula (AI) is thought to contain a subjective meta-representation of interoceptive signals (Craig et al., 2000). Interoception is not a unitary construct. Various taxonomies have been proposed that delineate interoception across neural, behavioral, subjective and metacognitive domains (Critchley & Garfinkel, 2017; Garfinkel et al., 2015; Khalsa et al., 2018; Quadt et al., 2018). Measures to date largely center around a) *interoceptive accuracy*, measured by objective behavioral tests, b) subjective report of interoceptive signals, also termed *interoceptive sensibility*, typically measured by questionnaires, and c) *interoceptive awareness* (also termed *interoceptive insight*), the metacognitive ability to judge one’s interoceptive accuracy, typically measured by confidence-accuracy correspondence. Over recent years, several groups have investigated if interoception differs along these three dimensions between autistic and non-autistic individuals, though research to date has largely focused on the cardiac axis.

There are a number of theories offering perspectives on autistic perception (Brock et al., 2002; Casey et al., 1993; Frith & Happé, 1994; Mottron et al., 2001). These theories tend to focus on specific neural or psychological mechanisms and can be restricted in their capacity to account for a range of

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empirical findings. An early account of divergent perception in autism is the weak central coherence theory (Frith & Happé, 1994), stating that autism is marked by increased focus on local stimuli and decreased integration of stimuli into their global context (Happé, 1996). Other researchers have proposed that autism is characterized by ‘temporal binding deficits’ arising out of weak neural synchronization (Brock et al., 2002), or by general perceptual enhancement (Mottron, Burack, Dawson, Soulières, & Hubert, 2001). A monotropic account of autism (Murray, 2018; Murray et al., 2005) proposes that attention allocation is atypical in autism, focusing more intensely and more narrowly on just a few interests at a time, making parsing of multiple information streams much more cognitively demanding.

In the last decade, several accounts have emerged that attempt to describe sensory processing differences associated with autism from a Bayesian, or predictive processing perspective (e.g. Brock, 2012; Cruys et al., 2014; Friston et al., 2013; Karvelis et al., 2018; Lawson et al., 2014, 2017; Palmer et al., 2017; Pellicano & Burr, 2012; van Boxtel & Lu, 2013). These generally argue that in autism, bottom-up signals in both the exteroceptive (Pellicano & Burr, 2012) and interoceptive domain (Quattrocki & Friston, 2014) are given more weight in the perceptual process than top-down prior models about these signals. This may then lead to attentional biases in favor of sensory signals, potentially causing atypical perception and behavior.

In one of the initial Bayesian accounts of autism, Pellicano and Burr (2012) hypothesized that top-down expectations about incoming sensory stimuli are attenuated in autism, leading to ‘hypo-priors’, and, consequently, a greater reliance on real-time, bottom-up sensory input. A greater weighting of sensory signals in Bayesian perceptual inference might either increase or decrease the accuracy of perception depending on the context: When the current sensory input is reliable or prior expectations are not well-informed it can increase accuracy, but in noisy environments it is likely to decrease accuracy. Further elaborations converged on the idea that while priors might be intact in autism, their function to attenuate bottom-up error signals is reduced. These error signals are then weighted as highly precise and can therefore travel back up the hierarchy and influence prior models,

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exaggerating their effect on future predictions of incoming sensory signals (Cruys et al., 2014; Friston et al., 2013; Lawson et al., 2014, 2017; Palmer et al., 2017; Quattrocki & Friston, 2014).

The goal of this review is twofold. Firstly, we provide a broad review of studies investigating both exteroceptive and interoceptive sensory differences observed in autism. We aim to uncover shared or interacting mechanisms, and to summarize how existing theories attempt to account for autistic information processing across perceptual domains. If autism is characterized by a general difference in how the brain receives or processes incoming information, this might affect neural processing of stimuli from different sensory domains in similar ways. Secondly, we investigate the extent to which the divergent exteroceptive and interoceptive perceptual abilities of autistic people may jointly account for what are currently understood to be the prototypical social and cognitive characteristics of autism. Thirdly, we outline a unified framework in which we summarize the links between biological and behavioral findings, computational mechanisms and diagnostic features of autism that are discussed throughout this review. We end with a recommendation for future research to embrace the diversity and heterogeneity of the autistic population by building an understanding of sensory profiles in individuals rather than trying to frame autistic sensory experiences in absolute terms.

Literature selection

The studies considered in this review fulfill the following eligibility criteria. Studies are original articles published between 2000 and 2020 in a peer-reviewed journal written in English. Studies assess visual, auditory, tactile, multisensory or interoceptive processing using perceptual tasks, neural measures or self-report. Experimental outcomes are compared between a sample of participants diagnosed with autism, applying standardized diagnostic methods (DSM, ICD, ADI or ADOS) and non-autistic control participants. Samples must contain at least 10 participants that are matched for chronological age. Studies applying perceptual tasks must match both samples for cognitive abilities, while this requirement is not applied to studies using subjective questionnaires. Finally, in order to draw conclusions about sensory processes in autism that are not confounded by social processing

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differences, this review does not include studies involving social stimuli (e.g. faces). One exception are audio-visual speech stimuli, as these constitute a primary area of research into multisensory binding in autism. However, we only review studies focusing on phonetic and non-semantic aspects of speech processing. Moreover, we included meta-analyses of perceptual tasks in autism, even if they did not adhere to the eligibility criteria we applied for original studies.

The literature on exteroceptive processing in autism is extensive and contains numerous inconsistencies. Therefore, we focus on either replicated results or novel methods. Conversely, literature on interoceptive processing in autism is, at present, relatively scarce. As such, we have also included studies relating measures of interoception with autistic traits in non-autistic individuals. Some authors argue that differences in interoception observed in autism are not linked to autistic traits per se, but rather to alexithymia (Shah et al., 2016), which can be defined as a difficulty to describe or identify one's emotions. While alexithymia is not included in the diagnostic criteria for autism, it has an estimated 50% co-occurrence rate among autistic people, compared to just 10% in the general population (Berthoz & Hill, 2005; Hill et al., 2004). Therefore, we additionally included studies relating measures of interoception to alexithymia.

