Contents lists available at ScienceDirect







journal homepage: www.elsevier.com/locate/neuropsychologia

Startle modulation in autism: Positive affective stimuli enhance startle response

Julia L. Wilbarger^{a,*}, Daniel N. McIntosh^{b,**}, Piotr Winkielman^c

^a Department of Kinesiology, Occupational Therapy Program, University of Wisconsin-Madison, 3176 Medical Science Center, 1300 University Avenue, Madison, WI 53706, United States

^b Department of Psychology, University of Denver, 2155 South Race Street, CO 80208, United States

^c Department of Psychology, University of California, San Diego, CA, United States

ARTICLE INFO

Article history: Received 15 September 2008 Received in revised form 29 December 2008 Accepted 19 January 2009 Available online 30 January 2009

Keywords: Startle Affective startle modulation Emotion Affect Motivation Electromyography (EMG)

ABSTRACT

Behavioral evidence suggests that emotion processing deficits in individuals with autism spectrum disorders (ASD) may occur at the level of basic (early, rapid, automatic) affective processes. Consistently, neurological evidence indicates that key brain areas associated with basic affective processing are atypical in ASD. The current study sought to better specify these deficits by comparing different components of basic affective processing in 14 adolescents and adults with ASD and 14 typical controls matched for age and verbal ability. Participants viewed affective pictures, and their responses were assessed with (i) affective eyeblink startle modulation, an indicator of the brain's aversive motivational system; (ii) facial electromyography, an online indicator of implicit valence appraisal; and (iii) self-report, an indicator of overt valence appraisal. The results show that in contrast to the typical pattern, in which exposure to negative stimuli increases startle whereas exposure to positive stimuli decreases startle, individuals with ASD showed startle potentiation to both positive and negative stimuli. Atypical potentiation during positive stimuli occurred despite individuals with ASD demonstrating appropriate implicit valence appraisals, reflected in their facial EMG responses, and appropriate overt appraisals, reflected in their self-reported ratings of the stimuli. Potentiation of startle to both positive and negative stimuli suggests a disruption in basic affective processes in ASD at the level of the early motivational response. This atypical pattern of responses has implications for understanding social and emotion deficits in ASD and calls for further investigation of basic affective processes.

© 2009 Elsevier Ltd. All rights reserved.

Clinical experience and research reveal that individuals with autism spectrum disorders (ASD) have a mosaic of social and emotional skills. People with ASD show atypicalities in several areas of social and emotional functioning (Fein, Pennington, Markowitz, Braverman, & Waterhouse, 1986; Hobson, 2005; Kanner, 1943; Rogers & Pennington, 1991; Sigman, Kasari, Kwon, & Yirmiya, 1992; Sigman & Ruskin, 1999). These disruptions include altered responsiveness to social and affective signals, atypical processing of faces, and greater generation of negative emotional expressions (Dawson et al., 2002; Dissanavake, Sigman, & Kasari, 1996; Hobson, 1995, 1999; Kasari & Sigman, 1996; Rieffe, Terwogt, & Stockmann, 2000; Rogers & Pennington, 1991). However, not all areas of social and emotional functioning are disrupted. Individuals with ASD express a full range of emotion, show attachment behaviors, and comprehend a variety of emotional situations (Braverman, Fein, Lucci, & Waterhouse, 1989; Rogers & Pennington, 1991; Sigman et al., 1992;

** Corresponding author.

Sigman & Ruskin, 1999). Additionally, some ASD deficits in affective processing may be better attributed to cognitive or language factors (Dawson, Soulieres, Gernsbacher, & Mottron, 2007; Ozonoff, Pennington, & Rogers, 1990).

The above pattern of findings suggests that social and emotional processing in ASD is selectively disrupted, rather than uniformly impaired. This calls for a careful examination of different aspects of affective processing to specify which functions are atypical. The present study contributes to this goal by assessing several components of basic affective processing using physiological and behavioral measures.

Successful affective processing involves several basic components, including assignment of salience to stimuli, determination of positive or negative valence, activation of aversive and appetitive systems which prime approach and avoidance behaviors, and generation of affective experience. These early, rapid, spontaneous, and largely automatic processes help guide behavior, especially in fast, dynamic, online interactions with the environment, such as reciprocal social exchanges (Bradley & Lang, 2007; Cacioppo, Tassinary, & Berntson, 2000; Dawson et al., 2002; Lang, 1995). Some of these processes are so rudimentary that several writers proposed that human infants are biologically prepared to perceive and recipro-

^{*} Corresponding author. Fax: +1 608 262 1639.

E-mail addresses: jlwilbarger@education.wisc.edu (J.L. Wilbarger), daniel.mcintosh@du.edu (D.N. McIntosh).

^{0028-3932/\$ -} see front matter © 2009 Elsevier Ltd. All rights reserved. doi:10.1016/j.neuropsychologia.2009.01.025

cally respond to social and emotional information (Balaban, 1995; Meltzoff & Moore, 1995; Stern, 1995; Valenza, Simion, & Cassia, 1996). Consequently, disruptions in these basic skills may contribute to atypical social and emotional development.

Behavioral and neuroscience research suggests that basic affective processes, such as those involved in creating emotional reciprocity, are impaired in autism (Dawson, Webb, & Wijsman, 2005; Dissanayake et al., 1996; Pennington, 2002; Rogers & Pennington, 1991). For example, individuals with ASD are impaired on rapid and spontaneous facial mimicry (McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006; Oberman, Winkielman, & Ramachandran, 2009). They also show undifferentiated and inconsistent rapid facial responses to emotional expressions (Beall, Moody, McIntosh, Hepburn, & Reed, 2008) and demonstrate increased latencies in early event related potential (ERP) brain responses to faces (Webb, Dawson, Bernier, & Panagiotides, 2006; McPartland, Dawson, Webb, Panagiotides, & Carver, 2004; Dawson et al., 2005).

Behavioral evidence of atypicalities in basic affective processes is consistent with the neuropsychological evidence of ASD deficits in basic affective and social brain networks, especially the temporal lobe, the orbital frontal cortex, and the prefrontal cortex (Amaral, Bauman, & Schamann, 2003; Bachevalier, 2000; Baron-Cohen, Ring, Bullmore, Wheelwright, & Williams, 2000; Brothers, 1997; Dalton et al., 2005). In particular, work has focused on the amygdala, a temporal lobe structure involved in processing faces, assignment of affective significance to stimuli, and organization of defensive responses (Aggleton, 2000). Compared to typical peers, in ASD the amygdala shows functional and structural differences (Aylward et al., 1999; Bauman & Kemper, 1985; Bauman & Kemper, 2005) and atypical activation to affective and social stimuli (Baron-Cohen et al., 2000; Critchley et al., 2000; Dalton et al., 2005; Hazenedar et al., 2000; Pierce, Muller, Ambrose, & Courchesne, 2001). In nonhuman primates, removal of or damage to areas of the temporal lobe, including the amygdala, result in deficits in social and affective functioning that parallel some deficits in ASD (Amaral et al., 2003; Bachevalier & Loveland, 2006).

Although behavioral and neuroscience evidence suggests ASD deficits in basic affective processes, it is not clear which specific components are atypical. To examine this, the current study used three different methods that tap into motivational, valence, and explicit appraisal components: (i) affective startle modulation; (ii) facial electromyography; and (iii) self-reports of stimulus valence. As described in the next section, affective startle modulation measures the influence of the valenced stimuli on the rapid and reflexive responses of the aversive motivational system. Typically, negative stimuli activate the aversive response system (enhancing startle) whereas positive stimuli dampen its activation (reducing startle). In contrast, facial EMG provides an online measure of implicit valence appraisals. Typically, positive stimuli activate facial muscles associated with smiling whereas negative stimuli activate facial muscles associated with frowning. Finally, self-report ratings of stimulus valence tap the overt appraisal of the stimulus as well as the socialized understanding of the stimulus value. Assessing all these three components together helps better specify the typical and atypical operation of basic affective processes that underlie social and emotional functioning in people with ASD.

