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Associations Between Interoceptive Cognition and Age in Autism Spectrum Disorder and Typical Development

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Interoceptive awareness is linked to emotional and social cognition, which are impaired in individuals with autism spectrum disorder (ASD). It is unknown how this ability is associated with age in either typical or atypical development. We used a standard test of interoceptive accuracy (IA) to investigate these questions in children and adults with and without ASD. Perceived number of heartbeats over 4 time intervals was compared with actual heart rate to determine IA. Effects of group, age, IQ, heart rate, and mental counting ability on accuracy were assessed using multiple regression. Post hoc correlations were performed to clarify significant interactions. Age was unrelated to IA in both groups when IQ $\geq$115. When IQ $<$115, this relationship was positive in typical development and negative in ASD. These results suggest that cognitive ability moderates the effect of age on IA differently in autism and typical development.

Keywords: autism; interoception; intelligence; development

Autism spectrum disorder (ASD) is a lifelong developmental disorder associated with atypical reciprocal social communication and patterns of restricted/repetitive behavior. Notably, the *Diagnostic and Statistical Manual of Mental Disorders* (5th ed.,

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DSM-5) definition of ASD has recently been expanded to include abnormal sensory responses as a core diagnostic feature (American Psychiatric Association, 2013). Most sensory research in ASD has focused on processing of exteroceptive input from the visual and auditory systems, but very little research has considered the perception of internal bodily sensations—a sensory modality known as interoception.

Interoception encompasses a wide variety of sensations such as hunger, thirst, body temperature, itch, and sensations from organ activity such as respiration and heartbeat (Craig, 2002, 2003). A better understanding of sensory experiences in this domain has the potential to inform several current models of ASD. For example, many researchers have suggested that violations of predictive coding may underlie ASD symptomatology (Palmer, Paton, Kirkovski, Enticott, & Hohwy, 2015; Palmer, Seth, & Hohwy, 2015; Van Boxtel & Lu, 2013). This theory suggests that individuals with ASD have difficulty using prior sensory experience to form the basis for accurate predictions of future sensory events in the external world. Interoception has also been conceptualized within a predictive coding framework (Seth, 2013; Seth, Suzuki, & Critchley, 2012), whereby use of prior *internal* sensory cues is crucial for making associations between one's emotional state and external events. Some even speculate that interoceptive prediction errors *specifically* play a role in the etiology of ASD (Ondobaka, Kilner, & Friston, 2015; Quattrocki & Friston, 2014), although this has been debated (Brewer, Happé, Cook, & Bird, 2015) and has yet to be empirically tested. Difficulty predicting internal sensations may limit an individual's ability to form associations between those sensations and salient social or emotional events in the external world, which may contribute to social and communication problems. Furthermore, deficits in interoceptive predictive coding may render interoceptive cues less salient over time, causing them to be habitually disregarded and potentially resulting in a positive feedback loop (e.g., impaired attention causes cues to be less predictive, which then reinforces inattention).

Interoception is also thought to play a role in theory of mind (ToM)—the ability to cognitively identify with another individual (Ondobaka et al., 2015). This has been posited as a fundamental deficit in ASD (Baron-Cohen, Leslie, & Frith, 1985). ToM is associated with emotional awareness, empathy, and sense of "self," all of which are related to interoception (Barrett, 2004; Fukushima, Terasawa, & Umeda, 2011; Schauder, Mash, Bryant, & Cascio, 2015; Suzuki, Garfinkel, Critchley, & Seth, 2013; Tsakiris, Tajadura-Jiménez, & Costantini, 2011; Wiens, 2005) and are impaired in ASD (Baron-Cohen & Wheelwright, 2004; Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012; Paton, Hohwy, & Enticott, 2012; Uljarevic & Hamilton, 2012).