Exteroceptive processing

Visual processing

Basic visual discrimination

In the visual domain, a compelling number of studies measuring visual acuity (Bölte et al., 2012; Kéïta et al., 2010; Tavassoli et al., 2016), orientation (Freyberg et al., 2016; Grubb et al., 2013; Koh et al., 2010; but see Bertone et al., 2005; Dickinson et al., 2016;), motion direction (Manning et al., 2015), and flicker discrimination of simple stimuli (Bertone et al., 2005; Pellicano et al., 2005) indicate that basic visual discrimination abilities of autistic individuals are mostly indistinguishable from those of control participants. While conflicting with the perceptual enhancement hypothesis (Mottron et al., 2001), assuming that such visual discrimination abilities are elevated in autism, these

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findings suggest that differences observed in more complex visual tasks, which will be reviewed in the following, are indeed not driven by differences in low-level stimulus perception.

Visual search

A widely replicated finding related to visual processing in autism is superior performance in visual search tasks requiring participants to determine if a target stimulus is present in a cluttered field of distractors. Autistic participants respond quicker than controls in conjunctive search, where two features need to be integrated to find the target (O’Riordan, 2004; O’Riordan et al., 2001; O’Riordan & Plaisted, 2001; Shiraama et al., 2017), as well as in difficult disjunctive search, where the target is defined by a unique feature (Hessels et al., 2014; Joseph et al., 2009; O’Riordan, 2004; O’Riordan et al., 2001; Shiraama et al., 2017). Moreover, the autism advantage is stronger when the target is absent (Hessels et al., 2014; Joseph et al., 2009; Keehn & Joseph, 2016; O’Riordan, 2004; O’Riordan et al., 2001; O’Riordan & Plaisted, 2001; Shiraama et al., 2017), and at large set sizes (Hessels et al., 2014; O’Riordan, 2004; O’Riordan et al., 2001; Shiraama et al., 2017). This advantage in visual search remains when applying backwards masking (Shiraama et al., 2017), or dynamical search (Joseph et al., 2009), both of which disrupt top-down serial search strategies.

Even though superior visual search in autism has been widely replicated, some studies report no difference between samples (Constable, 2010; Edmondson et al., 2020; Grubb et al., 2013; Iarocci & Armstrong, 2014; Keehn et al., 2013; Lindor et al., 2018). As visual search requires fine control of saccades, discrepancies between findings might be influenced by differences in motor abilities (Lindor et al., 2018), as many autistic individuals show atypical motor responses (Donnellan et al., 2013; Fournier et al., 2010; D. Green et al., 2009).

In sum, there appears to be evidence for superior visual search abilities in autism, particularly in difficult search conditions. However, it is worth noting that while these effects have been replicated across numerous studies, they have not been universally obtained. This is consistent with a recent meta-analysis that found evidence for a low to moderate autism advantage in visual search across 15 studies (Constable et al., 2020), and more pronounced for conjunctive search.

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Parallel processing

According to perceptual load theory (Lavie, 1995), the amount of information presented to an individual determines to what degree distracting information will be processed. With low perceptual load, distractors interfere with task performance, while this interference disappears with high perceptual load. Autistic participants require a higher perceptual load to ignore distracting visual information (Remington et al., 2009, 2012), which indicates higher perceptual capacity. Drawing on these findings, it has been argued that the autism advantage in visual search might be accounted for by increased parallel processing, and consequently decreased automatic filtering of stimuli. Speculatively, this might also explain why the autism advantage in visual search prevails when the target is absent and at large set sizes, as in these cases, many stimuli are processed simultaneously.

Local-global processing

It has been widely claimed that the visual processing style of autistic participants is locally, rather than globally, focused (Happé, 1999; Happé & Frith, 2006; Mottron et al., 2003). A common method to probe local-global perception is the figure disembedding task (Witkin, 1971), which requires participants to respond to local aspects of a stimulus, while ignoring its global features.

In two meta-analyses on disembedding tasks, one found no difference between autistic and control participants (Van Der Hallen et al., 2015), while the other demonstrated a small superiority of autistic participants (Muth et al., 2014), where neither age nor IQ accounted for inconsistencies between studies. Higher accuracy among the autistic cohort has recently been observed in a more rigorous version of the figure disembedding task (Van der Hallen et al., 2018), supporting a local processing style where autistic individuals pay attention to local, rather than global aspects of complex stimuli (Nayar et al., 2017; Wang et al., 2015).

Addressing the notion that autistic individuals have difficulties with global processing, a number of studies investigated global motion coherence perception, where participants need to report the overall direction of motion of a randomly moving cloud of dots. A recent meta-analysis investigating 20 motion coherence studies found a small group difference, indicating that non-

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autistic participants are more accurate, faster, and require less information compared to autistic participants (Van der Hallen et al., 2019). Two studies (Robertson et al., 2012, 2014) found that differences in global motion perception might depend on stimulus duration, where a non-autistic advantage is only present at very short stimulus durations. Together, these results suggest that autistic participants tend to focus on local aspects of stimuli, and in line with weak central coherence theory (Happé & Frith, 2006), may have difficulties integrating local stimuli in the global context.

Binocular rivalry

In binocular rivalry paradigms, two distinct visual stimuli are presented simultaneously to each of the participant's eyes, and perception switches between both percepts. Notably, switch rates are diminished in autistic adults (Freyberg et al., 2015; Robertson et al., 2013; Spiegel et al., 2019), and show longer durations of mixed percepts, during which both stimuli are perceived simultaneously (Freyberg et al., 2015; Robertson et al., 2013). However, another study found no difference in mixed percept durations (Said et al., 2013). Inconsistencies between studies might be explained by differences in stimulus complexity, as complex stimuli evoke stronger lateral inhibition (Alais & Melcher, 2007). Differences in binocular rivalry have not been replicated in autistic children (Karaminis et al., 2017), possibly indicating a developmental effect.

These findings potentially speak to reduced lateral inhibition between neuronal populations encoding competing, complex stimuli during binocular rivalry (Tong et al., 2006) in autistic adults.

Oscillatory differences

Atypical oscillatory responses to visual stimuli in the gamma frequency band (30-120 Hz) have been observed in autism. Evoked oscillations in the gamma range in response to complex or illusory stimuli are decreased (Buard et al., 2013; Stroganova et al., 2012), compared to typical gamma band responses to simple visual stimuli (Milne et al., 2009; Stroganova et al., 2012). Conversely, gamma power is elevated in autism during sustained visual attention (Orekhova et al., 2007).