1. Motivational response system: affective startle modulation

The modulation of a startle response during exposure to affective stimuli has been used extensively to study aversive and appetitive response systems in the brain (Davis, 1997; LeDoux, 2000). This method has several benefits. Responses are not contingent upon motor planning, language, or participants' voluntary actions (Ornitz, Lane, Sugiyama, & de Traversky, 1993). Startle modulation is evident across the lifespan, from infancy through adulthood (Balaban, 1995; McManis, Bradley, Berg, Cuthbert, & Lang, 2001). The method is validated across several clinical populations, including individuals with anxiety disorders and sociopathy (Patrick, Cuthbert, & Lang, 1994; Patrick & Zempolich, 1998).

In typical humans and other animals, negative stimuli prime an aversive motivational response (supporting avoidance behaviors) by enhancing startle magnitude to a sudden loud noise whereas positive stimuli prime an appetitive motivational response (supporting approach behaviors) by dampening the startle responses (Bradley, Cuthbert, & Lang, 1990; Cuthbert, Bradley, & Lang, 1996; Davis, 1997). Importantly, simple startle responses are intact among individuals with ASD (Bernier, Dawson, Panagiotides, & Webb, 2005; McAlonan et al., 2002; Ornitz et al., 1993). Thus, the extent and direction of startle modulation by affect helps assess the functioning of basic motivational systems in people with ASD.

Affective startle modulation is supported by neural systems involved in basic affective processing, such as the amygdala. For example, electrical stimulation of the amygdala directly enhances startle reflex amplitude, while lesions abolish it (Davis, 1997; Lang, 1995). Thus, atypical startle modulation responses in individuals with ASD may point to a disruption in amygdala function.

Despite the value of the affective startle modulation as a probe into the early affective and motivational systems, only one study has examined it in ASD, and it obtained inconclusive results (Salmond, de Haan, Friston, Gadian, & Vargha-Khadem, 2003). Salmond and colleagues compared startle modulation to "nice" and "scary" images in children and adolescents with ASD and typical peers. Unexpectedly, in both typical and ASD groups, startle magnitudes were smaller during the negative stimuli than the positive. The typical group results are especially surprising as they run counter to the highly robust finding of startle enhancement during negative stimuli in adults. The interpretation of the study is further complicated by the absence of a neutral condition. Without it, it cannot be determined if there was a suppression of startle to the negative stimuli or an elevation of the positive. Still, these results could be interpreted as reflecting the characteristics of their sample and the characteristics of the manipulation. First, the participants were largely young males (13:1 for ASD, >50% of typical controls). Interestingly, previous research found that typical boys (but not typical girls) demonstrated increased startle responses with exposure to positive versus neutral stimuli and *suppressed* startle with exposure to negative versus neutral stimuli (McManis et al., 2001). Additional data showed that the typical boys did not demonstrate as strong of arousal activation (skin conductance) or affective responses (corrugator activity) to the negative stimuli as girls or adults. McMannis and colleagues proposed that the results indicate incomplete activation of the defensive response system in the young boys. Second, it is worth pointing out that the Salmond and colleagues study did not control for the arousal value for the stimuli. Thus, assuming the mild nature of researcher-selected images for children, the observed decreased amplitude (reflecting orienting) to negative stimulus would be expected, rather than a defensively related increase found at higher levels of intensity for negative stimuli. As shown in previous research, decreased activation to negative or threat stimuli is also occasionally found in adult males, and also across genders when the stimulus intensity is low (Bradley & Lang, 2007; Cuthbert et al., 1996). Finally, the startle probe in Salmond and colleagues (2003) was set at a significant lower volume than is customary for startle research, which could further weaken activation of the aversive motivation system. In short, the previous research on affective startle modulation in ASD is not conclusive regarding the presence and nature of any atypicalities.

In the present study, we address limitations in the previous study. We compared responses across positive, negative, and neutral images from standardized image sets. The positive and negative images were equated for arousal levels with mean arousal ratings sufficient to differentiate startle modulation between positive and negative stimuli. Based on previous behavioral and neurological findings, we predicted that individuals with ASD would demonstrate disruptions in startle modulation to affective stimuli, supporting an atypical connection between affective appraisal and motivational response.

2. Spontaneous online evaluation: facial electromyography

To assess online, implicit evaluation of stimuli, the current study assessed automatic activation of the facial muscles associated with the expression of emotion (Cacioppo, Martzke, Petty, & Tassinary, 1988; Dimberg, 1982; Winkielman & Cacioppo, 2001). In particular, activity over the *corrugator supercilii*, which knits the brow as in a frown, typically shows greater activity during exposure to negative stimuli. The *zygomaticus major*, which pulls the lips back as in a smile, shows increased activity during exposure to positive stimuli, decreased activity during exposure to negative stimuli (Dimberg, 1982).

The research using facial EMG in individuals with ASD is relatively sparse. However, during passive viewing of facial expressions, adults and children with ASD have not shown typical, rapid, affective muscular reactions to others' facial expressions of emotion. Both diminished and enhanced EMG activity has been documented (Beall et al., 2008; Magnée, de Gelder, van Engeland, & Kemner, 2007; McIntosh et al., 2006). When asked to classify emotions of viewed faces, however, children with ASD do show matching emotional facial expressions, but their responses are delayed when compared to those of typically developing children (Oberman et al., 2009). These observed differences in facial responses to affective stimuli in ASD may reflect disruptions in mimicry or behavioral matching, or they may reflect atypical affective responses to the faces (Moody & McIntosh, 2006; Moody, McIntosh, Mann, & Weisser, 2007). Because these previous studies did not examine responses to non-facial stimuli, it is unclear if these differences are motor or affective responses to faces (an affective response to a face may be the same as a motor matching response to the face). Equally unclear is if the differences are specific to social stimuli. In the current study, we examined affective EMG in response to a wider variety of stimuli to evaluate whether people with ASD show a general difference in the automatic appraisal of the affective valence of stimuli. If theories supporting atypical appraisals of emotional stimuli are correct, and the earlier findings reflect this difference, then individuals with ASD should show diminished affective EMG responses to emotional stimuli.

3. Overt evaluations: self-report of experienced affect

We also collected self-reports of experienced affect. This is important because what people consciously feel and explicitly report after viewing a stimulus may differ from the basic motivational response to the stimulus (assessed via startle) and from the implicit valence appraisals (assessed via facial EMG) or both. Based on evidence that people with ASD comprehend emotional situations and express a full range of emotion (Sigman & Ruskin, 1999), we did not expect significant group differences on the selfreport measure. The prediction of group similarity on self-report measures, but not on basic affect measures, is also consistent with proposals that individuals with ASD use slower, more intentional compensatory processes to perform social-emotional tasks (e.g., Rutherford & McIntosh, 2007).

Table 1

Group demographics and matching information.

Group	Ν	Age, mean (SD)	PPVT score, mean (SD)	ASQ score, mean (SD)	Number of males
ASD	14	21.9 (7.5)	104 (21)	22.7 (3.3)	11
Typical	14	21.1(5.7)	112 (12)	1.2 (1.3)	12

4. Method

4.1. Participants

Fourteen high functioning adolescents and adults with ASD were matched to a group of 14 typically developing individuals on chronological age and verbal ability as measured by the Peabody Picture Vocabulary Test (Dunn & Dunn, 1997) (see Table 1). Participants were recruited from Denver, Colorado, area clinics, support groups, community advertisements, and the university research pool. Participants were paid or received course credit. Consent and/or assent were obtained from all participants or their legal guardians. All procedures were approved by the University of Denver Institutional Review Board for the use of human subjects.

Individuals with ASD met the criteria for either Autistic Disorder (AD) or Asperger's (ASP) syndrome using the DSM-IV TR (APA, 2001) and on either the Autism Diagnostic Inventory-Revised (ADI-R) (Lord, Rutter, & Le Couteur, 1994) or the Autistic Diagnostic Observation-Generic (ADOS-G) (Lord et al., 1997). All participants' parents completed an Autism Screening Questionnaire (ASQ) (Berument, Rutter, Lord, Pickles, & Bailey, 1999).¹ Individuals in the ASD group scored above the suggested cut-off (15 points) discriminating between ASD and pervasive developmental disorders (PDD). Typical participants scored well below the cut-off point. Individuals were excluded from participation if they had a significant hearing or visual impairment or other medical conditions prohibiting full participation or if they had autism associated with another condition such as Fragile X syndrome or Tuberous Sclerosis.