Further evidence for a relationship between interoception and socioemotional abilities in ASD comes from the functional neuroimaging literature. The posterior insula is the primary cortical processor of interoceptive sensation, which is then hypothesized to be ascribed affective significance by the anterior insula (Craig, 2009, 2014; Uddin, 2015). The anterior insula has specifically shown enhanced activation during heartbeat detection tasks (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004). This area has also been implicated in several social-emotional processes, including awareness of others' emotions, social behavior (Craig, 2002; Garfinkel & Critchley, 2013; Terasawa, Shibata, Moriguchi, & Umeda, 2012), and determining the emotional salience of external events (Uddin, 2015). Furthermore, several studies of ASD have found aberrant functional connectivity of the anterior and posterior insula at rest (Ebisch et al., 2011; Uddin, 2015) and atypical activity in the anterior insula during social-emotional tasks (Caria & de Falco, 2015). This suggests that common mechanisms relevant to salience processing could potentially underlie interoception and established deficits in ASD.

Although a direct link between interoception and ASD symptoms remains unclear, the available evidence suggests the possibility of differences in the manner and extent to which individuals with ASD detect, attend to, and interpret interoceptive signals. Such an alteration is likely to have cascading effects on social interactions and other cardinal features of ASD. Initial investigations of interoceptive ability in ASD have applied distinct methodological approaches and yielded mixed results. Schauder et al. (2015) reported no group differences in interoceptive accuracy (IA) in children with and without ASD using a heartbeat-tracking paradigm (Schandry, 1981) in which heartbeat counts are compared to actual heartbeat counts over discrete time intervals. In contrast, Fiene and Brownlow (2015) showed that adults on the autism spectrum reported less body awareness than controls using self-report measures of general body awareness and thirst.

Although these findings appear at odds, several explanations may account for the discrepancy. First, the vastly different methods employed by each study (psychophysiological measurement vs. self-report) may in fact be sensitive to independent constructs within the larger concept of interoception. Garfinkel, Seth, Barrett, Suzuki, and Critchley (2015) identified three distinct subcategories of interoceptive measurement: accuracy, sensibility, and awareness. Accuracy is measured through direct comparison of estimated and actual signals and is only possible when actual signals can be quantified (as in the heartbeat tracking paradigm used by Schauder et al., 2015). This represents a limited range of interoceptive information. In contrast, sensibility is measured through self-reported experience of internal cues (as in Fiene & Brownlow, 2015) and can be assessed for any interoceptive submodality, including those that are not readily quantifiable such as thirst. Finally, awareness is defined as the degree to which an individual's subjective report and objective measurements correspond.

Garfinkel, Tiley, O'Keeffe, Harrison, Seth, and Critchley (2016) combined the methods discussed earlier to address each of these domains in a sample of adults with ASD. They found that compared to controls, the ASD group tracked their heartbeats with less accuracy but reported greater internal sensitivity (i.e., sensibility). This discrepancy implies reduced interoceptive awareness. These results contradict both Schauder et al. (2015; i.e., no group differences in accuracy) and Fiene and Brownlow (2015; i.e., impairments in self-reported sensibility). It is important to note that Garfinkel et al. (2016) did not report cognitive ability (IQ) of their participants, which may be a significant confound in their reported findings. Thus, differences across the distinct interoceptive domains currently do not form a coherent narrative, but direct comparison across the few studies conducted thus far has limited utility until replication with convergent methods is achieved.

Another compelling explanation for the differences in studies to date is the narrow developmental scope of study samples (i.e., children vs. adults). Studies limited to one age group may provide an incomplete narrative. We propose considering interoception as a dynamic, developmental characteristic for which individuals with ASD may have a different lifelong trajectory than neurotypical individuals. To our knowledge, the relationship between age and interoception has not been studied in ASD. In fact, there is very little research on this association in typical development. One study did find a negative relationship between age and interoceptive ability from young adulthood to late adulthood in a typical sample (Khalsa, Rudrauf, & Tranel, 2009), but interoception has yet to be studied across a broader range of ages that includes the developmentally critical stages of childhood and adolescence. This approach has already been adopted in the study of related processes, such as somatosensation (Gescheider, Bolanowski, Hall, Hoffman, & Verrillo, 1994), empathy (Decety & Michalska, 2010), and visual-proprioceptive mechanisms of body awareness and ownership (Bremner, Hill, Pratt, Rigato, & Spence, 2013; Cowie, Makin, & Bremner, 2013; Jaime, Longard, & Moore, 2014), at different ages. Because autism is a lifelong developmental disorder, studying relevant phenomena at different life stages is critical to understanding their role in the long-term functioning of individuals with ASD.