When presented with periodic visual stimuli, neural ensembles can synchronize their activity with the frequency of the stimulus, as well as with multiples of the stimulus frequency, a process

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known as neural entrainment (Lazarev et al., 2001). Autistic participants show reduced neural entrainment at the stimulation frequency (Snijders et al., 2013), as well as at multiples of the stimulation frequency (Lazarev et al., 2009). Next to these local effects within brain regions, synchronization of oscillations between brain regions also appears to be atypical. Specifically, beta-range interhemispheric synchronization in sensory cortices (Lazarev et al., 2013; Peiker et al., 2015), and alpha-range feedback connectivity from V4 to V1 is decreased for autistic individuals when presented with visual stimuli (Seymour et al., 2019). The latter effect has been reported in conjunction with reduced cross-frequency coupling between alpha and gamma oscillations in V1.

This evidence suggests that the synchronization of neural oscillations within and between brain regions in response to visual stimuli is less strong in autistic individuals.

Visual predictions

Autistic individuals appear to rely to a lesser extent on prior knowledge in tasks related to depth perception, resulting in more veridical perception of stimuli (Bedford et al., 2016; Mitchell et al., 2010; Ropar & Mitchell, 2002). Moreover, in a cued visual association task, autistic participants gazed longer at the correct location when the incorrect location was predicted by the cue (Greene et al., 2019). These findings indicate a possible decreased reliance on top-down predictions during visual perception in autism.

Auditory processing

Auditory mismatch negativity

Auditory deviance processing in autism has been frequently investigated by examining mismatch negativity (MMN) in auditory oddball paradigms. Results are highly heterogeneous, and MMN amplitude differences seem to strongly depend on stimulus features (speech sounds or non-speech sounds), as well as deviance type (frequency, duration, or phoneme category). A recent meta-analysis of 28 studies reports that autistic participants show reduced MMN amplitudes in response to speech-sound phoneme deviants, as well to non-speech duration deviants, but not to other stimuli (Chen et al., 2020). An earlier meta-analysis reports no main effect of group on MMN amplitude, and

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emphasizes the importance of counterbalancing features of standard and deviant stimuli (Schwartz et al., 2018). Out of 22 reviewed studies, only six were counterbalanced. Among those, MMN amplitudes are decreased in autistic participants for non-speech, but not for speech-sounds. In both meta-analyses, age differences contribute to the heterogeneity of results, with MMN differences being more pronounced in children, and less in adults.

Overall, current evidence from MMN studies does not suggest that deviance processing is generally divergent in autism, but rather indicates a strong dependence on stimulus characteristics, age, and task design.

Sound segregation

Autistic individuals have been found to exhibit difficulties with automatic filtering of auditory stimuli, such as streams of tones with distinct frequency ranges (Lepistö et al., 2009). When participants are required to identify auditory stimuli among distractors with common features, reduced automatic filtering in autism leads to processing advantages (Lin et al., 2015).

Moreover, autistic individuals show an increased ability to extract local features from melodies, while the perception of global features of the melody is indistinguishable between groups (Bouvet et al., 2014; Mottron et al., 2000), paralleling findings of enhanced visual disembedding.

In sum, when presented with complex auditory stimuli made up of several parts, autistic participants may filter and group stimuli less, and may display an increased tendency to perceive each part independently, potentially indicating weak stimulus binding.

Oscillatory differences

Atypical oscillatory responses to auditory stimuli in autistic participants have been described frequently. Findings differ between evoked oscillations, which are phase-locked to the onset of a stimulus and induced activity, which is phase-independent and marks a change in oscillatory power after onset of a stimulus. Specifically, evoked gamma power (40-60 Hz) is decreased in response to pure tones, while induced gamma power is increased (Edgar, Fisk, et al., 2015; Edgar, Khan, et al., 2015; Rojas et al., 2008). This is reflected by reduced inter-trial coherence in autism (sometimes

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referred to as phase locking factor) (Edgar, Khan, et al., 2015; Gandal et al., 2010; Rojas et al., 2008), which expresses how consistent the phase of neural oscillations is over trials. Autistic participants further show reduced neural entrainment to acoustic click trains in the gamma range (Seymour et al., 2020; Wilson et al., 2007).

These results parallel findings from the visual domain and indicate that the precise timing of neural oscillations to the onset of a stimulus is affected in autism, while the production of neural oscillations per se is indistinguishable from that of non-autistic individuals.

Auditory predictions and habituation

The attenuating effect of predictions and habituation on auditory processing appears to be diminished in autistic participants. One approach to investigate auditory predictions is to vary the predictability of deviant stimuli in an auditory oddball paradigm. For autistic participants, the MMN amplitude to deviant stimuli decreases less over time than for control participants (Hudac et al., 2018), and less attenuation by a higher occurrence rate of the deviant stimulus was observed (Goris et al., 2018). These findings can be interpreted as results of decreased top-down predictions in the auditory domain, mirroring findings observed for diminished visual predictions. Alternatively, they might reflect decreased habituation to recurring deviant stimuli in autism, which relies on local neural populations in the auditory cortex. These two processes are hard to tease apart (Garrido et al., 2009) but can be unified by the Bayesian approach to perception, as detailed in the “Theoretical Frameworks” section below.

Tactile processing

Tactile habituation

When tactile stimulation starts at an imperceptible level and slowly increases in strength, it is harder to perceive than tactile stimulation of constant strength (Zhang et al., 2011). This tactile habituation effect has consistently found to be reduced in autistic participants (Puts et al., 2014, 2017; Tavassoli et al., 2016), and is thought to depend on lateral GABAergic inhibition (Blankenburg et al., 2003; Tommerdahl et al., 2010). Magnetic resonance spectroscopy (MRS) studies have demonstrated

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decreased GABA levels in somatosensory cortex of autistic adults (Sapey-Triomphe et al., 2019) and children (Puts et al., 2017).

These findings indicate that atypical tactile processing in autism might manifest in part as decreased sensory habituation caused by reduced neuronal inhibition.

Oscillatory differences

As in the visual and auditory domains, reduced gamma wave synchronization in autism has been observed in response to tactile stimuli. The entrained response to a 25 Hz vibrotactile stimulus at 50 Hz (within the gamma range) was found to be diminished for autistic participants compared to non-autistic controls (Khan et al., 2015), which the authors attribute to increased feedforward, but decreased feedback functional connectivity.