4.2. Measures

4.2.1. Verbal ability

The Peabody Picture Vocabulary Test (PPVT) is a receptive language scale that demonstrates good reliability and validity. Average correlation to the Wechsler Intelligence Scale for Children (WISC) Verbal Scale is .91. Responses require only pointing and do not rely on expressive language. Standard scores are available for individuals 3 years to adult. Groups were matched within one standard deviation on PPVT standard scores.

4.2.2. Startle modulation

Affective startle modulation was assessed by magnitude of eye-blink startle measured by EMG activity over the area of *orbicularis oculi* muscle following a 90 db, 50 ms white noise instantaneous rise startle probe. Two electrodes, 5 mm apart, were centered below the bony orbit of the left eye (Berg & Balaban, 1999; Blumenthal et al., 2005). Each eye blink was scored for activity between 30 ms and 150 ms after the onset of the startle probe. A period of 120 ms was chosen to capture eye-blink responses with longer latencies as seen in individuals with autism (Ornitz et al., 1993). Activity was expressed as the difference between muscle activity during the startle period and a 120 ms baseline period before the startle probe.

4.2.3. Affective facial EMG

Electrodes placed on the left brow and the left cheek measured EMG activity over the corrugator supercilii (frown) and zygomaticus major (smile), respectively. All EMG procedures followed guidelines established by Fridlund and Cacioppo (1986). Activity was computed by subtracting muscle activity during a 2 s baseline period before the picture presentation from activity during the first 2 s of the 6 s picture viewing.

4.2.4. Picture ratings

Participants rated the affective valence of the images using the self-assessment manikin (SAM) a 9-point picture symbols scale (Bradley & Lang, 1994; Lang, Greenwald, Bradley, & Hamm, 1993). The SAM has been used for children as young as 7 years and is thought to be language and culture-free. Participants looked at each stimulus picture as long as they liked and then indicated on a computer keyboard how they felt when they looked at the pictures.²

¹ The ASQ has subsequently been published as the Social Communication Questionnaire by Western Psychological Services, Los Angeles.

² The instructions were to "PRESS the number between 1 and 9 that best tells HOW YOU FEEL when you look at the picture."

Table 2

Mean normative ratings for valence and arousal for the IAPS picture stimuli by valence category.

	Picture Valence				
	Negative	Neutral	Positive		
Valence ratings					
Mean	2.35	5.32	7.88		
Range	1.78-3.72	4.47-6.64	7.38-8.34		
Alerting ratings					
Mean	5.36	3.75	5.19		
Range	4–7.35	2.77-5.51	4.1-6.44		

4.3. Picture stimuli

Participants viewed a total of 54 images; 45 from the International Affective Picture System (IAPS) (CSEA-NIMH, 1994) and nine from a standardized set of facial expressions (Matsumoto & Ekman, 1988)³ Six pictures each of three valences (negative, positive, neutral) were presented in blocks of 18 trials. Positive images included nature scenes, food, and positive facial expressions. Negative images included spiders, snakes, car crashes, negative facial expressions, and people in distress. Neutral images included objects such as kitchen utensils and faces with neutral expressions. Half the pictures in each valence category had social content (e.g., faces, people engaged in some type of activity⁴), and half did not (e.g., environments, animals or objects). Because no systematic content effects were found, all analyses included all stimulus types and content effects will not be discussed further. The stimuli were suitable for presentation to individuals across a range of ages and cognitive abilities.

The IAPS images have normative data for the intensity of affective valance and arousal value, validated through self-report rating procedures and psychophysiological measures (Bradley & Lang, 2007). Positive and negative images were matched for arousal ratings. By nature, the neutral affective images have lower arousal ratings. The positive and negative are in a relative moderate range because images of graphic violence or erotica were excluded. The mean normative valence and arousal ratings for the negative, neutral, and positive pictures are displayed in Table 2.

4.4. Procedures

After arrival, participants were oriented to the study; diagnostic information, consent, and assent were obtained; and the PPVT was administered. During the lab session, participants were seated comfortably, their skin was prepared with isopropyl alcohol and mild skin abrasive, and 4mm silver/silver chloride surface electrodes were attached (impedances less than $15 \text{ k}\Omega$). After a brief habituation period, participants engaged in the picture viewing (startle) procedure. Startle procedures were based on previous studies (Bradley et al., 1990; Cuthbert et al., 1996). Fifty-four pictures were shown in three randomly presented blocks of 18. Stimuli were randomized within each block of 18 by presentation software (E-Prime). Each block had an equal number of each valence and social condition. No other constraints were placed on the presentation. Pictures were shown for 6 s on a computer screen, followed by an inter-stimulus interval (ISI) of 10-17 s. A startle probe was presented binaurally through Beyerdynamic TDE-65 sound attenuating headphones during two thirds of the pictures in each block. On these trials, the startle probe was presented pseudorandomly at 2.5, 3.5 or 4.5 s after the onset of the picture. Three versions of the experiment were counterbalanced such that across participants each picture was paired with the acoustic probe an equal number of times. Startle probes were also presented pseudorandomly during the blank screen ISIs. The probe time was varied during trials and additional probes were presented during the ISI to control for conditioning to and anticipating of the sound stimuli. After each block, the participant viewed the stimuli again, this time rating them for affective valence on the Self-Assessment Manikin (Bradley & Lang, 1994). All picture and sound stimuli were presented and responses recorded via computer using E-Prime software (Schneider, Eschmann, & Zuccolotto, 2002). Participants were also videotaped to control for movement and attention artifacts.

Table 3

Means and standard deviations for startle modulation for Picture Valence for each group and Picture Valence.

Group	Picture Valence				
	Negative, mean (SD)	Neutral, mean (SD)	Positive, mean (SD)		
Typical Autism (ASD)	.29(.36) .10(.23)	.06 (.34) 19 (.27)	14 (.43) .14 (.22)		

4.5. Apparatus

A Neuroscan 32-channel Synamps amplifier controlled by SCAN software collected, amplified, and filtered 3 channels of EMG with millisecond accuracy. A PC computer controlled and synchronized data collection and stimulus presentation. The startle probe was amplified and sent to the headphones via a Technica amplifier. Sound levels were calibrated with a Radio Shack Audiometer.

4.6. EMG data acquisition, reduction and analysis

EMG signals were amplified by a factor of 150 at the head box located near the participant and by a factor of 500 at the amplifier. Signals were filtered on-line with a low pass of 500 Hz and a high pass of 10 Hz. Data were sampled at 2048 Hz. The baseline and response period signals for each muscle were rectified, integrated, and a magnitude was calculated offline using CNS Suite data reduction program (Ohio State University Social Neuroscience Laboratory, 1999). The magnitude of EMG response was determined using a Waveform Moment Analysis (WAMA), which calculates a mean of EMG activity across the selected measurement time window (Cacioppo & Dorfman, 1987).

Electromyographic data from each of the three muscles were logarithmically transformed to normalize the distribution of scores and reduce the influence of extreme values. Scores were standardized by block for each individual to reduce the influence of drift and make the data comparable across subjects. All EMG trials for the affective startle modulation and affective facial responses were screened via review of videotapes and raw EMG data. Videotapes were reviewed for lack of attention to the screen, extraneous movement, and lack of eye blinks during startle trials in the participants. We also examined the raw EMG data for activity not related to stimuli (noise) in the pre-stimulus and post-stimulus periods or a lack activity of 10% or greater over the baseline period within the startle probe window. Approximately 10 percent of trials were eliminated, the majority of which were due to movements artifacts; this proportion did not differ across groups. The criteria for trial elimination were based on previous publications (e.g. Berg & Balaban, 1999; Cuthbert et al., 1996).

