SOCIAL NEUROSCIENCE, 2006, 1 (3–4), 349–363

Psychology Press
Taylor & Francis Group

Impaired recognition of negative basic emotions in autism: A test of the amygdala theory

Chris Ashwin
University of Essex, Colchester, UK

Emma Chapman
University of Cambridge, Cambridge, UK

Livia Colle
University of Turin, Turin, Italy

Simon Baron-Cohen
University of Cambridge, Cambridge, UK

Autism and Asperger Syndrome are autism spectrum conditions (ASC) characterized by deficits in understanding others' minds, an aspect of which involves recognizing emotional expressions. This is thought to be related to atypical function and structure of the amygdala, and performance by people with ASC on emotion recognition tasks resembles that seen in people with acquired amygdala damage. In general, emotion recognition findings in ASC have been inconsistent, which may reflect low numbers of participants, low numbers of stimuli and trials, heterogeneity of symptom severity within ASC groups, and ceiling effects on some tasks. The present study tested 39 male adults with ASC and 39 typical male controls on a task of basic emotion recognition from photographs, in two separate experiments. On a control face discrimination task the group with ASC were not impaired. People with ASC were less accurate on the emotion recognition task compared to controls, but only for the negative basic emotions. This is discussed in the light of similar findings from people with damage to the amygdala.

Facial expressions convey important information about the emotional state of others (Darwin, 1872/1965). The ability to decode facial information quickly and successfully would have been highly adaptive in the social world. Indeed, nonverbal information from the face is so important that humans may have developed specialized perceptual mechanisms for processing emotional expressions (Ekman, 2003; Young, 1998). There is evidence that sensitivity to facial expressions of emotion is present very early in life, since even young infants are able to discriminate different basic emotional expressions in the face (Field, Woodson, Greenberg, & Cohen, 1982; Haan & Nelson, 1998; Walker, 1982; Walker-Andrews, 1997). Recognizing the emotions of others is a key component in the development of a theory of mind (ToM), although ToM is often narrowly considered in terms of understanding volitional (e.g., wanting) and

Correspondence should be addressed to: Chris Ashwin, Department of Psychology, University of Essex, Wivenhoe Park, Colchester C04 3SQ, UK. E-mail: cashwin@essex.ac.uk

CA and SBC were supported by the Medical Research Council (MRC) UK and the National Alliance for Autism Research (NAAR) during the period of this work.
We are grateful to the volunteers who participated in the research, particularly those with ASC for their generous co-operation.

www.psypress.com/socialneuroscience DOI:10.1080/17470910601040772

epistemic (e.g., believing) states, rather than broadly covering all mental states (including the affective). Recent models have viewed ToM as just one component of empathizing, which involves understanding the emotional and mental states of others and responding to these with an appropriate emotion (Baron-Cohen, 1995, 2003; Blair, 2005).

High-functioning autism (HFA) and Asperger syndrome (AS) are neurodevelopmental conditions characterized by deficits in social and communicative functioning and restrictive and repetitive behavior (APA, 1994; ICD-10, 1994). Both of these are autism spectrum conditions (ASC), with common features including difficulties in social reciprocity, relationships, and impaired social-emotional functioning (Baron-Cohen, Tager-Flusberg, & Cohen, 2000b; Volkmar, Lord, Bailey, Schultz, & Klin, 2004; Volkmar, Paul, Klin, & Cohen, 2005). Reduced attention to faces and decreased eye contact with others are early signs of ASC (APA, 1994; Hobson, 1993; Osterling & Dawson, 1994; Osterling, Dawson, & Munson, 2002; Phillips, Baron-Cohen, & Rutter, 1992). People with ASC have difficulties understanding others' minds, with deficits in recognizing facial expressions of emotion thought to be a key aspect of these conditions (Baron-Cohen, 1995; Golan, Baron-Cohen, & Hill, 2006; Grelotti, Gauthier, & Schultz, 2002; Hobson, 1993; Klin, Jones, Schultz, Volkmar, & Cohen, 2002a).

Even though social and emotional difficulties in ASC have been emphasized from the earliest descriptions (Asperger, 1944; Kanner, 1943), the exact nature of the emotional deficits remains unclear. There have been many studies looking at the perception of emotional expressions in ASC, however no consensus has emerged. While some studies have found differences in the perception of basic emotional expressions in people with ASC (Celani, Battacchi, & Arcidiacono, 1999; Davies, Bishop, Manstead, & Tantam, 1994; Hobson, 1986; Hobson, Ouston, & Lee, 1988; Njiokiktjien, Verschoor, de Sonneville, Huyser, Op het Veld, & Toorenaar, 2001), others have reported no differences (Adolphs, Sears, & Piven, 2001; Baron-Cohen, Wheelwright, & Jolliffe, 1997; Castelli, 2005; Grossman, Klin, Carter, & Volkmar, 2000; Ogai et al., 2003; Ozonoff, Pennington, & Rogers, 1990; Prior, Dahlstrom, & Squires, 1990; Teunisse & de Gelder, 1994). Some studies have found deficits in ASC for processing *surprise* and more complex social and emotional information from the face, with intact performance when tested on other basic emotions (Adolphs et al., 2001; Baron-Cohen, Spitz, & Cross, 1993a; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Baron-Cohen et al., 1997; Bormann-Kischkel, Vilsmeier, & Baude, 1995; Capps, Yirmiya, & Sigman, 1992). Surprise is considered a more cognitive emotion than other basic emotions, as it involves inferring that the other person's mental state involved expecting or believing something different (Baron-Cohen et al., 1993a). These findings have led to an idea that emotion deficits in ASC may involve difficulties with more complex emotions, rather than basic emotions (Adolphs et al., 2001; Baron-Cohen et al., 1993a; Golan et al., 2006).