A related finding is that tactile perception thresholds of autistic participants appear unaffected by the presentation of a competing vibrotactile stimulus (Tommerdahl et al., 2008), while perception thresholds of non-autistic individuals increase three- to four-fold when a competing stimulus is presented. It is argued that this indicates reduced oscillatory synchronization between nearby neural ensembles in autism, potentially impeding the binding of the two stimuli, resulting in an increased likelihood that they will be perceived individually.

Multisensory processing

Perception of synchrony

The closer two stimuli from different sensory modalities are perceived in time, the more likely they are to be bound into a unified percept (Stevenson et al., 2016). The time window in which multisensory stimuli are likely to be perceptually bound is termed the multisensory temporal binding window (Wallace & Stevenson, 2014). Temporal binding windows can be assessed by synchrony or temporal order judgments of stimuli from different sensory modalities. A recent meta-analysis of 12 studies reports, with moderate effect size, weak multisensory temporal binding in autistic individuals (Meilleur et al., 2020), which is more pronounced for audio-visual speech stimuli than for non-speech

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stimuli. For non-speech stimuli, the authors report a high variation of findings between studies, which is likely due to differences in stimulus features and modalities.

The typical fast habituation to asynchronous non-linguistic audio-visual stimuli observed in non-autistic participants (Van der Burg et al., 2013) is diminished for autistic individuals (Noel et al., 2017; Turi et al., 2016). This may again point to reduced habituation in autism, this time manifesting for multisensory integration. Whereas non-autistic participants can adapt within one trial to asynchrony between two stimuli, autistic participants have a reduced tendency to adjust their perception of synchrony based on past stimuli.

Multisensory facilitation

Multisensory facilitation occurs when perception of a stimulus is facilitated by an additional stimulus in another modality. Reduced multisensory facilitation for autistic participants has been found in audio-visual response time tasks (Brandwein et al., 2013; Ostrolenk et al., 2019), as well visual search with auditory cues (Collignon et al., 2013). Findings from multisensory tasks consistently indicate that autistic individuals have difficulties in multisensory stimulus binding and show reduced multisensory facilitation, which might give rise to problems with speech comprehension (Stevenson et al., 2018).

Self-report

Autistic self-reports (Kern et al., 2006; Minshew & Williams, 2007), and reports by parents of autistic children (Ben-Sasson et al., 2007; Minshew & Hobson, 2008; Silva & Schalock, 2012; Tomchek & Dunn, 2007) consistently identify an atypical subjective experience of exteroceptive stimuli. Interestingly, according to self- and parent-reports, autism is associated both with increased under- and over-reactivity to sensory stimuli. In line with this, sensory under- and over-reactivity correlates in a large sample of autistic children (N = 222), and sensory over-reactivity tends to co-occur with repetitive behaviors and strong attentional focus (Liss et al., 2006). It is speculated that overly focused attention and repetitive behaviors might be compensatory mechanisms for sensory over-reactivity, as they limit the scope of incoming information and might thus moderate arousal levels.

Interoceptive processing

Heartbeat perception

Interoception - the tracking and responding to physiological states of the body, such as hunger, thirst, temperature, fatigue or pain - is often experienced atypically in autistic individuals (Fiene & Brownlow, 2015), as we will detail below. Interoception is a crucial component for recognizing and interpreting emotions both in the self and in other, as well as for intuitive decision making (Dunn et al., 2010; Fukushima et al., 2011; Herbert et al., 2011): abilities that have traditionally been considered impaired in autism. Interoception is additionally thought to play a central role in anxiety (Paulus & Stein, 2010) which often co-occurs alongside autism (Brosnan et al., 2016; Garfinkel et al., 2016; Silani et al., 2008).

To date, the majority of interoceptive research in autism has focused on the cardiac domain, potentially because heartbeats are discrete and easily measurable (Larsson et al., 2020). Historically, the majority of cardiac interoception paradigms tended to use either tracking or discrimination-based tasks. In heartbeat tracking tasks (Schandry, 1981), participants are required to count their heartbeats over different time intervals (typically between 25 and 60 seconds) without taking their pulse, and the accuracy is based on the ratio of perceived to actual heartbeats. It is common practice not to instruct participants on how or where to detect heart beats, and the location of heart beat sensations during these tasks has been neglected by research, although there are now investigations in the spatial and temporal relationships in heartbeat detection tasks (Betka et al., 2020). Findings to date using this tracking task are mixed, with some studies demonstrating higher accuracy in non-autistic adults (Mul et al., 2018) and children (Nicholson et al., 2019; Palser et al., 2018). This is also supported by Garfinkel and colleagues (2016), although the study does not meet eligibility criteria for our review, as samples were not matched for cognitive abilities. Conversely, other studies found no differences in interoceptive accuracy between autistic and non-autistic adults (Failla et al., 2019; Nicholson et al., 2018, 2019; Shah et al., 2016), or children (Schauder et al., 2015). These mixed findings might be partially due to differing exclusion criteria: Schauder and colleagues (2015) excluded participants if they reported no

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heartbeats, assuming this indicates poor understanding of the instructions. Consequently, all participants with very low interoceptive accuracy were excluded. If these individuals were over-represented in the autistic participant group, this could account for no observed differences between groups in this study. Additionally, mixed findings might also reflect the heterogeneity of autism, where reduced interoceptive sensibility may only be observed in some samples, and/or may be driven by the presence and degree of co-occurring conditions. It has been suggested that differences in alexithymia between non-autistic and autistic individuals may drive apparent reduced interoceptive accuracy in autism. Where alexithymia has been equated between the autistic and non-autistic groups, no differences in interoceptive accuracy has been observed, and reduced interoceptive accuracy inversely correlates with heightened alexithymia (Shah et al., 2016). This inverse relationship between interoceptive accuracy and alexithymia has also been found in non-autistic populations (Herbert et al., 2011), although not consistently (Mul et al., 2018; Nicholson et al., 2018, 2019; Zamariola, Maurage, et al., 2018). The variation of results concerning the relationship between autism and interoceptive accuracy might further be accounted for by individual differences in autistic characteristics, age, or the presence of additional mental health conditions. For example, autistic people are known to experience elevated levels of depression and anxiety (Simonoff et al., 2008), and both are associated with differences in interoceptive processing (Garfinkel et al., 2016; Paulus & Stein, 2010). Alexithymia and interoceptive accuracy have been found to correlate in non-autistic adults, but only when controlling for depression and anxiety scores (Murphy, Brewer, et al., 2018).