In this study, we used a cross-sectional design to determine whether IA is associated with age in individuals aged 8–54 years and, if so, whether this relationship is similar in ASD. We expanded on our sample of children previously reported in Schauder et al. (2015), including both new children and adults with and without ASD. We decided to focus on IA as defined by Garfinkel et al. (2015) because of its simplicity and quantifiable nature. Although collecting both accuracy and sensibility data would be ideal, there are very few validated measures of IA available and none that would be appropriate to use across the range of ages we studied.

We anticipated a specious relationship between IA and age because of age-related differences in resting heart rate (Fleming et al., 2011). Individuals with a higher resting heart rate may tend toward less accurate responses, simply because there are more heartbeats to count over a shorter interval. Therefore, we included heart rate as a predictor in our model. Our primary prediction was that IA would be positively associated with age in our typically developing sample, as in related neurocognitive abilities such as proprioception (Cowie et al., 2013), empathy (Decety & Michalska, 2010), and emotion recognition (Gao & Maurer, 2010). However, given previous findings in ASD of typical IA in childhood (Schauder et al., 2015) but diminished interoceptive accuracy and awareness (Garfinkel et al., 2016) in adulthood, we hypothesized that the opposite relationship may emerge in ASD (i.e., interoceptive accuracy is negatively associated with age).

METHOD

Participants

Adults. Nineteen adults with ASD and 19 typically developing (TD) adults, ages 18–54 years, participated in this study. Participants had IQ scores of at least 70, as measured by the two-subtest (Vocabulary and Matrix Reasoning) version of the Wechsler Abbreviated Scales of Intelligence—Second Edition (WASI-II; Wechsler, 2011). ASD diagnoses were confirmed through research-reliable administrations of the Autism Diagnostic Interview-Revised (ADI-R; Lord, Rutter, & Le Couteur, 1994) and the Autism Diagnostic Observation Schedule—Second Edition (ADOS-2; Gotham et al., 2007), and the judgment of a licensed clinical psychologist based on *DSM-5* criteria. TD individuals were excluded if they had a history of any psychiatric or learning disorder or had a first-degree relative with ASD. The Adult Self Report (ASR; Achenbach & Rescorla, 2003) was used as a standardized measure to screen for specific psychiatric concerns. Participants in both groups were excluded for genetic and neurological disorders as well as significant head injuries. Participants had normal or corrected-to-normal vision and gave informed consent. Procedures were approved by the Vanderbilt Institutional Review Board.

Children. In total, 52 children and adolescents with ASD and 42 TD children and adolescents, ages 8–17 years, were enrolled in the study. Inclusion criteria were identical to those used for adults, with a few exceptions. The Child Behavior Checklist (CBCL; Achenbach & Rescorla, 2001), a parent-report measure, was used to screen TD children for psychiatric

TABLE 1. Participant Characteristics for Children, Adults, and All Participants

		ASD	TD	*t*, *p*
Age	All	18.08 (10.81)	17.72 (11.29)	−0.176, .860
	<18 years	12.16 (2.92)	11.03 (2.82)	−1.725, .089
	≥18 tears	29.63 (11.29)	31.47 (9.51)	0.544, .590
IQ	All	104.80 (15.68)	114.79 (11.68)	3.846, <.001*
	<18 years	106.08 (17.15)	114.72 (11.63)	2.556, .013*
	≥18 years	102.32 (12.40)	114.95 (12.10)	3.178, .003*
% male	All	78.6	74.1	0.552, .582
	<18 years	83.8	79.5	0.447, .635
	≥18 years	68.4	63.2	0.333, .741

Note. Mean values and group differences are shown, with standard deviations in parentheses. There were no significant diagnostic group differences in age or gender for children, adults, or overall. IQ significantly differed in both age groups and overall. ASD = autism spectrum disorder; TD = typically developing.

concerns (instead of the ASR, which is not standardized for children). Parents of TD individuals were additionally asked to complete the Social Communication Questionnaire (SCQ; Rutter, Bailey, & Lord, 2003). Individuals with SCQ scores above 15 were not enrolled. Of the eligible sample, data from 21 children with ASD and 24 children with typical development were included in an earlier report (Schauder et al., 2015). An additional 21 children with ASD and 15 children with typical development completed the same interoception task for the current experiment. Five children with ASD were excluded based on the examiner's judgment of task comprehension and compliance. The final sample consisted of 37 children with ASD and 39 children with typical development.