In studies that have reported performance across individual basic emotions, there is some evidence showing that people with ASC may have particular deficits involving *negative* basic emotions. For example, studies have shown less accurate recognition of fear (Howard et al., 2000; Pelphrey, Sasson, Reznick, Paul, Goldman, & Piven, 2002), anger (Giola & Brosgole, 1988), disgust (Golan & Baron-Cohen, submitted), anger and disgust (Ellis & Leafhead, 1996), and in continua of emotions involving sadness, fear and anger (Teunisse & de Gelder, 2001). These difficulties suggest the emotion-recognition deficits in ASC may reflect focal brain abnormalities. In particular, deficits in the recognition of *fear* and *anger* expressions in ASC have led to comparisons with people having damage to the amygdala, who show similar emotion recognition deficits (Baron-Cohen, Ring, Bullmore, Wheelwright, Ashwin, & Williams, 2000a; Boucher, Mayes, Cowell, Broks, Farrant, & Roberts, 2005; Howard et al., 2000; Pelphrey et al., 2002). Although the evidence is still limited for specific deficits of fear in ASC, the emotion recognition findings fit in well with other lines of evidence linking ASC to dysfunction of the amygdala.

For example, people with ASC show abnormalities in the perception of direct eye gaze (Grice, Halit, Farroni, Baron-Cohen, Bolton, & Johnson, 2005; Howard et al., 2000; Senju, Tojo, Yaguchi, & Hasegawa, 2005; Senju, Yaguchi, Tojo, & Hasegawa, 2003) and in rating the trustworthiness of faces of others (Adolphs et al., 2001). Both of these abilities involve the amygdala (Kawashima et al., 1999; Winston, Strange, O'Doherty, & Dolan, 2002) and people with amygdala damage are impaired on tasks measuring them (Adolphs, Tranel, & Damasio, 1998; Young, Aggleton, Hellawell, Johnson, Broks, & Hanley, 1995). In addition, functional neuroimaging studies have shown decreased activation of the amygdala in people with ASC during the processing of negative emotional expressions (Ashwin, Baron-Cohen, Wheelwright, O'Riordan, & Bullmore, in press; Baron-Cohen et al., 1999b; Critchley et al., 2000), including a lack of amygdala modulation across differing task demands (Ashwin et al., in press; Wang, Dapretto, Hariri, Sigman, & Bookheimer, 2004). There are also findings from structural neuroimaging studies of differences in the size of the amygdala in autism (Abell et al., 1999; Aylward et al., 1999; Pierce, Muller, Ambrose, Allen, & Courchesne, 2001; Schumann et al., 2004; Sparks et al., 2002), and differences in neural communication between the amygdala and the rest of the brain (Welchew et al., 2005). Neuropathological studies of the brain at autopsy have shown cell abnormalities in the amygdala in ASC (Bauman & Kemper, 1985, 1988, 1994), and monkeys who receive lesions of the amygdala early in life show behaviors similar to autism (Bachevalier, 1994, 2000). These converging lines of evidence have led to the theory that a key dysfunction in ASC involves the amygdala (Adolphs et al., 2001; Bachevalier & Loveland, 2006; Baron-Cohen et al., 2000a; Boucher et al., 2005; Howard et al., 2000; Schultz, Romanski, & Tsatsanis, 2000; Schultz, 2005).

Early studies of emotion recognition by amygdala patients reported rather specific deficits for fear expressions and, to a lesser extent, anger (Adolphs, Tranel, Damasio, & Damasio, 1994; Broks et al., 1998; Calder, Young, Rowland, Perrett, Hodges, & Etcoff, 1996). However, recent findings have shown evidence that damage to the amygdala may actually cause more profound impairments affecting the recognition of multiple negative basic emotions, including fear, anger, sadness, and disgust (Adolphs, 1999, 2002; Adolphs & Tranel, 2004; Adolphs et al., 1999; Anderson, Spencer, Fulbright, & Phelps, 2000; Buchanan, Tranel, & Adolphs, 2004; Schmolck & Squire, 2001). One reason earlier investigations may have failed to find more extensive deficits for negative basic emotions beyond fear could be due to the low numbers of participants in those studies (Adolphs, 2002, 2003). In a more comprehensive study involving nine patients with bilateral amygdala damage, most of the amygdala patients showed evidence for broader impairments in the recognition of multiple negative basic emotional expressions (Adolphs et al., 1999). Therefore evidence is accruing that bilateral damage to the amygdala may affect recognition across the negative basic emotions including fear, anger, disgust, and sadness (Adolphs, 2002, 2003; Adolphs & Tranel, 2004). The emotion recognition impairments appear to be worse with more extensive damage of the amygdala (e.g., bilateral amygdala damage compared to unilateral damage), and with earlier onset of amygdala dysfunction (Adolphs, 2002; Adolphs et al., 1999; Benuzzi et al., 2004; Brierley, Medford, Shaw, & David, 2004; Meletti, Benuzzi, Nichelli, & Tassinaria, 2003; Meletti et al., 2003; Schmolck & Squire, 2001). Since the defining behavioral characteristics of ASC emerge early in life, if early and extensive dysfunction of the amygdala is a key factor in the development of these conditions, then we might expect to see evidence for deficits in recognizing *multiple* basic negative emotional expressions from the face.

Previous investigations of emotion recognition in ASC are hard to interpret and compare because many included small numbers of participants, they often involved few stimuli examples and trials, used tasks with ceiling effects, involved heterogeneity of symptom severity across ASC groups, and generally failed to run replication studies. These factors can reduce the power to find any group differences and limit the validity of findings. The present study attempts to overcome some of the limitations in previous studies by including a larger number of participants, using more stimulus examples and a task not affected by ceiling effects, including participants with similar symptom severity, and replicating the study across two separate experiments involving different groups of participants.

The aims of the current research were to compare the recognition of facial expressions of basic emotions from photographs in groups of males with ASC compared to matched groups of typical male controls across two separate experiments. In previous studies not finding differences in people with ASC on emotion recognition tasks, it has been suggested that emotion deficits may not be evident in ASC when participants have higher verbal ability, or when they are older, perhaps due to compensatory strategies (Grossman et al., 2000; Prior et al., 1990). Therefore the present study included all high-functioning adult participants and matched the groups for verbal IQ, full-scale IQ, and age.