In heartbeat discrimination tasks (Katkin et al., 1983; Whitehead et al., 1977; Wiens & Palmer, 2001), participants are asked to judge if a series of auditory or visual stimuli is synchronous or asynchronous to their own heartbeat. No differences in interoceptive accuracy measured by heartbeat discrimination tasks were found between non-autistic and autistic adults (Mul et al., 2018), or children (Palser et al., 2018). However, the number of trials in these studies was below the recommended number of 40 trials recommended by some to acquire reliable results (Kleckner et al., 2015). While the heartbeat discrimination task has been widely used as a measure of interoceptive

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accuracy (Forkmann et al., 2016; Garfinkel et al., 2016; Katkin et al., 1983), successful performance on this task requires combining exteroceptive and interoceptive information. This highlights that established tests of interoceptive accuracy can require additional types of processing and cannot be considered 'pure' tests of interoception.

It has been argued that heartbeat tracking tasks may not actually test sensitivity to heart beats, but instead reflect the accuracy of participants' beliefs about their own heart rate (Brener & Ring, 2016), coupled with their capacity to accurately estimate time (Desmedt et al., 2020). Moreover, interoceptive accuracy is negatively correlated with heart rate (Ainley et al., 2020; Zamariola, Vlemincx, et al., 2018), as individuals have a tendency to under-report their heartbeats. Those individuals with a lower heart rate may thus appear more sensitive. While some authors claim that this undermines the validity of the paradigm (Zamariola, Maurage, et al., 2018), others argue that interoceptive perception necessarily depends on individual physiological properties, in this case heart rate (Ainley et al., 2020). Concerning the heartbeat discrimination task, it has been argued that accuracy depends on the temporal delays of heartbeats and heartbeat sensations, which differ between individuals (Brener & Ring, 2016). These arguments call out for further understanding and potential refinement of existing interoception methods as well as for the development of novel paradigms to assess interoceptive accuracy.

Novel interoceptive tasks

Novel approaches to measure interoceptive accuracy in noncardiac axes have recently been proposed. Targeting the respiratory domain, Murphy and colleagues (2018) have defined interoceptive accuracy as the strength of reliance on interoceptive cues (opposed to auditory cues) when estimating the speed of one's breath (Murphy, Catmur, et al., 2018). In a non-autistic sample, alexithymia, but not autistic traits, predicted a weaker reliance on interoceptive information. The authors also found that alexithymia, but not autistic traits, correlated with the accuracy of estimating muscular effort (Murphy, Catmur, et al., 2018). Finally, the consistency of subjective arousal ratings and skin conductance responses to emotionally arousing pictures has been proposed as a marker for

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interoceptive accuracy (Gaigg et al., 2018). Again, alexithymia, but not autistic traits, predicts weaker correspondence between arousal ratings and skin conductance response.

Interoceptive sensibility

While there is evidence for increased interoceptive sensibility in autistic adults (Garfinkel et al., 2016), typical interoceptive sensibility has been observed in autistic children (Palser et al., 2018). Interestingly, both studies report that the interoceptive trait prediction error (i.e. the difference in interoceptive sensibility and interoceptive accuracy) was higher in autistic participants opposed to controls. Autistic participants of all ages thus reported to be sensitive to interoceptive signals, but showed low accuracy relative to this self-report measure when assessed, resulting in greater interoceptive error in both autistic children and adults.

Decreased interoceptive sensibility in autistic adults has also been observed (Fiene & Brownlow, 2015; Mul et al., 2018). This apparent discrepancy might be due to the different questionnaires used to assess interoceptive sensibility. Garfinkel and colleagues (2016) as well as Palser and colleagues (2018) applied the Body Perception Questionnaire (BPQ; Porges, 1993), which assesses the frequency of being aware of bodily sensations, such as swallowing or stomach pain. Other research used the Multidimensional Assessment of Interoceptive Awareness (MAIA; Mehling et al., 2012) or the Body Awareness Questionnaire (BAQ; Shields et al., 1989), both of which assess the belief in accurate interpretation and control of body signals (e.g. *'I notice distinct body reactions when I am fatigued'*). Further work is needed to further delineate the different interoceptive components that may drive distinct self-report measures to assess whether they diverge selectively in autism.

Integration of interoceptive and exteroceptive processing

Cardio-visual temporal binding windows measured by a variant of the heartbeat discrimination task appear to be enlarged four-fold for autistic participants, as compared to non-autistic participants (Noel et al., 2018). This provides the first evidence for atypical integration of interoceptive and exteroceptive signals. This effect was several orders of magnitude larger than the enlargement of

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temporal binding windows for visuo-tactile and audio-visual stimuli. However, samples were not matched for cognitive abilities and replication is needed to draw clear conclusions.

Theoretical frameworks

There exists a range of neurobiological, psychological, and computational theories offering accounts for divergent sensory processing in autism (see Box 1). Rather than being mutually exclusive, many of these theories can be viewed as complementary. One strand of theories speaks towards a divergent manner of stimulus binding in autism, while another strand uses Bayesian accounts of sensory processing to explain atypical autistic perception. We will address how both theoretical frameworks account for the findings reviewed above, how they might relate to each other, and which links they suggest between perceptual and behavioral differences.

Weak stimulus binding

Weak central coherence theory (Happé, 1996; Happé & Frith, 2006) posits that autism is characterized by reduced binding of local stimuli into global percepts. In line with this, autistic individuals tend to show performance advantages in tasks where stimuli need to be perceived in isolation, such as visual search (Constable et al., 2020), disembedding (Van der Hallen et al., 2018), or auditory segregation tasks (Lin et al., 2015), and display a locally focused processing style (Nayar et al., 2017; Wang et al., 2015). Conversely, autistic individuals show difficulties in tasks where stimuli need to be combined or grouped, reflected by reduced perception of motion coherence (Van der Hallen et al., 2019), reduced multisensory facilitation (Brandwein et al., 2013), inaccurate perception of synchrony (Grossman et al., 2015), increased temporal binding windows (Meilleur et al., 2020), reduced filtering based on stimulus features (Lepistö et al., 2009), and diminished integration of interoceptive and exteroceptive information (Noel et al., 2018). Reduced automatic filtering of stimuli might result in sensory over-reactivity (Kern et al., 2006). It has been proposed (Hatfield et al., 2019) that autism is marked by a reduced capacity for global integration of interoceptive stimuli into an 'interoceptive scene', akin to the reduced stimulus binding observed in the exteroceptive domain. For instance, the physiological

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state of being thirsty can only be inferred by integrating several distinct interoceptive sensations. If global interoceptive integration is weakened in autism, Hatfield and colleagues argue, this might give rise to difficulties in interpreting and responding to bodily and emotional states. This argumentation is in line with reduced binding of external and internal signals might lead to increased salience (Garfinkel et al., 2016), along with reduced interpretability of the overall bodily state (Fiene & Brownlow, 2015), observed in some autistic adults.