For children, adults, and the combined sample, there were no group differences in mean age or proportion of male participants. However, there were statistically significant group differences in IQ (Table 1).

Data Collection

Interoception Task. We implemented a standard test of interoceptive accuracy, identical to that described in a previous study (Schauder et al., 2015). Participants used the mental tracking method (Schandry, 1981), in which they were asked to report the number of counted heartbeats over four time intervals: 25 s, 35 s, 45 s, and 100 s. Heart rate was monitored using a Biopac OXY 100C pulse oximeter with a Biopac TSD123A finger transducer, placed on the middle finger of the dominant hand. Physiological data were recorded using AcqKnowledge software (sampling rate of 50 Hz). Participants were asked to sit quietly with their hands in their laps and their eyes closed. They were instructed to count their heartbeats without feeling their chest, wrist, and so forth. (i.e., without physically taking their pulse in any way). Each trial was closely supervised, beginning and ending with a verbal cue from the examiner. At the end of each trial, participants verbally reported how many heartbeats they counted. Before data collection, a 30-s practice trial was performed to ensure task comprehension. If participants reported zero heartbeats, instructions were repeated and a second practice trial was given. If the participant still reported zero, testing was terminated. Participants who successfully completed the practice session went on to complete four more trials, one of each time interval. The order of time intervals was randomized across participants. Accuracy was calculated for each trial as the absolute value of the difference between the actual and reported number of heartbeats, divided by the actual number of heartbeats. An overall measure of accuracy was calculated as the average IA across all nonpractice trials. An average heart rate was obtained for each participant by first calculating average heart rate within each time trial and then averaging across trials.

Visual Counting Task. A visual counting task was included to control for possible effects of counting ability, attention, and motivation on measured IA. All adults in the final sample as well as 28 children with ASD and 21 children with typical development completed this activity. Participants were asked to count the number of times a dim circle flashed on a white computer screen over the same four time intervals used in the interoception task. The circle was constructed as an object in Microsoft PowerPoint using the 5% dot pattern as fill. The stimulus was programmed to flash at approximately the average heart rate for children ages 8–17 years (Fleming et al., 2011).

Data Analysis

Independent samples *t* tests were used to determine whether group differences existed in age, average heart rate, visual counting scores, and IQ. IQ and visual counting *t* scores and degrees of freedom were corrected for variance inequality as determined by Levene's test for equality of variances. Variables that significantly differed between groups (heart rate, IQ, and visual counting, see "Results" section) were included in our regression model, in addition to our variables of primary interest (diagnostic group and age). To test our prediction that heart rate would vary as a function of age, we examined the correlation between these variables.

We first explored relationships of interest independently in the ASD and TD groups using separate multiple regressions. We included age, IQ, heart rate, and visual counting score as predictor variables and average IA across all nonpractice trials as the outcome variable. We also examined interactions between age and IQ. Age values were logarithmically transformed to compensate for the skewness of the distribution toward younger ages. All variables were mean centered. The 28 missing visual counting scores were imputed using the mean value.

Next, we combined all subjects across diagnostic groups and performed a third multiple regression. This model was nearly identical to that described earlier, except that diagnostic group was included as an additional predictor of IA, and all two- and three-way interactions between group, age, and IQ were considered. Continuous variables remained centered, and groups were contrast coded as -0.5 (TD) and $+0.5$ (ASD).

Based on the results obtained in the multiple regression, we also performed a series of post hoc correlations for each diagnostic group to clarify the nature of two- and three-way interactions. To fully explore and visualize these relationships, IQ was necessarily dichotomized; participants were separated into IQ $<$115 and IQ $\geq$115. This cutoff score is clinically meaningful (1 standard deviation above the normative mean) and results in a more even distribution of participants among the four cells of interest (ASD/$<$115, ASD/$\geq$115, TD/$<$115, TD/$\geq$115) than a cutoff of 100 (the normative mean). Correlations were performed between age and IA and compared across IQ categories and diagnostic groups.