5. Results

5.1. Startle modulation

As described above, affective startle modulation taps the functioning of the basic appetitive-defensive motivational system. Based on reports of psychological and neurological atypicalities with core affect functioning, we predicted that participants with ASD would show atypical affective startle modulation. We first examined whether there were any effects related to the social content of the pictures. There were no significant main effects or interactions with the other factors for social content factor (p's = .39 - .80). Differences in affective startle modulation were then examined between the two groups (ASD, Typical) and for three different pictures valences (Negative, Neutral, Positive) (Table 3). A mixed model repeated measures ANOVA indicated a significant main effect of Picture Valence, F(2,52) = 5.23, p = .009, and a significant Group by Valence interaction, F(1,26) = 5.82, p = .005. There were no significant differences in startle response for probe time for either group or between groups (p's = .1-.45).

As displayed in Fig. 1, the typically developing group showed the expected pattern of startle potentiation during negative stimuli and suppression during positive stimuli. Startle responses during the negative stimuli were significantly larger than during the neutral stimuli, t(13)=2.28, p=.04 (all *t*-tests are two-tailed) and the positive stimuli, t(13)=2.94, p=.01. There was a trend for smaller startle responses during the positive stimuli compared to the neutral stimuli, t(13)=1.56, p=.10.

³ The source and identification numbers for the affective picture stimuli are listed. International Affective Picture Set (CSEA-NIMH, 1994) – negative non-social stimuli: 3280, 6230, 7380, 9290, 9340, 9560, 9561, 9830, 9910; negative social stimuli: 2800, 2900, 3230, 3301, 3350, 9220; neutral non-social stimuli: 1121, 1560, 1670, 7034, 7100, 7233, 7235, 7500, 7560; neutral social stimuli: 2214, 2250, 2383, 2487, 4605, 9070; positive non-social stimuli: 1440, 1710, 1750, 5700, 5910, 5982, 7230, 7330, 8501; positive non-social stimuli: 2070, 2150, 2340, 2550, 8420, 8470. JACFEE or JACNeuF Facial Images from Matsumoto and Ekman (1988) – negative: E1, E21, E31; neutral N1, N27, N46; positive: E36, E38, E40.

⁴ In all but five of the 27 social content images, facial expression could be clearly seen. In all positive facial expressions were happy and joyful, negative were balanced between anger, sadness and distress.



Fig. 1. Mean standardized log EMG activity over the area of the orbicularis oculi across 120 ms beginning 30 ms after a 50 ms 95 db burst of white noise measured while participants viewed affective picture stimuli. Individuals with ASD differ from the typical pattern by showing startle potentiation while viewing positive stimuli (last column).

As predicted, individuals with ASD did not show this typical pattern. They showed startle potentiation for *both* negative and positive stimuli relative to the neutral stimuli. Startle responses during negative and positive stimuli were significantly larger than responses during the neutral stimuli, t(13)=2.29, p=.04 and t(13)=2.75, p=.02, respectively. Startle responses during exposure to the negative and positive stimuli did not differ significantly from each other.⁵

Additional comparisons within each stimulus valence revealed that groups differed in responses to positive and neutral stimuli, but not to negative stimuli. Specifically, during the positive stimuli, the ASD group showed greater startle than the typical group, t(26) = 2.12, p = .04. During neutral stimuli, the ASD group showed lower startle than the typical group, t(26) = 2.15, p = .04. In short, individuals with ASD demonstrated a strikingly consistent pattern of potentiation to both positive and negative stimuli. Eighty-six percent of the ASD group demonstrated this pattern, whereas only one person (7%) in the typical group did so.

5.2. The role of arousal in startle magnitude

It is important to consider whether the increased startle magnitudes for both positive and negative stimuli in the ASD group are due to the higher arousal ratings of the positive and negative stimuli. To evaluate this possibility, bivariate correlations were performed between the arousal values and startle magnitudes. There were no significant correlations between startle magnitudes and arousal values for the individual stimuli. Correlations between startle magnitudes and the normative arousal ratings for the picture stimuli for the typical and ASD groups are respectively, .24 and .06 for positive stimuli, .08 and .05 for neutral stimuli, and .08 and .12 for negative stimuli. Arousal ratings do not appear to account for the startle modulation results.⁶



Fig. 2. Mean standardized log EMG activity over the areas of the (A) zygomaticus major and (B) corrugator supercilii across a 2 s interval while participants viewed three valences of affective stimuli. Responses were equivalent between individuals with ASD and typical individuals for both muscles and across Picture Valence.

5.3. Affective facial EMG

As described above, facial EMG taps into appraisal of Picture Valence reflecting higher-order, yet implicit processes. If atypicalities in ASD processing occur uniformly across multiple levels of affective processing, one should expect group difference on this measure. However, if higher-order processes are intact, one should expect no differences.

These predictions were tested in two Group (Typical, ASD) by Picture Valence (Negative, Neutral, Positive) repeated measures ANOVAs, one for each facial muscle (zygomaticus and corrugator) (Fig. 2A and B). Overall, there were no Group differences or Group by Valence interactions in zygomaticus or corrugator activity (p > .05). More specifically, in both groups the analysis revealed a standard pattern of facial reactions to affective pictures. For zygomaticus activity (e.g., smiling), there was a significant main effect for Picture Valence, F(2,66) = 13.44, p = .001, with greater zygomaticus activity during positive images compared to the negative and neutral images, *t*(35)=4.1, *p*<.001 and *t*(35)=4.1, *p*<.001, respectively. There was no difference in EMG activity over the zygomaticus between the negative and neutral conditions. For corrugator activity (e.g., scowling), there was also a significant effect for Valence, F(2,46) = 20.98, p = .001, with more corrugator activity during negative images than during positive and neutral images, t(35) = 4.89, p < .001, and t(35) = 2.69, p = .011, respectively. Corrugator activity was lower during positive compared to neutral images, t(35) = 5.13, p < .001. In conclusion, the EMG data indicated that this sample of high functioning individuals with ASD demonstrated typical appraisal of the valence of the stimuli shown through expressive responses.

5.4. Self-report picture rating

Finally, we collected participants' self-report of valence. This measure allowed us to determine whether any atypical physio-

⁵ The apparent suppression of startle responses to neutral pictures is an artifact of standardization. Responses were standardized for each individual. The standardized startle responses for the neutral stimuli are usually at the mean or zero point. This was true for the typical group. In the ASD group, the overall standardized mean startle responses are higher because of the increased magnitude of startle responses to the positive stimuli. This results in the responses to the neutral stimuli that fall below the mean or become negative.

⁶ In the current study, startle responses did not correlate with the established norms for arousal rating for any of the groups. However, individuals in the current study did not rate the pictures for arousal value, so we do not know if the established norms apply to the ASD group.

logical responses reflect different understandings of the affective qualities of the stimuli. The groups did not differ in their affective ratings of the pictures. A Group (Typical, ASD) by Picture Valence (Negative, Neutral, Positive) repeated measures ANOVA found no differences for Group or Group by Valence interactions (p > .05). There was a significant effect of Picture Valence, F(4,48) = 260.75, p = .001. Positive stimuli received the most positive (highest) ratings (M = 7.25, SD = 1.1) followed by neutral (M = 4.4, SD = .67) and negative stimuli (M = 2.62, SD = .87). These ratings are consistent with norms established for these stimuli (Center for the Study of Emotion and Attention, CSEA-NIMH, 1994).

6. Discussion

The current study assessed startle modulation, facial EMG, and self-reported affective responses during emotional stimuli to examine different components of affective processes in individuals with ASD and typical controls. There were three important findings.