Interpreting bodily states requires the integration of both interoceptive and exteroceptive signals. A pounding heart, sweat and heavy breathing might be a sign of arousal, fear or physical exertion and clues to disambiguate these can be found in the external environment. Weak integration of external and internal cues might thus give rise to both difficulties in responding to bodily needs and alexithymia, as the experience of emotions is thought to depend on the perception of bodily states (Damasio & Carvalho, 2013).

On a neural level, weak stimulus binding can translate into reduced synchronized neural activity in response to stimuli (Brock et al., 2002; Simon & Wallace, 2016), as gamma range synchronization is thought to underlie stimulus binding. Locally evoked synchronized gamma oscillations in response to stimuli (Buard et al., 2013; Edgar, Khan, et al., 2015; Khan et al., 2015), long-distance synchronization (Peiker et al., 2015), and cross-frequency coupling (Seymour et al., 2019) have been found to be decreased in autism, all of which are mechanisms involved in multisensory binding (Simon & Wallace, 2016). Interestingly, baseline oscillatory activity and induced gamma oscillations are increased in autism (Edgar, Fisk, et al., 2015; Edgar, Khan, et al., 2015; Rojas et al., 2008), suggesting that the temporal precision of gamma wave production, rather than their production per se, is atypical in autism.

On a molecular level, reduced evoked gamma range synchronization may be driven by an increased excitation/inhibition ratio in autism (Robertson et al., 2016; Rubenstein & Merzenich, 2003). GABAergic inhibition is necessary to produce phase-locked gamma waves in response to stimuli (Sohal et al., 2009), whereas downregulation of inhibitory activity might increase resting-state gamma

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oscillations (see: Edgar, Khan, et al., 2015, for a discussion). Findings of decreased GABA receptor expression in cortical areas in autism (Gaetz et al., 2014; Harada et al., 2011; Oblak et al., 2010; Puts et al., 2017; Sapey-Triomphe et al., 2019), as well as diminished sensory habituation (Puts et al., 2014, 2017), and atypical binocular rivalry (Robertson et al., 2013) constitute evidence for reduced neural inhibition in autism.

On the level of neural circuits, weak stimulus binding in the autistic brain might give rise to divergent patterns of functional connectivity. There is evidence for wide-spread under-connectivity (Di Martino et al., 2014; Just et al., 2004), but also over-connectivity (Courchesne et al., 2007; Supekar et al., 2013; Uddin et al., 2013) in the brains of autistic individuals. In particular, functional connectivity of the anterior insula, an area where interoceptive and exteroceptive information converge (Craig, 2009), is reported to be increased (Green et al., 2016; Supekar et al., 2013), or decreased in autism (Ebisch et al., 2011; von dem Hagen et al., 2013). It has been proposed that “idiosyncratic connectivity patterns of individuals with ASD may [...] stem from the altered interaction of the autistic individual with the external environment” (Hahamy et al., 2015). In line with this idea, one might speculate that inconsistent neural responses to stimuli, such as reduced phase-locked gamma oscillations, may contribute to highly individual neural connectivity patterns in autism.

Overall, reduced stimulus binding in autism accounts for a wide range of findings from perceptual tasks and can be linked to robust neural and molecular observations.

Box 1. Theories of autistic perception

Excitation-inhibition balance. Decreased GABA levels in autistic individuals lead to globally reduced neural inhibition (Robertson et al., 2016).

Neural synchronization hypothesis. Autism is characterised by reduced synchronization of neural oscillations, leading to difficulties in stimulus binding (Simon & Wallace, 2016).

Under-connectivity hypothesis. Long-range under-connectivity between frontal and posterior regions of the brain underlies the autistic phenotype (Just et al., 2012).

Intense world hypothesis. Increased local neural connectivity and plasticity leads to hyper-perception and -attention in autism (Markram 2007).

Weak central coherence. Autism is characterized by difficulties in processing information in its context, leading to a locally focused processing style (Happé & Frith, 2006).

Perceptual enhancement. Low level perceptual abilities are enhanced in autism (Motttron et al., 2001).

Monotropism. Autistic characteristics emanate from atypical attention allocation. In autism, attention allocation supports few synchronous interests, each highly aroused (monotropism), compared to typical attention allocation supporting multiple interests, less highly aroused (Murray, 2018; Murray et al., 2005).

Bayesian account. Attenuation of prediction errors in the exteroceptive (Lawson et al., 2014) and interoceptive domain (Quattrocki & Friston, 2014) is biased towards sensory error signals. This leads to an increased influence of error signals on predictive model generation that drive perception.

The Bayesian approach

Several Bayesian accounts of autism propose that the core mechanism underlying divergent autistic perception and behavioral characteristics is atypical perceptual inference in the exteroceptive (Cruys et al., 2014; Lawson et al., 2014; Pellicano & Burr, 2012) or interoceptive domain (Quattrocki & Friston,

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2014). These accounts are based on Bayesian, predictive coding principles (Friston & Kiebel, 2009) postulating that in non-autistic individuals, perception heavily relies on top-down models which predict the most likely incoming sensory input and are compared against actual signals from the body and external environment, generating an error signal that can then be used to update models. Importantly, predictive processing involves a mechanism that estimates the reliability and precision of both predictive models and incoming signals. This estimate determines how much influence predictions or error signals have in forming percepts and sensations.