RESULTS

Group Characteristics

When all participants were combined, there were significant group differences in IQ, $t(102) = 3.85$, $p < .001$; average heart rate, $t(112) = -3.89$, $p < .001$; and visual counting score, $t(69) = 2.94$, $p = .004$, such that the ASD group had lower IQ, higher heart rate, and lower visual counting accuracy. Mean age did not significantly differ between groups, $t(112) = -.176$, $p = .860$ (Table 2). In addition, logarithmically transformed age was significantly correlated with heart rate ($r = -.421$, $p < .001$).

Typical Development Multiple Regression

In the TD group, age, heart rate, IQ, visual counting score, and the IQ × Age interaction all together accounted for a significant proportion of variance in average IA, $R^2 = .357$, $F(5, 52) = 5.784$, $p < .001$. The conditional main effects of age ($\beta = .156$, $p = .146$) and IQ ($\beta = .002$, $p = .269$) were not significant, nor was the IQ × Age interaction ($\beta = -.013$, $p = .104$). There was a significant main effect of heart rate ($\beta = -.006$, $p < .001$), but no significant main effect of visual counting score ($\beta = .871$, $p = .356$).

Autism Spectrum Disorder Multiple Regression

In the ASD group, the overall multiple regression was significant, $R^2 = .312$, $F(5, 50) = 4.526$, $p = .002$. There were significant conditional main effects of age ($\beta = -.293$, $p = .039$) and IQ ($\beta = .005$, $p = .003$). However, the IQ × Age interaction did not reach significance ($\beta = .016$, $p = .091$). As in the TD group, there was a significant main effect of heart rate ($\beta = -.005$, $p = .021$), but the effect of visual counting score was not significant ($\beta = -.587$, $p = .271$).

Group Comparison Multiple Regression

When the ASD and TD groups were combined and diagnostic group was considered as a predictor, the omnibus F test was significant, $R^2 = .335$, $F(9, 104) = 5.824$, $p < .001$. Group

TABLE 2. Analysis of Potential Predictors of Interoceptive Accuracy

				Correlation with IA (r, p)		
	ASD	TD	t, p	ASD	TD	Overall
Heart rate	86.15 (14.65)	75.54 (14.49)	−3.888, <.001*	−.226, .094	−.528, <.001*	−.387, <.001*
IQ	104.80 (15.68)	114.79 (11.68)	3.846, <.001*	.350, .008*	.033, .803	.272, .003*
Visual count	0.946 (0.056)	0.973 (0.027)	2.941, .004*	−.065, .666	.350, .029*	.114, .298

Note. Mean values, standard deviations, and group differences are shown for additional variables included in our multiple regression. Heart rate, IQ, and visual counting score all differed significantly between the autism spectrum disorder (ASD) and typically developing (TD) groups. Heart rate and IQ were significantly correlated with IA overall, whereas visual counting score was not.

alone did not significantly predict average IA (β = .031, p = .412), nor did age (β = −.054, p = .530) or visual counting score (β = −.283, p = .508). The main effect of heart rate was significant (β = −.006, p < .001), as were the main effect of IQ (β = .004, p = .004), the two-way interaction between group and age (β = −.523, p = .001), and the three-way interaction between group, age, and IQ (β = .028, p = .022). The IQ × Group interaction and the IQ × Age interaction were not significant (β = .003, p = .252 and β = −.001, p = .896, respectively).

Post Hoc Correlations

Effects of Age by IQ Group. TD individuals with IQ <115 showed a significant positive correlation between age and IA (r = .539, p = .007), but this relationship was absent in TD participants with IQ ≥115 (r = .283, p = .105). In the ASD group, the IQ <115 group showed a significant negative correlation between age and IA (r = −.339, p = .032), but no relationship was observed in individuals with IQ ≥115 (r = .188, p = .485). For a summary of post hoc correlations, see Figure 1 and Table 3.

DISCUSSION

Interoceptive Accuracy in Typical Development

Our results establish, for the first time in typical development and ASD, a relationship between interoceptive accuracy and age through middle adulthood. In the TD group, when we accounted for age, heart rate, IQ, visual counting score, and the IQ × Age interaction, the only significant predictor of IA was heart rate. As we expected, individuals with lower heart rate tended to perform better on this particular task.