First, and most critically, the results supported our prediction of atypical startle modulation, with ASD individuals showing startle potentiation to both positively and negatively valenced stimuli. This pattern contrasts with typical affective modulation of startle responses, in which startle is suppressed during positive stimuli and increased during negative stimuli (Lang, 1995).7 As discussed in the introduction, unusual affective startle modulation in children and adolescents with ASD was also reported by Salmond et al. (2003). They found greater startle during positive versus negative stimuli. However, there was no such difference in the present data. The lack of an affectively neutral condition, uncertainty regarding arousal levels of the stimuli, and a weaker than usual startle probe in Salmond and colleague's study may explain the differences in findings. At minimum, the two studies together indicate that affective startle modulation is disrupted in ASD, with atypical startle potentiation during positive stimuli. Given the differences in methods, there is good evidence from the present study that there is also potentiation during negative stimuli.

The atypical potentiation during positive stimuli occurred despite the next pair of findings. Individuals with ASD made appropriate implicit appraisals of the positive and negative stimuli (demonstrated through facial EMG), and made appropriate selfreports of affective valence. These findings from the current study provide an important context for interpreting the affective startle modulation result.

The second finding of valence-appropriate EMG responses in ASD participants runs against suggestions that ASD individuals are impaired across different levels of affective processes. Instead, the current findings are consistent with recent reports that facial EMG responses in ASD may be atypical or typical, depending on whether the task requires spontaneous responses or encourages active valence processing. Specifically, during passive viewing of facial expressions children (Beall et al., 2008) and adults (McIntosh et al., 2006) with ASD do not consistently show the same pattern of rapid matching of emotional facial EMG responses as seen in typical children and adults. However, other work found that ASD individuals will show valence-congruent facial EMG responses when the task encourages explicit categorization or involves longer periods of viewing (Magnée et al., 2007; Oberman et al., 2009). The present study used a relatively long 2 s viewing window, but participants were not asked to explicitly categorize the stimuli. We may have tapped into responses that, while implicit, were more subject to higher-order influences because we measured EMG over a longer period of time than studies looking at rapid and spontaneous responses. In conclusion, it appears that individuals with ASD may use higher-order, atypical, or less rapid processes to make affective appraisals (Rutherford & McIntosh, 2007). Interestingly, the absence of any differences in valence appraisal based on the social versus non-social content of the stimuli suggests that observed differences are unrelated to differences in attention to faces. Still, further work evaluating this possibility directly would be useful.

Finally, the current study found no group differences on selfreports of affective experience. The finding that ASD individuals can appropriately evaluate standard affective stimuli is consistent with previous findings and further supports the idea that the higherorder process of valence appraisal is intact in individuals with ASD.

6.1. Possible implications of atypicalities in affective startle modulation

The observed atypical potentiation of startle during positive stimuli in ASD individuals, despite their intact higher-order valence appraisals, has several implications for understanding the basis of behavior and development in autism.

First, these results suggest a disruption in ASD in a specific early stage, automatic affective process: potentially due to either the atypical priming of an aversive motivational system or the lack of activation of appetitive influences during exposure to positive stimuli. One of the primary functions of affect is preparation for action towards or away from stimuli in the environment. The presence of affective stimuli automatically influences motivational responses such as startle, which is a basic automatic defensive response. Exposure to positive stimuli that activates appetitive motivation should suppress startle (Lang, 1995; Schmid, Koch, & Schnitzler, 1995). That positive stimuli enhanced startle responses in adults with ASD indicates a possible dissociation between the typical motivational response to affective stimuli and the higher-order assignment of valence to stimuli.

Several questions arise about possible consequences of this phenomenon. Full activation of the defensive response system involves a cascade of behavioral and physiological responses (Graham, 1984; Davis, 1997; LeDoux, 2000). Behaviorally, the results of defensive responses include freezing, fleeing or fighting. Although defensive types of behaviors such as avoidance or aggression are not uncommon in individuals with autism neither are they predominant behaviors across all individuals, particularly high functioning individuals with ASD. Therefore, atypical priming or the lack of suppression of the aversive response system to positive stimuli is likely to result in more subtle behavior such as diminished approach behaviors, decreased range of preference or increased general negative affect (Murphy & Zajonc, 1993; Winkielman, Berridge, & Wilbarger, 2005). Indeed, children with autism have been reported to demonstrate more negative emotional expressions, are more likely to demonstrate negative affect in positive situations, use more blended emotions, have gaze aversion, and show reduced social approach and attention (Kasari, Sigman, Yirimiya, & Mundy, 1998). Further, some autobiographical accounts by adults with ASD note discomfort with affective social contact and often describe the need to learn the rules of social engagement that seem to come so naturally to others (Jones, Quigley, & Huws, 2003; Grandin, 2000).

The second implication of finding atypical affective processing concerns the development of social and emotional skills. Several authors have proposed that deficits in the assignment of salience or reward to affective stimuli may explain key deficits in autism, such as face processing, joint attention and language (Baron-Cohen et al., 2000; Dawson et al., 2005; Gaigg & Bowler, 2007; Mundy & Neal, 2000; Winkielman, McIntosh, & Oberman, in press). The results of our study support the notion of a disruption in the assign-

⁷ Hess et al. (2007) found that in typical males, which make up most of our control sample, the startle modulation by affective faces was similar to the non-face stimuli (potentiation to angry, inhibition to happy). This is consistent with our findings where we saw no effects of social versus non-social content.

ment of reward value to stimuli rather than a *lack* of responsiveness to affective stimuli in ASD. Even if positive stimuli are not directly aversive, individuals with ASD may perceive positive stimuli as ambiguous or lacking reward. Accordingly, they may cognitively appraise them as positive, but experience a low-level defensive motivational (somatic) response. Such ambiguity may render positive stimuli unreliable, useless, or even noxious. For example, if a child's mother's smile towards a new toy primes the same physiological tendency for aversive responding as a frown at approach to a hot stove, at some point referencing a parent for affective cues may not yield salient information. Social referencing may therefore diminish.

Third, our results have implications for the study of the neurological substrates of ASD, and emphasize the importance of further investigation of aversive and appetitive response systems. Approach and avoidance behaviors involve multiple overlapping brain systems (Berridge, 2003; Rolls, 1999). Some of the brain systems involved in appetitive and defensive behavior have also been implicated in autism, including the temporal lobe, the amygdala, and oribitofrontal cortex (OFC) (Amaral et al., 2003; Aylward et al., 1999; Bachevalier, 2000; Bachevalier & Loveland, 2006; Baron-Cohen et al., 2000; Brothers, 1990; LeDoux, 1996; Rolls, 1999).

The amygdala is an important structure to consider as it has been implicated in autism, and is critical in affective modulation of startle responses (Davis, 1997). One key function of the amygdala is the coordination of output to the autonomic nervous system (ANS) for defensive responding such as in affective startle modulation. Our results imply that the output of this circuit function typically for the potentiation of startle during exposure to negative stimuli, but not for the suppression of startle during exposure to positive stimuli. This finding provokes the question of how key a neural system for the modulation of affect, such as the amygdala, functions in autism. Some researchers argue that the amygdala is responsible for the assignment of both significance and valence of stimuli (Davis, 1997; LeDoux, 2000). Others point to the role of the frontal reward system in the assignment of valence to affective stimuli, particularly in primates (Rolls, 1999). The OFC is particularly important in the assignment of reward value in the context of motivation (Rolls, 1999). Additionally, appetitive behavior is coordinated by a host of other brain structures that interface with the amygdala, such as the nucleus accumbens (NAC) and hypothalamus (Berridge, 2003). In particular, lesions or pharmacological disruptions in the NAC in animals have been shown to reduce the effect of appetitive stimuli startle attenuation (Koch, Schmid, & Schnitzler, 1996). Although currently there is little evidence of differences in the NAC in people with ASD (Langen, Durston, Staal, Palmen, & van England, 2007), animal models of autism in rats prenatally treated with valproic acid show deficits in the NAC related to hedonic functioning (Schneider, Ziòłkowska, Gieryk, Tyminska, & Przewłocki, 2007).