Bayesian accounts of autism converge on the idea that for autistic individuals, perception is driven less by top-down generative models than in non-autistic individuals, and is instead more influenced by incoming error signals (Palmer et al., 2017). In other words, autistic perception is thought to be dominated more by sensory evidence and less by prior beliefs. One explanation for this disbalance is a reduced attenuation of prediction errors by top-down prior predictions in autism, which renders prediction errors overly precise and context-insensitive. Consequently, individual prediction error signals strongly influence predictive models and thereby hamper the learning of general, widely applicable rules and structures (Lawson et al., 2014). Especially in complex, noisy and uncertain environments, requiring a high error tolerance, reduced sensory attenuation might exert pronounced effects on perception (Cruys et al., 2014). In the interoceptive domain, it has been suggested that overly precise interoceptive prediction errors in autism result in difficulties with autonomic regulation (Quattrocki & Friston, 2014). It is proposed that in non-autistic individuals, attention is shifted away from one's own body, enabling the contextualizing of bodily sensations with external stimuli. If this does not happen, due to a lesser attenuation of interoceptive error signals and ongoing attention on bodily sensations, these sensations will be amplified. Given the strong relationship between interoceptive processing and emotional states, this may ultimately lead to atypical emotional regulation (Quattrocki & Friston, 2014).

Research designed to test the implications of the Bayesian account has found reduced effects of top-down predictions on visual and auditory perception (Goris et al., 2018; Greene et al., 2019;

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Hudac et al., 2018; van Laarhoven et al., 2020). In line with this, a possible mediator of top-down prediction signals is feedback connectivity in response to stimuli, which has been found to be reduced in autism (Khan et al., 2015; Seymour et al., 2019). The Bayesian account further suggests that habituation to sensory stimulation is reduced in autism, as it relies on the attenuation of bottom-up signals (Lawson et al., 2014). This is supported by converging evidence for reduced tactile (Puts et al., 2014, 2017), and audiovisual (Noel et al., 2017; Turi et al., 2016) habituation.

An interesting finding to be considered under the Bayesian account is reduced auditory deviance processing observed for certain configurations of stimulus features in autism (Chen et al., 2020). Reduced deviance processing is thought to be driven either by reduced habituation to repeating stimuli, or by reduced predictions of upcoming stimuli (Garrido et al., 2009), and both effects are in line with the Bayesian account. Findings of sensory over-reactivity (Minshew & Williams, 2007) also fit with the notion that autistic individuals show reduced attenuation of bottom-up information. Finally, if bottom-up signals are weighed disproportionately high in autism, one might expect autistic individuals to excel at tasks requiring accurate discrimination of low-level stimulus features irrespective of their context. This is empirically reflected by the autistic advantage in visual search, disembedding, and segregation tasks (Constable et al., 2020; Lin et al., 2015; Van der Hallen et al., 2018).

Some of the behavioral characteristics associated with autism may be explained by a Bayesian account of atypical perceptual inference. As autistic individuals are thought to show reduced attenuation of prediction errors, social situations – noisy and complex in their nature – become inherently unpredictable, resulting in challenges with social interaction (Cruys et al., 2014). Repetitive behavior patterns and focused interests can be understood as compensatory mechanisms to reduce uncertainty by providing a predictable environment (Lawson et al., 2014). Moreover, if there is no strong attenuation of interoceptive prediction errors, autistic individuals might not attribute salience to socially relevant exteroceptive stimuli and show less attenuation of self-generated stimulation, leading to a stronger focus on their own sensations (Quattrocki & Friston, 2014). Supporting the notion

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that divergent interception might lead to behavioral differences, heightened interoceptive sensibility and accuracy in autism have been associated with divergent social-affective behavior and restricted behaviors, respectively (Palser et al., 2020).

Attenuation of prediction errors is thought to be mediated by neuromodulators, specifically noradrenaline and acetylcholine for the exteroceptive domain (Yu & Dayan, 2005), and oxytocin for the interoceptive domain (Quattrocki & Friston, 2014). Post mortem studies have established an association between autism and the loss of acetylcholine receptors (Martin-Ruiz et al., 2004; Perry et al., 2001). Moreover, increased tonic pupil size (Anderson & Colombo, 2009; Blaser et al., 2015), and increased phasic changes of pupil size in sensory tasks (Blaser et al., 2015; Lawson et al., 2017) might indicate atypical noradrenaline function in autism. Regarding oxytocin, plasma levels have been found to be increased (Green et al., 2001; Modahl et al., 1998), and a recent meta-analysis revealed an association between autism and differences of the oxytocin receptor gene (LoParo & Waldman, 2015). Finally, it has been proposed that attenuation of prediction errors is exerted via NMDA receptors (Friston, 2005) and differences of genes coding for NMDA receptors have been associated with autism (Lee et al., 2015).

Taken together, the Bayesian approach links differences in perceptual inference with common behavioral patterns in autism, and studies testing the implications of the Bayesian account provide consistent results. There is a fair amount of evidence indicating that neuromodulatory systems underlying attenuation of prediction errors might be atypical in autism (Green et al., 2001; Martin-Ruiz et al., 2004; Modahl et al., 1998; Perry et al., 2001). However, the Bayesian account does not derive from consistently observed neurobiological changes, such as atypical excitation-inhibition balance and weak neural synchronization.

A unified framework

How might reduced stimulus binding and atypical perceptual inference relate to one another? An interesting parallel is that both approaches postulate that autism is characterized by a lower tendency to combine different types of information (signals from different sensory modalities or bottom-up and

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top-down signals). If information integration is atypical in multiple ways, this might be reflected in highly individual functional connectivity patterns between brain regions encoding those different types of information. Indeed, this has been observed in autistic individuals (Hahamy et al., 2015).

The interaction between the neurobiological mechanisms proposed by both frameworks has not been systematically investigated. However, there is some evidence suggesting that atypical neuromodulatory systems, which are thought to underlie weakened sensory attenuation, might affect the inhibition/excitation ratio, which is the neural mechanism proposed to underlie weak stimulus binding. For instance, oxytocin influences GABAergic functioning in early in development (Quattrocki & Friston, 2014; Tyzio et al., 2006), and acetylcholine release decreases neural inhibition and plays a central role in the production of gamma oscillations (see Feldman & Friston, 2010, for a discussion).

Atypical perceptual inference and weak stimulus binding might interact and reinforce each other and jointly account for the diversity of autistic presentations. While weak stimulus binding can account for reduced bottom-up integration of stimuli, the Bayesian framework highlights decreased top-down effects on sensory processing.