Interoceptive Accuracy in Autism Spectrum Disorder

Using the same model in the ASD group, we found that IA significantly decreased with age, controlling for all other variables and interactions. This finding is consistent with neurobiological evidence suggesting that a putative neural substrate of interoception is correspondingly affected by age in individuals with ASD. Uddin et al. (2013) reported hyperconnectivity of the insula in children with ASD; however, studies of adults on the autism spectrum have found insular hypoconnectivity (Di Martino et al., 2014; Ebisch et al., 2011; von dem Hagen, Stoyanova, Baron-Cohen, & Calder, 2013). This would expectedly to give rise to the pattern of IA we observed, given the role of the insula in interoceptive awareness.

Comparison of Autism Spectrum Disorder and Typically Developing Interoceptive Accuracy

In the full multiple regression with group as a predictor, the conditional main effect of IQ appears to be driven by its significant impact in the ASD group, whereas the main effect of heart rate is attributable to independent effects in both groups. Despite an absence of group and age main effects, a significant proportion of variance in IA was accounted for by an interaction between these two variables. Closer examination of the preliminary group regressions shows that this interaction reflects a significant, negative relationship between age and IA in the ASD group, compared with a nonsignificant positive relationship in the TD group,

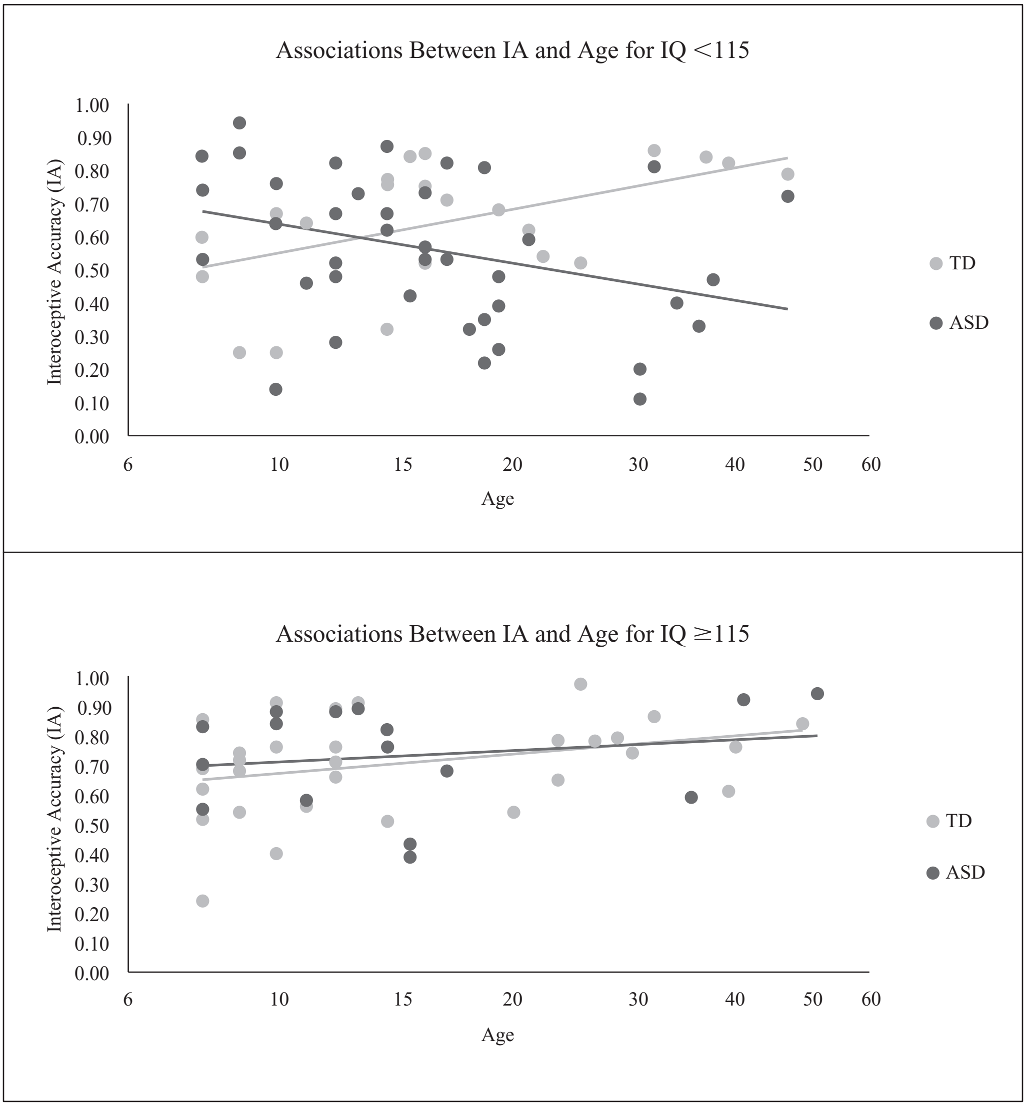

FIGURE 1. Age is logarithmically scaled and displayed in years. For participants with IQ <115, age was significantly positively correlated with IA in the typically developing (TD) group and significantly negatively correlated in the autism spectrum disorder (ASD) group. This relationship was not significant in either group for participants with IQ ≥115.

when all other predictor variables are accounted for. Our understanding of this relationship is greatly enhanced by the three-way interaction we observed between group, age, and IQ, illustrated in Figure 1. It is important to note that although the Group × Age interaction was independently significant, the IQ × Age and IQ × Group interactions were not. By dichotomizing IQ (<115/115+), we were able to better visualize and interpret this complex relationship.

It appears that in both ASD and typical development, there is no significant relationship between age and IA when IQ is at least 115. However, for people with IQ <115, the effect of age on

TABLE 3. Summary of Post Hoc Correlations

Diagnosis	IQ	*n*	Age/IA Correlation (*r*)	Significance (*p*)
TD	Under 115	24	.539	.007*