We expected the control group to perform very well in labeling the facial pictures of basic emotion expressions, but to show less accurate performance for negative emotions compared to the non-negative emotions, consistent with previous emotion recognition research (Ekman, 1982; Gosselin, Kirouac, & Dore, 1995; Kirita & Endo, 1995). Overall, we predicted the control group would show a concordance rate of at least 80% or higher for recognition of each of the basic emotional expression categories.

Our predictions for the ASC group were as follows: If emotion recognition deficits in ASC are limited to complex emotions and mental states, then we should find no group differences for any of the basic emotions, or deficits limited to surprise. If ASC involves more profound emotion recognition deficits, then we expect to see impaired recognition across multiple emotional expressions. Furthermore, if emotion recognition deficits in ASC are related to dysfunction of the amygdala, then we expect less accurate recognition for all the negative basic emotions along with intact performance for "non-negative" emotions, based on previous studies of patients with bilateral amygdala damage.

EXPERIMENT 1

The purpose of Experiment 1 was an initial investigation of the ability of people with and without ASC to label basic emotions from photographs of various basic emotion expressions of the face. Based on previous research with similar standardized photographs of emotional expressions, we expected the control group to perform well and show a concordance rate of 80% or greater for each of the emotion categories (Ekman & Friesen, 1976). If people with ASC have deficits in emotion recognition that are restricted to complex emotions and surprise, with relatively intact recognition of other basic emotions (Adolphs, Sears, & Piven, 2001; Baron-Cohen, Wheelwright, & Jolliffe, 1997; Golan, Baron-Cohen, & Hill, in press), then we expected to see no differences between the groups for any emotion, or deficits limited to surprise. If ASC involves dysfunction of the amygdala (Baron-Cohen et al., 2000; Boucher et al., 2005; Howard et al., 2000; Pelphrey et al., 2002; Schultz, 2005), then we expected to see reduced performance limited to recognizing fear, and anger to a lesser extent. Finally, if amygdala dysfunction in ASC is extensive and occurs early in life, then we expected to see broader deficits affecting multiple negative basic emotions.

Methods

Participants. We recruited 13 adult male participants with ASC (1HFA/12AS: mean age = 31.23 years, $SD = \pm$ 9.1; mean full-scale IQ = 108.6, $SD = \pm$ 17.1). All participants with ASC were diagnosed according to internationally accepted criteria (APA, 1994; ICD-10, 1994), and completed the Autism Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). We also recruited 13 adult male participants (mean age = 25.6 years, $SD = \pm$ 5.1; mean full-scale IQ = 117.9, $SD = \pm$ 9.6) with no history of any psychiatric condition from the community as a control group. IQ was measured for all participants (Wechsler, 1999), and both groups were matched on handedness and sex.

Stimuli. Photographs used in the experiment were taken from the Karolinska Directed Emotion Facial picture set (see Figure 1), a standard collection of emotional and neutral photographs for research purposes (Lundqvist, Flykt, & Ohman, 1998). Twelve examples each of the expressions fear, disgust, anger, surprise, and sadness were chosen based on how closely they matched the facial muscle pattern described by Ekman and colleagues (Ekman, 1992; Ekman & Friesen, 1975, 1976).

Since the valence of surprise is more ambiguous than other basic emotions, we had ten people rate the surprise photographs using a scale from -3 (most negative) to $+3$ (most positive), with 0 representing a neutral valence. None of the surprise pictures received a mean rating by the ten judges that was significantly different from 0, indicating that the surprise photographs used in the study were not seen as negative. The photographs were converted from color to grayscale and printed onto high-quality photographic A4-sized paper to display to the participants. Each picture was approximately 20×28 cm in size. The order of the expression pictures was randomized and they were put into a booklet for viewing.

Procedure. Participants were seated at a desk in a quiet room and shown pictures from the emotion booklet one at a time. A list of the possible emotion choices was in front of them during the task and included *fear*, *disgust*, *anger*, *sadness*, and *surprise*. They were first read the list of emotions and asked if they knew what each one meant. None of the participants in

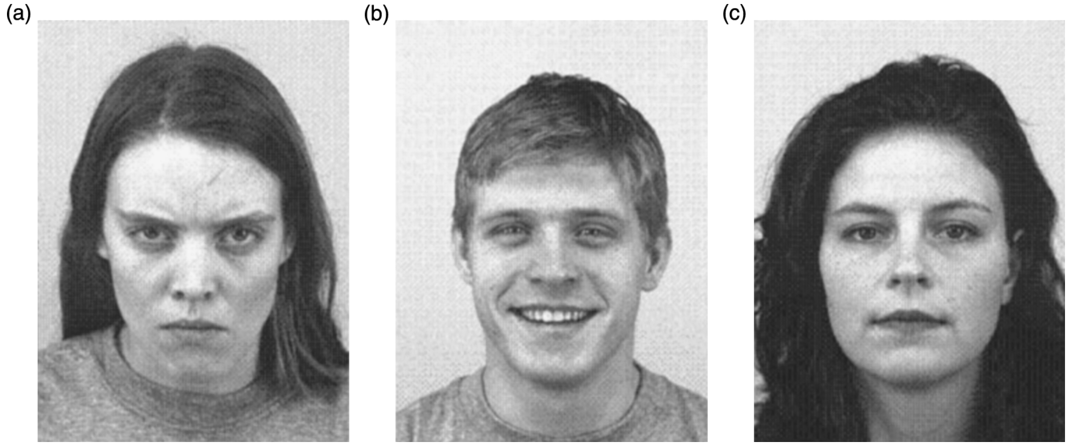

Figure 1. Examples of (a) angry, (b) happy, and (c) neutral stimuli used for the emotion labeling experiments.

either group had difficulty understanding any of the basic emotions. For the task, participants viewed the pictures one at a time and were asked to choose which one of the choices in front of them best described the person in the photograph. They were not given a time limit for a response.

Statistical analysis. The measure of interest was the percentage of correct responses out of 12. A general linear model (GLM) ANOVA with repeated measures was performed on the accuracy data with Emotion (Fearful vs. Angry vs. Sadness vs. Disgust vs. Surprise) as the within-subject factor and Group (Controls vs. ASC) as the between-subject factor. Post hoc *t*-tests were done where appropriate.