A unified framework can provide an account for how perceptual differences in autism may cascade towards social difficulties (figure 1). For example, difficulties in social interaction might be influenced by reduced binding of auditory and visual information during speech perception and from reduced reliance on top-down predictions. Reduced binding of interoceptive and exteroceptive information has the potential to hamper the attribution of salience to social stimuli and so may make it harder to interpret one's bodily and emotional state: which is crucial for the understanding of emotions in self and other. Moreover, avoidance of social situations, repetitive behaviors, and a strong attentional focus may be understood as compensatory mechanisms to prevent sensory overload and construct a predictable environment.

We urge researchers to consider that while there is much evidence of atypical processing at the neural, cognitive and perceptual level in autism, this does not translate to 'deficits' at the personal and social level. While the differences between autistic and non-autistic sensory processing and their

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potential consequences need to be considered and may, as described above, lead to differences in personal and social behavior, there is an important distinction to be made between these different levels of description. 'Deficient functioning' may be ascribed to autistic individuals on the basis of observed differences in neural, perceptual or cognitive processing, when in reality it might be a world not set out to accommodate and welcome these atypical profiles that leads to perceived deficits. We describe below why existing standards to measure 'function' in non-autistic populations do not always apply to the autistic population.

Crucially, autism is a highly heterogeneous condition and no single framework can describe the autistic population as a whole. Both the features suggested by our model, as well as the strength of causal relationships between those features are thought to apply to autistic individuals to varying degrees depending on individual profiles.

Limitations and future directions

Due to the large amount of studies reviewed in this paper, we did not systematically investigate effects of age or gender on sensory processing in autism. However, these and other factors likely affect results. We excluded all studies involving social stimuli (such as faces or semantic and pragmatic aspects of language processing), thus limiting the review to basic sensory processes. In the interest of brevity, we did not include studies into proprioceptive perception in autism. However, research suggests that proprioceptive processing is also atypical in autism: possibly resulting from weak integration of other sensory modalities (Cascio et al., 2012; Greenfield et al., 2015) in line with the argument provided in this review. Moreover, it has been reported that symptoms of autonomic dysregulation such as fatigue, pain or digestion issues occur frequently in autistic individuals (Csecs et al., 2020). Even though interoceptive processing and autonomic regulation are closely linked (Craig, 2003; Quattrocki & Friston, 2014), we did not discuss findings of autonomic functioning in this review. Finally, the review of sensory processing in the exteroceptive domain is far from exhaustive, and we limited our review to frequently replicated or novel findings.

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There are also important limitations regarding the reviewed studies. Many of the findings outlined in this review are inconsistent. Reasons for this variability may include small sample sizes in many studies as well as a strong dependence of outcomes on stimulus properties. Methodological features, such as stimulus types, number of trials, exclusion criteria and scoring methods often differ within sets of studies that employ the same task. Moreover, the method employed to match groups for cognitive abilities differs, possibly confounding the results. A further limitation is the lack of standardized self-report questionnaires. In the interoceptive domain, a significant issue is the absence of consensus about which percepts are considered interoceptive and which methods are best suited to test interoceptive accuracy.

Arguably, the biggest challenge for research on sensory processing in autism is the high level of heterogeneity across the autism spectrum. Despite the common neuro-developmental diagnosis, it is likely that the neurobiological mechanisms and genetic differences underlying these diverse phenotypes vary, and this may be reflected in divergent patterns of sensory experiencing among different autistic individuals. Also of note is the fact that of the studies we reviewed, the majority included only those autistic individuals with an IQ greater than 70: thus disregarding approximately 50% of the autistic population (Newschaffer et al., 2007). Within autism research, IQ has traditionally been linked to so-called 'functioning ability', however it is increasingly recognized that it is not really possible to match IQ to a specific and stable level of function (Kenworthy et al., 2010). Furthermore, the very notion of functioning ability is becoming outdated, based on the fact that it can be both misleading and stigmatizing (Botha et al., 2021; Bottema-Beutel et al., 2021). Unlike within the non-autistic population, IQ is a poor predictor of abilities, adaptability and performance for autistic people (Estes et al., 2011), largely on account of the 'spiky profile' of (Milton, 2012: 8) of cognitive abilities that autistic individuals tend to possess. The heterogeneity of the population might account for inconsistent findings observed in many paradigms discussed in this review. In line with this observation and the highly varied individual sensory experience in autism, we suggest that generalizations about differences between autistic and non-autistic people is too simplistic. Instead,

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both empirical and clinical research would benefit from approaching an understanding of individual sensory profiles and their potential implications for emotional and behavioral characteristics.

An interesting avenue for future research would be to combine interoceptive and exteroceptive processing tasks to investigate whether sensory processing differences exist in similar ways across modalities for autistic individuals and how perceptual atypicality may influence behavior. We further hope that future research will help elucidate how weak stimulus binding and atypical perceptual inference might interact on the molecular, neural and circuit levels in the autistic brain.

Conclusion

In this review, we outlined and linked a wide range of findings from studies investigating the exteroceptive and interoceptive processing of autistic individuals. A large part of these findings can be explained by reduced neural synchronization and consequently reduced binding of sensory stimuli into global percepts. Another set of findings speaks to atypical perceptual inference in autistic individuals, who seem to rely more on incoming evidence and less on prior predictions than non-autistic individuals. Weak stimulus binding and atypical perceptual inference – though described as distinct theories in the literature – might complement each other and describe the complex bottom-up and top-down differences of autistic perception, respectively. We aimed to unify scattered theories and findings of autistic perception into a more general framework and argue that that some of the prototypical social and cognitive characteristics of autism may be seen as consequences of, or compensatory mechanisms for, atypical exteroceptive and interoceptive perceptual processing. Crucially, the sometimes atypical perceptual abilities of autistic individuals should not be categorized simply as impairments. Instead, these divergent ways of processing incoming information within the brain can lead to both advantages and disadvantages, depending on task demands and environment. This final point is significant. For both autistic and non-autistic individuals, relative strengths and limitations in their exteroceptive and interoceptive processing have been identified. Perhaps what most meaningfully impacts upon whether these differing abilities are ultimately considered impairments or become disabling characteristics is the

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environment in which the individual resides. Built and social environments designed to meet the sensory profiles of non-autistic individuals may not be felicitous for autistic individuals: and vice versa. Shifting research efforts towards individualized approaches could foster the notion that instead of impaired perception, we need to understand sensory differences as individual facets of a highly diverse and heterogeneous phenotype with equally varying emotional, social, and behavioral implications.

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