	115+	34	.283	.105
ASD	Under 115	40	−.339	.032*
	115+	16	.188	.485

Note. Participants were assigned to one of four groups based on diagnosis and IQ score. Correlations between age and interoceptive accuracy (IA) are expressed as Pearson's *r*. Age and IA were significantly positively correlated in the typically developing (TD) group with IQ <115 and significantly negatively correlated in the autism spectrum disorder (ASD) group with IQ <115. Neither the ASD nor the TD group showed a significant relationship between age and IA when IQ ≥115.

*indicates that $p < .05$.

IA may be dependent on diagnostic group. In the ASD group, IA significantly *decreased* with age; in the TD group, IA significantly *increased* with age. Therefore, age appears to have considerable, opposite impacts on IA in ASD and TD individuals with average or below-average IQ. However, these effects are absent in people with particularly high IQ, regardless of diagnostic group.

General Discussion

Our results fit in with current research implicating interoception in the etiology of ASD. Accurate perception and interpretation of interoceptive cues is central to both discerning one's own physical and emotional state and to understanding others' experiences of emotion. During a complex social interaction, the ability to detect subtle physiological changes may help one better flexibly engage in a dynamic social environment. Studies of predictive coding in ASD have suggested that difficulty interpreting interoceptive cues may indirectly affect social behavior by disrupting the ability to predict others' thoughts and actions (Ondobaka et al., 2015; Quattrocki & Friston, 2014). In ASD, we saw a negative relationship between age and interoceptive accuracy, which was driven by individuals with IQ <115. We propose that this is a logical extension of the predictive coding hypothesis.

Interoceptive cues with little predictive value are not useful and can even be a distraction in the presence of other, more predictive information. Therefore, over many years, people with ASD may eventually develop alternative attentional strategies to reduce the salience of these cues over time. Furthermore, individuals with ASD with higher attentional capacity (which is associated with IQ; Engle, 2002) may find that although internal cues are not particularly useful, active suppression is not necessary to sustain attention to more valuable social information. Altogether, this could explain both the age and IQ effects we observed in the ASD group and how IQ moderates the effect of age on IA. Although this interpretation is speculative, it is certainly an interesting possibility that deserves further exploration.