Results

There were no significant differences between groups for age $t(24) = 1.93$, *ns*, or IQ $t(24) = 1.71$, *ns*. AQ scores for the sample with AS ($N = 13$, mean AQ score $= 35.6$, $SD = 6.3$, 76.9% scoring 32+) were very similar to the findings from previously published studies ($N = 58$, mean AQ score $= 35.8$, $SD = 6.5$, 80% scoring 32+; Baron-Cohen et al., 2001).

The ANOVA looking at accuracy revealed a main effect of Group $F(1, 34) = 57.0$, $p < .001$, with the control group performing better than the ASC group on the emotion labeling task (see Figure 2). There was also a main effect of Emotion $F(3, 32) = 14.48$. $p < .001$, with the recognition of fear being worse than all other emotions apart from disgust. Disgust was recognized worse than anger and sadness, which were the best recognized emotions. There were no other significant differences for the emotions.

Importantly, there was an interaction between Group and Emotion, $F(1, 34) = 4.25$, $p < .05$. Planned comparison *t*-tests showed that the ASC group performed worse at labeling fear, $t(24) = 3.89$, $p < .01$, disgust, $t(24) = 2.30$, $p < .05$, and anger, $t(24) = 2.95$, $p < .01$. There were no group differences for surprise, $t(24) = 0.23$, $p = .823$, *ns*, while the difference for sad approached significance, $t(24) = 3.89$, $p = .078$.

Discussion

The results of Experiment 1 showed that people with ASC were less accurate at recognizing basic

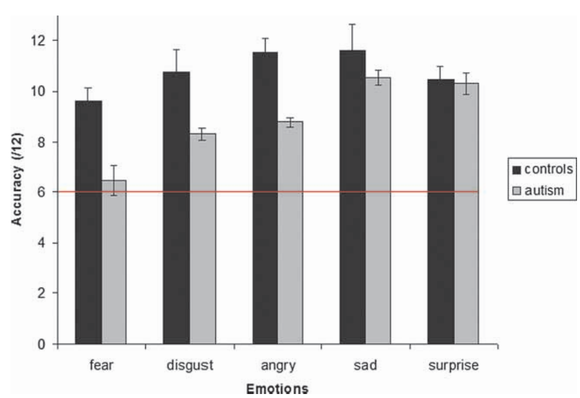

Figure 2. Mean scores and standard errors from the facial expression emotion labeling task in Experiment 1 including five basic emotions and 13 participants in each group. The ASC group was significantly worse than the controls in recognizing fear, disgust, and anger, while sadness showed a trend towards significance. Chance performance is shown with a red line.

emotions from facial expressions in photographs compared to the control group. However, this group difference emerged mainly from the three basic negative emotions of fear, anger, and disgust. There were no group differences for surprise and sadness, although sadness approached significance ($p = .078$). This suggests that ASC may involve more general difficulties in basic emotion recognition than previously suggested, and shows that deficits are more apparent for basic emotions with negative valence. The participants in the ASC group were all high-functioning, their performance on the task was above chance, and they showed normal recognition for some of the emotions. This suggests the findings did not emerge from *general* impairments in face or object processing, or from an inability to recognize emotional expressions from the face, but rather from *specific* deficits in recognizing basic emotional expressions with negative valence. The groups were matched for both IQ and age, so these factors cannot explain the results. The control group showed a concordance rate of at least 80% for each of the basic emotions, showing that the expressions displayed in the stimuli were recognized as the appropriate emotion by the control group.

However, Experiment 1 did not include neutral expressions and other basic emotions defined by cross-cultural work (Ekman, 2003; Ekman & Friesen, 1971, 1975). In addition, Experiment 1 involved only 13 participants in each of the groups, perhaps limiting the power to see some group differences and raising the possibility of false positives. Therefore in Experiment 2 we replicated the study with larger groups of participants, and included neutral expressions and all the basic emotional expressions defined by Ekman and colleagues (Ekman & Friesen, 1975, 1976). Finally, in order to more directly test if emotion recognition deficits might be due to more general impairments in face processing, and not specific emotional expressions, we also included the Benton face recognition task (Benton, Hamsher, Varney, & Spreen, 1983).

EXPERIMENT 2

The purpose of Experiment 2 was to investigate basic emotion recognition ability in ASC with larger numbers of participants and a wider range of emotions, including happy and neutral expressions, which were not included in Experiment 1. We were interested in testing if the findings from Experiment 1 would replicate in different groups of participants with and without ASC, which would provide greater validity to the results. In particular, we wanted to test if people with ASC in Experiment 2 would show reduced performance in recognizing the negative emotions of fear, disgust, anger, and sadness, with no group differences for the non-negative expressions of happiness, surprise, and neutral. Given the nature of the deficits found in Experiment 1 for the ASC group, we also wanted to look at the types of errors for the negative emotions to compare them with those made by amygdala-damaged patients. Once again, we expected the typical control group to show an 80% concordance rate for recognizing all of the basic emotions.

Methods

Participants. We recruited 26 adult male participants with ASC (2HFA/24AS: mean age = 31.6 years, $SD = \pm 10.6$; mean verbal IQ = 118.2, $SD = \pm 14.4$; mean full-scale IQ = 121.2, $SD = \pm 13.5$) from people who had previously participated in research for our lab. As in Experiment 1, all participants with ASC were diagnosed according to internationally accepted criteria (APA, 1994; ICD-10, 1994), and completed the Autism Spectrum Quotient (AQ; Baron-Cohen et al., 2001). None of these 26 individuals with ASC had taken part in Experiment 1. We also recruited 26 adult male participants (mean age = 30.7 years, $SD = \pm 11.1$; mean verbal IQ = 119.3, $SD = \pm 12.2$; mean full-scale IQ = 121.3, $SD = \pm 13.7$) with no history of any psychiatric condition from the community to serve as a control group. All participants completed a measure of intelligence (Wechsler, 1999), and both groups were matched on handedness (22:4, right to left, for both groups).