Recent proposals about social and affective deficits in ASD have implicated both the amygdala and the OFC. Dalton et al. (2005) propose that attention to face stimuli activates affective processing circuitry including the amygdala and the OFC and produces negatively valenced hyperarousal which in turn leads to characteristic gaze aversion to faces. Dawson et al. (2005) have proposed a social motivation hypothesis for explaining affective processing deficits in ASD involving reward circuitry of the amygdala and OFC. The authors propose that the usual affective or social stimuli fail to activate the expected reward circuitry. In particular, this negatively influences attention to affective and social stimuli resulting in significant deviations in the development of affective processing capacities and a disadvantage in emotion processing tasks.

Animal models of autism have pointed to deregulation of the amygdala response to affective stimuli (Amaral et al., 2003; Bachevalier, 2000; Markram, Rinaldi, Mendola, Sandi, & Markram, 2008). Rats prenatally treated with valproic acid, which disrupts development of the amygdala, demonstrate not only many behavioral features of autism but also demonstrate lack of inhibition and dysregulation of the amygdala (Markram et al., 2008). The treated rats have greater levels of anxiety, decreased prepulse inhibition, and exaggerated and prolonged fear conditioning. Cellular recording from the amygdala showed increased excitability, hyperplasticity, sensitization, and impaired inhibition. Based on these results Markram et al. (2008) propose an "aversive world" hypothesis in autism, one in which individuals may be overly averse responsive.

The currently observed atypicality in the phenomenon of affective startle modulation, a phenomenon which has been closely linked to aversive and appetitive neural systems such as the amygdala and the nucleus accumbens in previous research, is consistent with neurofunctional deficits in autism. However, as direct or specific neural activity was not measured, the data do not directly address its role in the observed disruptions. Nonetheless, the data do underscore the importance of further examination of the neurological underpinnings of aversive and appetitive motivation, and the assignment of significance and valence to affective stimuli in people with ASD. Further study can clarify whether the results found here are more related to disruptions in the priming of aversive responses or the suppression of appetitive activation for the positive stimuli. An additional alternative to explore is the potential role of disruptions in the early assignment of valence to the stimuli. Lack of valence discrimination may leave responses open to non-valence specific influences such as an arousal dimension.

Finally, our findings have important implications for interventions for individuals with ASD. If exposure to affective stimuli activates an aversive motivational response or increases generalized arousal, then intervention strategies might best be directed towards facilitating modulation or regulation of responses. The results here also suggest a dissociation between rapid and automatic processing, and more voluntary and cognitively oriented strategies for interpreting affective stimuli. This finding should be taken into account in intervention for individuals with ASD. Awareness of the possible dissociation of somatic and cognitive responses to social or emotional situations at the least should be acknowledged in the intervention process. Strategies for increased understanding of emotional and social information might be paired with strategies for managing the possible stress associated with processing emotional or social stimuli.

6.2. Limitations

The interpretation of the current results is limited to high functioning adolescents and adults with autism or Asperger's syndrome. All the individuals in this study had normal or above average cognitive and verbal abilities. Individuals with lower cognitive and language skills may show differences in the self-report of affective appraisals and possibly facial EMG. In fact, the disjunctions observed here may reflect the ability of our sample to compensate for the lack of low-level basic valence discrimination with higher order, rule-driven processes (Rutherford & McIntosh, 2007). At the same time, the typical nature of facial EMG responses suggests that our sample did not only report proper valence, but also responded with their faces accordingly. In any case, the observed pattern of increased potentiation to positive stimuli was striking and the findings strongly suggest further study of a broader group of people with ASD, including younger and more affected individuals.

It is possible that the results of this study could be related to poor modulation of arousal and attention in general. The participants in this study did not rate the stimuli on an arousal dimension. Without participants' ratings, the contribution of arousal to the startle responses remains unclear. The ASD participants' unique perception of the arousal values of the stimuli may have contributed to the results. Although, as found in other studies (Bradley & Lang, 2007), the magnitude of startle did not correlate significantly with the arousal values of the stimuli, and attention was controlled by video review of looking behavior. Nonetheless, direct measurement of arousal ratings or physiological arousal such as the use of electrodermal responses or heart rate would shed light on this question.

7. Conclusion

In typically developing individuals, a combination of affective processes that mark certain stimuli as important or salient and direct action towards relevant stimuli typically support appropriate social and emotional behavior. Consequently, deviations in those processes may result in functional deficits. The present study reveals that focused examination of separate components of affective processes can enhance understanding of differences related to ASD, revealing both strengths and deficits. These data add specific support to the idea that an important aspect of the emotion disruption in ASD is in early stage, automatic, affective processes. The possibility that affective stimuli activate the aversive motivation system in the nervous system should be considered in theories for understanding social and emotional functioning in ASD as well as the corresponding intervention approaches.

Acknowledgements

This research was conducted at the University of Denver, CO, USA and supported by a grant from the National Alliance for Autism Research to McIntosh and Winkielman. We appreciate the assistance and input of Bruce Pennington, Yuko Munakata, Adi Curiel, John Curtin, Mark Starr, Sally Rogers and the time and commitment of the individuals who participated in this research.

References

- Aggleton, J. P. (2000). *The Amygdala: A functional analysis* (2nd ed.). Oxford, UK: Oxford University Press.
- Amaral, D. G., Bauman, M. D., & Schamann, C. M. (2003). The amygdala and autism: Implications from non-human primate studies. *Genes, Brain and Behavior*, 2, 295–302.
- American Psychiatric Association. (2001). Diagnostic and Statistical Manual of Mental Disorders-IV-TR. Washington, DC: American Psychiatric Association.
- Aylward, E. H., Minshew, N. J., Goldstein, G., Honeycutt, N. A., Augustine, A. M., Yates, K. O., et al. (1999). MRI volumes of amygdala and hippocampus in non-mentally retarded autistic adolescents and adults. *Neurology*, 53, 2145–2150.
- Bachevalier, J. (2000). The amygdala, social cognition and autism. In J. P. Aggleton (Ed.), The amygdala: A functional analysis. Oxford, UK: Oxford University Press.
- Bachevalier, J., & Loveland, K. A. (2006). The orbitofrontal-amygdala circuit and self-regulation of social-emotional behavior in autism. *Neuroscience and Biobehavioral Reviews*, 30, 97–117.
- Balaban, M. T. (1995). Affective influences on startle in five-month-old infants: Reactions to facial expressions of emotion. *Child Development*, 66, 28–36.
- Baron-Cohen, S., Ring, H. A., Bullmore, E. T., Wheelwright, S., & Williams, S. C. R. (2000). The amygdala theory of autism. *Neuroscience and Biobehavioral Reviews*, 24, 355–364.
- Bauman, M. L., & Kemper, T. L. (1985). Histoanatomic observations of the brain in early infantile autism. *Neurology*, 35, 866–874.
- Bauman, M. L., & Kemper, T. L. (2005). Neuroanatomic observations of the brain in autism: a review and future directions. *International Journal of Developmental Neuroscience*, 23(2–3), 183–187.
- Beall, P. M., Moody, E. J., McIntosh, D. N., Hepburn, S. L., & Reed, C. L. (2008). Rapid facial reactions to emotional facial expressions in typically developing children and children with autism spectrum disorder. *Journal of Experimental Child Psychology*, 101, 206–223.
- Berg, K., & Balaban, M. (1999). Startle elicitation: Stimulus parameters, recording techniques, and quantification. In M. Dawson, A. Shell, & A. Bohmelt (Eds.), Startle modification: Implications for neuroscience, cognitive science, and clinical science (2nd ed., pp. 21–50). Cambridge UK: Cambridge University Press.
- Bernier, R., Dawson, G., Panagiotides, H., & Webb, S. (2005). Individuals with autism spectrum disorder show normal responses to a fear potential startle paradigm. *Journal of Autism & Developmental Disorders*, 35, 575–583.

Berridge, K. (2003). Pleasures of the brain. Brain & Cognition, 52, 106-128.

Berument, S. K., Rutter, M., Lord, C., Pickles, A., & Bailey, A. (1999). Autism screening questionnaire: Diagnostic validity. *British Journal of Psychiatry*, 175, 444–451.