The present findings have important implications for our understanding of interoceptive accuracy in both typical and atypical development. Critically, they identify IQ as an important influence on age effects, with unique consequences for ASD and TD individuals. Although the role of IQ in this relationship was not hypothesized a priori, this finding is in line with research suggesting that interoception and certain forms of intelligence share neurobiological underpinnings. In particular, the anterior insular cortex and the anterior cingulate cortex, which are thought to be primary regions serving interoceptive awareness (Craig, 2014), have been associated with both fluid intelligence (Yuan et al., 2012) and the "multiple demand" network underlying general intelligence (Duncan, 2010). Our results demonstrate that a more direct relationship between specific areas of intelligence and interoception is likely and warrants further study designed specifically for that purpose.

Limitations and Future Directions

Although this study sheds some light on the unexplored domain of interoceptive development, future research is warranted to clarify the nature of the relationships we have observed. Most important, a longitudinal study would provide information about the developmental trajectory of interoception. Although our cross-sectional design precludes any definitive conclusions about development, it is a necessary first step in establishing the importance of age as a predictor of IA. Our results speak to the promise of a more time- and cost-intensive longitudinal study. Another area of limitation pertains to our participant characteristics. Gender-specific patterns of neural development (Lenroot et al., 2007) suggest that sex differences in age associations with IA may exist. However, our sample included so few females (23.7% overall) that our current results may only generalize to males. In addition, future studies should focus on recruiting subjects in particular age ranges in equal numbers to avoid skewness in the distribution of ages that was present in our study. Our sample could have also been improved by matching controls on both age and IQ, although this can be difficult when using large samples of participants with ASD.

Considering what this study implies about the role of IQ in interoception, future studies should consider including a more comprehensive measure of intelligence. Our participants were tested on only the Vocabulary and Matrix Reasoning subscales of the WASI-II; these are thought to provide a reasonable measure of general intelligence (*g*; Wechsler, 2011). However, experimenters specifically interested in the role of intelligence in IA will find a more comprehensive test useful (e.g., Wechsler Intelligence Scale for Children—Fourth Edition, Wechsler Adult Intelligence Scale—Fourth Edition) so that different domains of intelligence (e.g., fluid intelligence, perceptual reasoning, working memory) can be independently, reliably explored in relation to interoception.

Finally, some limitations are inherent in the heartbeat-tracking task we used. The difficulty of this task may warrant cautious interpretation of its use in children. There are no published age norms on performance for this task; however, the lack of a main effect of age in our TD and combined sample suggests that the task is difficult for everyone regardless of age. A negative relation between IA and age in the ASD group actually suggests that children with ASD were *more* successful than their adult counterparts. Furthermore, we applied stringent exclusion criteria for task understanding and compliance. The difficulty of this task may make it vulnerable to guessing. A plausible alternative is a "tapping" method, which is a response synchronization measure in which individual taps corresponding to perceived heartbeats are timed and matched against actual heartbeats; this may be less susceptible to guessing. Finally, some participants may be able to feel their pulse through their pulse oximeter, giving them a spurious advantage in this task. Replacing the pulse oximeter with electrocardiogram (ECG) may improve validity, but many individuals with ASD may not tolerate this more invasive method.

Recall the three dimensions of interoceptive ability defined by Garfinkel et al. (2015): accuracy (measured by comparing heartbeat judgments with physiological data), sensibility (self-reported sensitivity), and awareness (agreement between accuracy and sensibility). Our experiment only speaks to accuracy; future research may use questionnaires in combination with laboratory measures, similar to Garfinkel et al. (2016), to incorporate interoceptive accuracy, sensibility, and awareness into a single model. Although Garfinkel et al. (2016) described all three dimensions of interoceptive ability, a major limitation of the study was the absence of intelligence measurements. The results of this study suggest that IQ must always be accounted for in this area of research. Finally, it may be interesting to expand the focus of this study to an even broader range of ages, including young childhood and older adulthood. One study found inferior interoceptive ability in old age compared to young adulthood in a healthy sample (Khalsa et al., 2009). Our own findings raise several relevant questions: Are TD people with exceptional cognitive capabilities less susceptible to these age effects? Do the similar patterns we observed in high-IQ individuals with ASD and typical development persist into old age? These are important considerations for future research, which will help to establish a more sophisticated understanding of the role of interoceptive cognition in developmental disorders.

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