Stimuli. The same photographs used in Experiment 1 were included in Experiment 2, with the addition of 12 examples each of happy and neutral expressions taken from the Karolinska Directed Emotion Facial set of emotional expressions (Lundqvist et al., 1998). Since the valence of neutral pictures can be ambiguous, ten judges rated the neutral photographs using a scale from -3 (most negative) to $+3$ (most positive), with 0 representing a neutral valence. Each of the pictures received a mean rating by the ten judges that did not significantly differ from 0, indicating that the neutral photographs were not seen as negative.

We also included the Benton Face Recognition Test (Benton et al., 1983) as a measure of face discrimination ability. This task involved a target face at the top of a page, with six novel faces below. Participants chose which of the six faces matched the identity of the target face. We used the short form involving thirteen different trials.

Procedure. The procedure for Experiment 2 was identical to Experiment 1, with the addition of the 12 neutral and 12 happy expression photographs, which were randomly interspersed into the booklet. A list of the seven expression options was placed in front of every participant during the experiment.

Statistical analysis. The measure of interest was the percentage of correct responses out of 12. A GLM ANOVA with repeated measures was performed on the accuracy data with Emotion (Fearful vs. Angry vs. Sadness vs. Disgust vs. Happy vs. Surprise vs. Neutral) as the within-subject factor and Group (Controls vs. ASC) as the between-subject factor. Post hoc *t*-tests were carried out where appropriate.

Planned post hoc comparisons were performed with the combined data for the negative emotions (fear, anger, disgust, and sadness), and the combined data for the non-negative emotions (happy, surprised, and neutral) to directly test the recognition of negative and non-negative emotions both within and between the two groups. First we compared the negative versus non-negative emotions for each group separately with paired samples *t*-tests, to see if each group was processing negative versus non-negative emotions differently. Then we carried out comparisons between the two groups for both the negative and non-negative emotions with independent samples *t*-tests, to see if there were group differences in how they processed negative or non-negative emotions.

Results

There were no significant differences between groups for age, $t(50) = 0.31$, *ns*, verbal IQ, $t(50) = 0.29$, *ns*, or full scale IQ, $t(50) = 0.02$, *ns*. The results for the AQ scores for the sample with AS ($N = 26$, mean AQ score $= 38.3$, $SD = 6.0$, 88.5% scoring 32+) were very similar to the findings from previously published studies ($N = 58$, mean AQ score $= 35.8$, $SD = 6.5$, 80% scoring 32+; Baron-Cohen et al., 2001). On the Benton Face Recognition Task, the ASC group (mean score $= 39.6$, $SD = \pm 6.1$) and control group (mean score $= 41.0$, $SD = \pm 5.5$) did not differ, $t(50) = 0.86$, *ns*.

The statistics on the emotion recognition accuracy data revealed a main effect of Group, $F(1, 50) = 13.9$, $p < .001$, with the control group performing better than the ASC group (see Figure 3). There was also a main effect of Emotion, $F(6, 45) = 26.1$. $p < .001$, with recognition of fear once again worse than all other emotions apart from disgust. Happy was better recognized than all other emotions, while there were no other significant differences (see Figure 3).

Importantly, there was an interaction between Group and Emotion, $F(6, 45) = 5.9$, $p < .001$. Planned comparison *t*-tests showed that the control group performed better than the ASC group on fear $t(50) = 4.16$, $p < .001$, disgust, $t(50) = 4.56$, $p < .001$, anger, $t(50) = 2.49$, $p < .02$, and sadness, $t(50) = 2.40$, $p < .05$. There was no difference between the groups for happiness, $t(50) = 0.26$, $p = .80$, surprise, $t(50) = 0.15$, $p = .88$, or neutral $t(50) = 0.79$, $p = .92$ (see Figure 3).

The within-group comparison of the accuracy data for the negative and non-negative emotions showed a significant difference for the ASC group, $t(77) = 9.24$, $p < .001$, with the accuracy for negative emotions lower than the non-negative emotions. The male control group did not

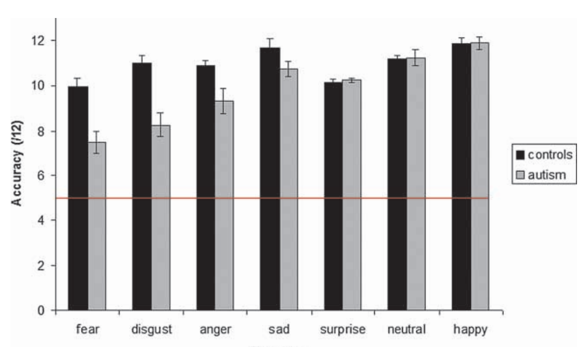

Figure 3. Mean scores and standard errors from the facial expression emotion labeling task in Experiment 2 including seven basic emotions and neutral and 26 participants in each group. The ASC group performed significantly worse than the controls in recognizing fear, disgust, anger, and sadness, with no group differences for the other expressions and neutral. Chance performance is shown with a red line.

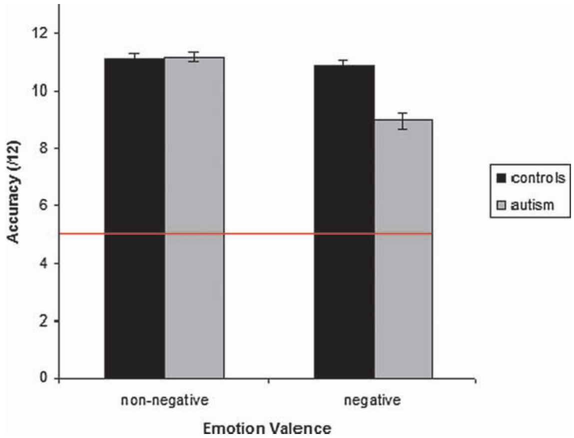

Figure 4. Mean scores and standard errors from the facial expression emotion labeling task in Experiment 2 for the negative and non-negative valence expressions for each group. The ASC group performed significantly worse than the controls in recognizing the negative basic emotions, with no group difference for the non-negative emotions. Chance performance is shown with a red line.

show a difference between the negative and non-negative emotions, $t(77) = 1.93$, $p = .057$, *ns*, however this value was approaching significance (see Figure 4).