- Blumenthal, T. D., Cuthbert, B. N., Filion, D. L., Hackley, S., Lipp, O. V., & van Boxtel, A. (2005). Committee report: Guidelines for human startle eyeblink electromyographic studies. *Psychophysiology*, 42, 1–15.
- Bradley, M. M., & Lang, P. J. (2007). Emotion and motivation. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), *Handbook of psychophysiology* (3rd ed., pp. 581–607). New York: Cambridge University Press.
- Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *Journal of Behavioral Therapy and Experimental Psychiatry*, 25, 49–59.
- Bradley, M. M., Cuthbert, B. N., & Lang, P. J. (1990). Startle reflex modulation: Emotion or attention? Psychophysiology, 27, 513–522.
- Braverman, M., Fein, D., Lucci, D., & Waterhouse, L. (1989). Affect comprehension in children with pervasive developmental disorders. *Journal of Autism and Devel*opmental Disorders, 17, 301–316.
- Brothers, L. (1990). The social brain: A project for integrating primate behavior and neurophysiology in a new domain. *Concepts in Neuroscience*, 1, 27–51.
- Brothers, L. (1997). Friday's footprints: How society shapes the mind. Oxford, UK: Oxford University Press.
- Cacioppo, J. T., & Dorfman, D. (1987). Waveform movement analysis in psychophysiological research. Psychological Bulletin, 102, 421–438.
- Cacioppo, J. T., Martzke, J. S., Petty, R. E., & Tassinary, L. G. (1988). Specific forms of facial EMG response index emotions during an interview: From Darwin to the continuous flow hypothesis of affect-laden information processing. *Journal of Personality and Social Psychology*, 54, 592–604.
- Cacioppo, J. T., Tassinary, L. G., & Berntson, G. G. (2000). Psychophysiological sciences. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), Handbook of psychophysiology (2nd ed., pp. 3–26). New York: Cambridge University Press.
- Center for the Study of Emotion and Attention (CSEA-NIMH). (1994). International affective picture system (photographic slides). Gainesville, FL: The Center for Research in Psychophysiology, University of Florida.
- Critchley, H., Daly, E., Bullmore, E., Williams, S. C. R., Van Amelsvoort, T., Robertson, D. M., et al. (2000). Functional neuroanatomy of social behavior: Changes in cerebral blood flow when people with autistic disorder process facial expressions. *Brain*, 123, 2203–2212.
- Cuthbert, B. N., Bradley, M. M., & Lang, P. J. (1996). Probing picture perception: Activation and emotion. *Psychophysiology*, 33, 103–111.
- Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., & Goldsmith, H. H. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nature Neuroscience*, 8, 519–526.
- Davis, M. (1997). The neurophysiological basis of acoustic startle modulation: Research on fear motivation and sensory gating. In P. Lang, R. Simons, & M. M. Balaban (Eds.), Attention and orienting: Sensory and motivational processes (pp. 69–98). Mahwah, NJ: Lawrence Erlbaum.
- Dawson, G., Webb, S., Schellenberg, G. D., Dager, S., Friedman, S., Aylward, E., et al. (2002). Defining the broader phenotype of autism: Genetic, brain, and behavioral perspectives. *Development and Psychopathology*, 14, 581–600.
- Dawson, G., Webb, S. J., & Wijsman, E. (2005). Neurocognitive and electrophysiological evidence of altered face processing in parents of children with autism: Implications for a model of abnormal development of social brain circuitry in autism. Development and Psychopathology, 17, 679–697.
- Dawson, M., Soulieres, I., Gernsbacher, M. A., & Mottron, L. (2007). The level and nature of autistic intelligence. *Psychological Science*, 18, 657–662.
- Dimberg, U. (1982). Facial reactions to facial expressions. *Psychophysiology*, 19, 643–647.
- Dissanayake, C., Sigman, M., & Kasari, C. (1996). Long-term stability of individual differences in the emotional responsiveness of children with autism. *Journal of Child Psychology and Psychiatry*, 37, 461–467.
- Dunn, L. M., & Dunn, L. M. (1997). Peabody Picture Vocabulary Test (3rd ed.). Circle Pines, MN: American Guidance Services.
- Fein, D., Pennington, B., Markowitz, P., Braverman, M., & Waterhouse, L. (1986). Towards a neuropsychological model of infantile autism: Are social deficits primary? Journal of the American Academy of Child and Adolescent Psychology, 25, 198–212.
- Fridlund, A. J., & Cacioppo, J. T. (1986). Guidelines for human electromyographic research. Psychophysiology, 23, 567–589.
- Gaigg, S. B., & Bowler, D. M. (2007). Differential fear conditioning in Asperger's syndrome: Implications for an amygdala theory of autism. *Neuropsychologia*, 45, 2125–2134.
- Graham, F. K. (1984). An affair of the heart. In M. G. H. Coles, J. R. Jennings, & J. A. Stern (Eds.), Psychophysiological perspectives: Festschrift for Beatrice and John Lacey (pp. 171–187). New York: Van Nostrand Reinhold.

Grandin, T. (2000). Thinking in pictures. New York: Doubleday.

- Hazenedar, M. M., Buchsbaum, M., Wei, T., Hof, P., Cartwright, C., Bienstock, C., et al. (2000). Limbic circuitry in patients with autistic spectrum disorders studied with positron emission tomography and magnetic resonance imaging. *American Journal of Psychiatry*, 157, 1994–2001.
- Hess, U., Sabourin, G., & Kleck, R. E. (2007). Postauricular and eye-blink startle responses to facial expressions. *Psychophysiology*, 44, 431–435.
- Hobson, P. R. (2005). Autism and emotion. In F. R. Volkmar, R. Paul, A. Klin, & D. Cohen (Eds.), Handbook of autism and pervasive developmental disorders. Vol. 1. Diagnosis, development, neurobiology, and behavior (3rd ed., pp. 406–422). Hoboken, NJ: John Wiley & Sons, Inc.
- Hobson, P. R. (1995). Apprehending attitudes and actions: Separable abilities in early development? Development and Psychopathology, 7, 171–182.
- Hobson, P. R. (1999). Beyond cognition: A theory of autism. In P. Lloyd & C. Fernyhough (Eds.), Perspectives on the Nature of Autism (pp. 253–281). New York: Routledge.