The comparison between groups for the negative and non-negative accuracy data revealed that there was no difference in accuracy for the non-negative emotions, $t(154) = 0.21$, $p = .84$, *ns*. However, the groups were significantly different on the negative emotions, $t(206) = 6.27$, $p < .001$, with the ASC group less accurate than the control group (see Figure 4).

The main errors made by the control group for fear pictures included surprise (62.5%), disgust (17.9%), sadness (10.7%), and anger (8.9%). They confused disgust pictures mainly for anger (50%) and sadness (46.2%), while the errors for anger pictures included disgust (60.5%) and sadness (31.6%). The main errors by the ASC group for fear pictures were surprise (36.8%), disgust (33.6%), anger (18.4%) and sadness (8%). The errors for disgust pictures were anger (63%), sadness (18.5%), and fear (14.1%), while the errors for anger included disgust (62.5%), sadness (20.3%), and fear (9.4%).

Discussion

The results from Experiment 2 broadly replicated the results from Experiment 1, revealing impaired performance by people with ASC for the negative emotions of fear, disgust, anger and sadness, and no group differences for any of the non-negative expressions of happy, surprise, and neutral. The findings in the experiment are robust as they were replicated with larger numbers of participants who were not involved in Experiment 1. The results show that difficulties in labeling basic emotions in people with ASC involve deficits in recognizing negative emotions, which is consistent with early extensive amygdala dysfunction. The most notable findings in the errors were found for fear expressions. The controls mainly confused fear for surprise, while the ASC group confused fear for surprise much less often, and almost as often as they confused fear for disgust. This is consistent with findings from bilateral amygdala patients, namely that while controls confuse fear for surprise much of the time, people with bilateral amygdala damage confuse fear less often with surprise, and find disgust to be more similar to fear than controls (Adolphs, 2002; Adolphs, Tranel, & Damasio, 2003; Adolphs et al., 1999).

The deficits found in this study for the ASC group cannot be attributable to differences in verbal or full scale IQ, or age. The controls had a concordance rate greater than 80% for each of the basic emotions, showing that the emotional expressions were recognized accurately by the control group. However, some of the emotions may have been close to showing ceiling effects, which may have contributed to some of the results. The control males did not show reduced performance for negative emotional expressions compared to the non-negative emotions, although it approached significance, suggesting that typical performance is equal across emotional valence for basic emotions.

GENERAL DISCUSSION

The results of the present investigation demonstrate deficits in recognizing basic emotional expressions from photographs in high-functioning adults with ASC compared to typical adult control males. The emotion recognition deficits were seen across all the negative basic emotional expressions, with no differences between groups for the non-negative emotion expressions. The control group did not show a difference in accuracy for the negative compared to the non-negative expressions. The findings are robust as they were found in two separate experiments involving different participants, and controlled for factors that may have contributed to reduced power in previous experiments. The finding of broad impairments for recognizing all the negative basic emotions by people with ASC is consistent with deficits seen in people with early and extensive damage to the amygdala, as was the pattern of errors seen for fear expressions. The results of the present study lend further support to the amygdala theory of autism (Baron-Cohen et al., 2000a) and related models that hypothesize a key involvement of the amygdala in ASC (Bachevalier, 2000; Bachevalier & Loveland, 2006; Boucher et al., 2005; Howard et al., 2000; Schultz et al., 2000; Schultz, 2005).

Such profound deficits in basic emotion processing could have significant effects on social-emotional development and functioning in ASC, especially for understanding others' minds (Baron-Cohen, Tager-Flusberg, & Cohen, 1993b; Baron-Cohen et al., 2000b), and call for a reassessment of the role of even basic emotion recognition in the development of ToM and empathy (Baron-Cohen, 2005). Some researchers separate ToM/empathy into cognitive and affective components (Baron-Cohen, 2003; Blair, 2005; Brothers & Ring, 1992), with the cognitive component involving beliefs about beliefs (the traditional view of ToM), and the affective component involving the recognition and response to the emotional expressions of others. These are not necessarily completely separate processes, as the neural circuits for ToM and emotion recognition overlap to some degree (Frith & Frith, 1999; Saxe, 2006). While deficits in cognitive empathy/ToM have been more consistently reported in ASC (Baron-Cohen, Leslie, & Frith, 1985; Baron-Cohen et al., 1993b; Baron-Cohen et al., 2000b), evidence is less clear about the affective component and have led some to propose that this area may be intact in autism (Blair, 2005). The findings from this study appear to provide clear evidence for deficits in the affective component of ToM/empathizing in ASC too, at least in the recognition of emotional expressions from the face. Therefore deficits in reading non-verbal communicative signals from others may be more extensive in ASC than previously thought, and impact both cognitive and affective areas of ToM/empathizing.

Information from lower-level and domain-specific abilities such as the perception of gaze direction and emotional expressions may provide the scaffolding for normal development and functioning of ToM (Baron-Cohen, 1995; Stone, 2005; Stone & Gerrans, 2005). Without important information about the affective states of others, early social-emotional development in ASC would be curtailed, leading to delayed or deficient functioning in higher-level abilities such as ToM/empathizing that utilize this information. Basic emotion recognition deficits would also interfere with everyday interaction, leading a person with ASC to either ignore or be unaware of how another person may be feeling.

This raises the interesting question of whether the empathy deficits in ASC are primarily perceptual in nature—a difficulty reading the expressions on the face—or are more central, related to comprehension, or both. At the very least, the current study allows us to conclude that there are difficulties in social perception in people with ASC. As regards comprehension, there are clinical anecdotal accounts of people with ASC feeling guilt or remorse when it has been pointed out to them that they acted inappropriately given the other person's mental state. This suggests that they may understand that the other person is capable of feeling sad or hurt or angry, etc., but just may not infer the other person's emotional state from perceptual information at the right time. We do not suppose these perceptual difficulties are limited to the visual modality, as they have also been reported in relation to auditory emotion recognition tasks (Golan & Baron-Cohen, submitted; Rutherford, Baron-Cohen, & Wheelwright, 2002). Other studies, however, implicate difficulties in comprehension itself, as revealed in the Faux Pas test (Baron-Cohen, O'Riordan, Stone, Jones, & Plaisted, 1999a), where there is no perceptual element. This raises the possibility that deficits are present in both social perception and social comprehension.

Some studies have found few or no deficits in people with ASC on tasks of basic emotion recognition from the face. This has led to ideas that social-emotion difficulties in ASC may be more evident for complex emotional expressions and mental states (Adolphs et al., 2001; Baron-Cohen et al., 1993a; Baron-Cohen et al., 1997; Golan et al., 2006). The failure of other studies to find deficits in specific basic emotions as profound as were seen in the present study may be attributable to a number of factors. These include low numbers of participants, few stimulus examples and trials, heterogeneity of symptom severity in ASC groups, tasks that involved ceiling effects, and a general lack of replication studies.

All of these can reduce the power to find group differences, and limit the validity of any results that are found. Deficits in basic emotion recognition do become evident in ASC when these factors are controlled for. Previous findings from various independent studies have shown deficits in ASC affecting all the negative basic emotions (Ellis & Leafhead, 1996; Giola & Brosgole, 1988; Howard et al., 2000; Pelphrey et al., 2002; Teunisse & de Gelder, 2001), but this is the first study as far as we are aware reporting deficits across all the basic negative emotions in ASC within the same participant groups.

A lack of difference in basic emotion recognition in ASC has also been attributed to the effects of age and ability of participants, as older and high-functioning people are thought to develop compensatory strategies for processing basic emotions (Adolphs et al., 2001; Baron-Cohen et al., 1997; Grossman et al., 2000; Klin, Jones, Schultz, & Volkmar, 2003). However, the participants in the present study were all high-functioning adults and the groups were matched for age and both verbal and full-scale IQ. Therefore the present results cannot be attributable to differences in verbal ability, general intelligence, or age. The ASC group also performed normally on a task of face discrimination, as well as recognition of non-negative basic expressions, showing that the deficits in ASC in recognizing negative basic emotional expressions did not emerge from more general deficits in face-processing. The results of the study are also not simply due to task difficulty, since the control group recognized sadness better than surprise, while the ASC group showed impairments for sadness alongside intact recognition for surprise. If task difficulty was producing the results we would have expected the opposite pattern of results by the ASC group for sadness and surprise. Although we controlled for many limitations, performance for some of the emotions may have been close to producing ceiling effects. Future studies should involve tasks with graded or subtle basic emotional expressions, so that recognition ability across all the emotions is above chance level but not close to ceiling performance.

While the present results support the idea of amygdala dysfunction in ASC, some other recent research has shown evidence for intact functioning, size, or neural activation of the amygdala in people with ASC (Bernier, Dawson, Panagiotides, & Webb, 2005; Dziobek, Fleck, Rogers, Wolf, & Convit, 2006; Grelotti et al., 2005; Pierce, Haist, Sedaghat, & Courchesne, 2004; Salmond, de Haan, Friston, Gadian, & Vargha-Khadem, 2003). While these results seem contradictory to those reported here, it is important to note that the amygdala is involved in many functions and contains many distinct nuclei, only some of which may be impaired in ASC (Pierce et al., 2004). Even when intact amygdala function is found it may still be abnormal in context, such as being activated for cartoon characters but not for faces (Grelotti et al., 2005). Models of amygdala dysfunction in ASC do not propose a complete lack of amygdala function, but suggest atypical functioning, particularly during critical early developmental periods (Baron-Cohen et al., 2000a; Boucher et al., 2005; Frith, 2001; Schultz et al., 2000; Schultz, 2005). Task characteristics and stimuli type, as well as ecological validity, are also likely play a role in the findings (Ashwin, Wheelwright, & Baron-Cohen, 2006). In sum, although some evidence has questioned the involvement of the amygdala as key in ASC, the evidence showing atypical amygdala function still outweighs evidence against it. Clearly more work is needed to determine the nature of this amygdala dysfunction, when it emerges, and how it is involved in the behaviors seen in ASC.

It is interesting that people with ASC in the present study were impaired in judgments for emotions that involve mainly perception of the eyes and regions around the eyes during recognition, while recognition was normal for emotional expressions that generally involve perception centering more around the mouth region (Schyns, Bonnar, & Gosselin, 2002). This is consistent with previous face-processing research showing that people with ASC use the eyes less than controls when making judgments of the face, and rely more on the mouth region (Baron-Cohen et al., 1997; Klin, Jones, Schultz, Volkmar, & Cohen, 2002b; Pelphrey et al., 2002). This suggests that differences in viewing patterns of the face may underlie the deficits in emotion recognition, which may differentially affect negative emotional expressions more than non-negative expressions. Adolphs, Gosselin, Buchanan, Tranel, Schyns, and Damasio (2005) recently showed that deficits for fear expressions in an amygdala patient involved abnormal viewing patterns of the face involving decreased time looking at the eyes and increased time looking at the mouth. The study involved the recognition of fear and happy expression photos in a person with bilateral amygdala damage. They found that the amygdala patient had difficulty recognizing fear expressions, and that this was related to her looking more at the mouth than the eyes during the processing of fear. The same differences were not found for recognizing happy expressions, which relies more on the perception on the mouth region (Adolphs et al., 2005; Schyns et al., 2002).

A similar mechanism involving the amygdala and decreased looking time towards the eyes may be involved in ASC. Recent neuroimaging evidence shows this may indeed be true, as the magnitude of amygdala activation in people with ASC was found to be positively correlated with time spent looking at the eye region of the face (Dalton et al., 2005). This corroborates studies showing people with ASC look less at eyes and more at mouths during emotional expression processing (Klin et al., 2002a, 2002b; Pelphrey et al., 2002). Interestingly, the performance in labeling fear by the amygdala patient was improved by simply telling her to look at the eyes, which offers possibilities for potential treatment methods to focus on in people with ASC. Training in emotion recognition using whole face and voice stimuli has already demonstrated that improvement is possible, even over as short a period as 10 weeks of 2 hours per week, using computer-presented video or audio files of actors expressing emotions (Golan & Baron-Cohen, submitted).