- Jones, R., Quigley, C., & Huws, J. C. (2003). First-hand accounts of sensory-perceptual experiences in autism: A qualitative analysis. *Journal of Intellectual & Developmental Disabilities*, 28, 112–121.
- Kanner, L. (1943). Autistic disturbance of affective contact. Nervous Child, 2, 217–250.
- Kasari, C., & Sigman, M. (1996). Expression and understanding of emotion in atypical development: Autism and Down syndrome. In M. Lewis, M. Sullivan, & M. Wolan (Eds.), *Emotional development in atypical children* (pp. 109–130). Mahwah, NJ: Lawrence Erlbaum Associate.
- Kasari, C., Sigman, M., Yirimiya, N., & Mundy, P. (1998). Affective development and communication in young children with autism. In A. Kaiser & D. B. Gray (Eds.), *Enhancing children's communication: Research foundation of intervention*. Baltimore, MD: Brooks.
- Koch, M., Schmid, A., & Schnitzler, H.-U. (1996). Pleasure-attenuation of startle is disrupted by lesions of the nucleus accumbens. *Neuroreport*, 7, 1442–1446.
- Lang, P. J. (1995). The emotion probe: Studies of motivation and attention. American Psychologist, 50, 372–385.
- Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, facial, visceral, and behavioral reactions. *Psychophysiology*, 30, 261–273.
- Langen, M., Durston, S., Staal, W. G., Palmen, S. J. M. C., & van England, H. (2007). Caudate nucleus in enlarged in high functioning medication naive subjects with autism. *Biological Psychiatry*, 62, 262–266.
- LeDoux, J. E. (1996). The emotional brain: The mysterious underpinnings of emotional life. New York: Simon & Schuster.
- LeDoux, J. E. (2000). The amygdala and emotion: A view through fear. In J. P. Aggleton (Ed.), *The amygdala: A functional analysis* (2nd ed., pp. 289–310). Oxford, UK: Oxford University Press.
- Lord, C., Risi, S., Lambrecht, L., Cook, E., Bennet, L. L., DiLavore, P., et al. (1997). The Autism Diagnostic Observation Schedule-Generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders*, 30, 205–223.
- Lord, C., Rutter, M., & Le Couteur, A. (1994). Autism Diagnostic Interview-Revised: A revised version of a diagnostic interview for caregivers of individuals with possible pervasive developmental disorders. *Journal of Autism and Developmental Disorders*, 24, 659–685.
- Magnée, M. J. C. M., de Gelder, B., van Engeland, H., & Kemner, C. (2007). Facial electromyographic responses to emotional information from faces and voices in individuals with pervasive developmental disorder. *Journal of Child Psychology* and Psychiatry, 48, 1122–1130.
- Markram, K., Rinaldi, T., Mendola, D. L., Sandi, C., & Markram, H. (2008). Abnormal fear conditioning and amygdala processing in an animal model of autism. *Neuropsychopharmacology*, 33, 901–912.
- Matsumoto, D., & Ekman, P. (1988). Japanese and Caucasian Facial Expressions of Emotion (JACFEE) and Neutral Faces (JACNeuF). *Report available from Intercultural and Emotion Research Laboratory*, Department of Psychology, San Francisco State University.
- McAlonan, G. M., Daly, E., Kumari, V., Critchley, H. D., van Amelsvoort, T., Suckling, J., et al. (2002). Brain anatomy and sensorimotor gating in Asperger's syndrome. *Brain: A Journal of Neurology*, 125, 1594–1606.
- McIntosh, D. N., Reichmann-Decker, A., Winkielman, P., & Wilbarger, J. L. (2006). When the social mirror breaks: Deficits in automatic, but not voluntary, mimicry of emotional facial expressions in autism. *Developmental Science*. 9, 295–302.
- McManis, M. H., Bradley, M. M., Berg, W., Cuthbert, B. N., & Lang, P. J. (2001). Emotional reactions in children: Verbal, physiological, and behavioral responses to affective pictures. *Psychophysiology*, 38, 222–231.
- McPartland, J., Dawson, G., Webb, S. J., Panagiotides, H., & Carver, L. J. (2004). Event-related brain potentials reveal anomalies in temporal processing of faces in autism spectrum disorder. *Journal of Child Psychology and Psychiatry*, 45, 1235–1245.
- Meltzoff, A. N., & Moore, M. K. (1995). Infants understanding of people and things: From body imitation to folk psychology. In J. L. Bernudez, A. Marcel, & N. Eilan (Eds.), The body and the self (pp. 41–69). Cambridge, MA: Bradford/MIT Press.
- Moody, E. J., & McIntosh, D. N. (2006). Mimicry and autism: Bases and consequences of rapid, automatic matching behavior. In S. J. Rogers & J. Williams (Eds.), *Imitation and the social mind: Autism and typical development* (pp. 71–95). New York: Guilford Press.
- Moody, E. J., McIntosh, D. N., Mann, L. J., & Weisser, K. R. (2007). More than mere mimicry? The influence of emotion on rapid facial reactions to faces. *Emotion*, 7, 447–457.

- Mundy, P., & Neal, R. (2000). Neural plasticity, joint attention, and a transactional social-orienting model of autism. *International Review of Research in Mental Retardation*, 20, 139–168.
- Murphy, S. T., & Zajonc, R. B. (1993). Affect, cognition, and awareness: Affective priming with optimal and suboptimal stimulus exposures. *Journal of Personality and Social Psychology*, 64, 723–739.
- Oberman, L. M., Winkielman, P., & Ramachandran, V. S. (2009). Slow echo: Facial EMG evidence for the delay of spontaneous, but not voluntary emotional mimicry in children with autism spectrum disorders. *Developmental Science*, doi:10.1111/j.1467-7687.2008.00796.x, in press.
- Ohio State University Social Neuroscience Laboratory (1999). CNS Suite Data Analysis Software.
- Ornitz, E., Lane, S., Sugiyama, T., & de Traversky, J. (1993). Startle modulation studies in autism. Journal of Autism and Developmental Disorders, 23, 619–637.
- Ozonoff, S., Pennington, B., & Rogers, S. J. (1990). Are there emotion perception deficits in young autistic children? *Journal of Child Psychology and Psychiatry*, 31, 343–361.
- Patrick, C. J., & Zempolich, K. A. (1998). Emotion and aggression in the psychopathic personality. Aggression and Violent Behavior, 3, 523–534.
- Patrick, C. J., Cuthbert, B. N., & Lang, P. J. (1994). Emotion in the criminal psychopath: Fear image processing. Journal of Abnormal Psychology, 103, 523–534.
- Pennington, B. F. (2002). The development of psychopathology: Nature and nurture. New York: Guilford.
- Pierce, K., Muller, R. A., Ambrose, J. A. G., & Courchesne, E. (2001). Face processing occurs outside of the fusiform 'face area' in autism: Evidence from functional MRI. *Brain*, 124, 2049–2073.
- Rieffe, C., Terwogt, M. M., & Stockmann, L. (2000). Understanding atypical emotions among children with autism. *Journal of Autism & Developmental Disorders*, 30, 195–203.
- Rogers, S. J., & Pennington, B. (1991). A theoretical approach to the deficits in infantile autism. Development and Psychopathology, 3, 137–162.
- Rolls, E. T. (1999). The brain and emotion. Oxford, UK: Oxford University Press.
- Rutherford, M. D., & McIntosh, D. N. (2007). Rules versus prototype matching: Strategies of perception of emotional facial expressions in the autism spectrum. *Journal* of Autism and Developmental Disorders, 37, 187–196.
- Salmond, C. H., de Haan, M., Friston, K. J., Gadian, D. G., & Vargha-Khadem, F. (2003). Investigating individual differences brain anomalies in autism. *Philosophical Transactions of the Royal Society London*, 358, 405–413.
- Schneider, T., Ziòłkowska, B., Gieryk, A., Tyminska, A., & Przewłocki, R. (2007). Prenatal exposure to valproic acid disturbs the enkephalinergic system functioning, basal hedonic tone, and emotional responses in an animal model of autism. *Psychopharmacology*, 193(4), 547–555.
- Schneider, W., Eschmann, A., & Zuccolotto, A. (2002). E-Prime user's guide. Pittsburgh, PA: Psychology Software Tools, Inc.
- Schmid, A., Koch, M., & Schnitzler, H.-U. (1995). Conditioned pleasure attenuates the startle response in rats. Neurobiology of Learning and Memory, 64, 1–3.
- Sigman, M., & Ruskin, E. (1999). Continuity and change in the social competence of children with autism, Down syndrome, and developmental delays. *Monographs* of the Society for Research in Child Development, 64, 1–142.
- Sigman, M., Kasari, C., Kwon, J.-H., & Yirmiya, N. (1992). Responses to the negative emotions of others by autistic, mentally retarded and normal children. *Child Development*, 63, 796–807.
- Stern, D. (1995). The interpersonal world of the infant. New York: Basic.
- Valenza, E., Simion, F., & Cassia, V. M. (1996). Face preference at birth. Journal of Experimental Psychology, 22, 892–903.
- Webb, S. J., Dawson, G., Bernier, R., & Panagiotides, H. (2006). ERP evidence of atypical face processing in young children with autism. *Journal of Autism and Developmen*tal Disorders, 36, 881–890.
- Winkielman, P., & Cacioppo, J. T. (2001). Mind at ease puts a smile on the face: Psychophysiological evidence that processing facilitation elicits positive affect. *Journal of Personality and Social Psychology*, 81, 989–1000.
- Winkielman, P., Berridge, K. C., & Wilbarger, J. L. (2005). Unconscious affective reactions to masked happy versus angry faces influence consumption behavior and judgments of value. *Personality and Social Psychology Bulletin*, 1, 121–135.
- Winkielman, P., McIntosh, D. N., & Oberman, L. (in press). Embodied and disembodied emotion processing: Learning from and about typical and autistic individuals. *Emotion Review 1*, 178–190.