CONCLUSION

Previous studies of emotional expression recognition have failed to provide a clear picture of whether emotion perception impairments exist in people with ASC and, if so, what they may be. The present study controlled for factors that may have confounded previous research and found that high-functioning adults with ASC showed broad deficits in recognizing negative basic emotional expressions from the face, with intact recognition of non-negative emotions, compared to controls. These findings are similar to patients with early and extensive damage of the amygdala, thus providing further support to models of ASC that propose key involvement of the amygdala, early in development (Baron-Cohen et al., 2000a). Since sensitivity to emotional expressions emerges very early in development (Field et al., 1982; Haan & Nelson, 1998; Walker, 1982; Walker-Andrews, 1997), is thought to be a building block for further empathy/ToM development (Harris, 1989), and is a key component of normal empathy/ToM, deficits in basic emotional expression recognition in ASC may have profound effects for developing an understanding of the emotional and mental states of others, and for utilizing this ability in daily life.

REFERENCES

Abell, F., Krams, M., Ashburner, J., Passingham, R., Friston, K., Frackowiak, R., et al. (1999). The neuroanatomy of autism: A voxel-based whole brain analysis of structural scans. *Neuroreport*, *10*(8), 1647–1651.

Adolphs, R. (1999). Social cognition and the human brain. *Trends in Cognitive Sciences*, *3*(12), 469–479.

Adolphs, R. (2002). Recognizing emotion from facial expressions: Psychological and neurological mechanisms. *Behavioral and Cognitive Neuroscience Reviews*, *1*(1), 21–61.

Adolphs, R. (2003). Is the human amygdala specialized for processing social information? *Annals of the New York Academy of Sciences*, *985*, 326–340.

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*, *433*(7021), 68–72.

Adolphs, R., Sears, L., & Piven, J. (2001). Abnormal processing of social information from faces in autism. *Journal of Cognitive Neuroscience*, *13*(2), 232–240.

Adolphs, R., & Tranel, D. (2004). Impaired judgments of sadness but not happiness following bilateral amygdala damage. *Journal of Cognitive Neuroscience*, *16*(3), 453–462.

Adolphs, R., Tranel, D., & Damasio, A. (1998). The human amygdala in social judgment. *Nature*, *393*(6684), 470–474.

Adolphs, R., Tranel, D., & Damasio, A. R. (2003). Dissociable neural systems for recognizing emotions. *Brain and Cognition*, *52*(1), 61–69.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, *372*(6507), 669–672.

Adolphs, R., Tranel, D., Hamann, S., Young, A. W., Calder, A. J., Phelps, E. A., et al. (1999). Recognition of facial emotion in nine individuals with bilateral amygdala damage. *Neuropsychologia*, *37*(10), 1111–1117.

Anderson, A. K., Spencer, D. D., Fulbright, R. K., & Phelps, E. A. (2000). Contribution of the anteromedial temporal lobes to the evaluation of facial emotion. *Neuropsychology*, *14*(4), 526–536.

APA. (1994). *DSM-IV diagnostic and statistical manual of mental disorders* (4th ed.). Washington, DC: American Psychiatric Association.

Ashwin, C., Baron-Cohen, S., Wheelwright, S., O'Riordan, M., & Bullmore, E. T. (in press). Differential activation of the social brain during fearful face-

processing in adults with and without autism. *Neuropsychologia*.
Ashwin, C., Wheelwright, S., & Baron-Cohen, S. (2006). Finding a face in the crowd: Testing the anger superiority effect in autism. *Brain and Cognition, 61*, 78–95.
Asperger, H. (1944). Die ''Autistischen Psychopathen'' im Kindesalter. *Archiv fur Psychiatrie und Nervenkrankheiten*, *117*, 76–136.
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*(9), 2145–2150.
Bachevalier, J. (1994). Medial temporal lobe structures and autism: A review of clinical and experimental findings. *Neuropsychologia*, *32*, 627–648.
Bachevalier, J. (2000). The amygdala, social cognition, and autism. In J. Aggleton (Ed.), *The amygdala: Neurobiological aspects of emotion, memory and mental dysfunction* (pp. 509–543). New York: Wiley-Liss.
Bachevalier, J., & Loveland, K. A. (2006). The orbitofrontal-amygdala circuit and self-regulation of social-emotional behavior in autism. *Neuroscience and Biobehavioural Reviews*, *30*(1), 97–117.
Baron-Cohen, S. (1995). *Mindblindness: An essay on autism and theory of mind*. Boston: MIT Press/Bradford Books.
Baron-Cohen, S. (2003). *The essential difference: Men, women and the extreme male brain*. London: Penguin books.
Baron-Cohen, S. (2005). The empathizing system: A revision of the 1994 model of the mindreading system. In B. Ellis & D. Bjorklund (Eds.), *Origins of the social mind*. London: Guilford Publications.
Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a ''theory of mind''? *Cognition*, *21*, 37–46.
Baron-Cohen, S., O'Riordan, M., Stone, V., Jones, R., & Plaisted, K. (1999a). Recognition of faux pas by normally developing children and children with Asperger syndrome or high-functioning autism. *Journal of Autism and Developmental Disorders*, *29*(5), 407–418.
Baron-Cohen, S., Ring, H. A., Bullmore, E. T., Wheelwright, S., Ashwin, C., & Williams, S. C. (2000a). The amygdala theory of autism. *Neuroscience and Biobehavioural Reviews*, *24*(3), 355–364.
Baron-Cohen, S., Ring, H. A., Wheelwright, S., Bullmore, E., Brammer, M., Simmons, A., et al. (1999b). Social intelligence in the normal and autistic brain: An fMRI study. *European Journal of Neuroscience*, *11*, 1891–1898.
Baron-Cohen, S., Spitz, A., & Cross, P. (1993a). Can children with autism recognize surprise? *Cognition and Emotion*, *7*, 507–516.
Baron-Cohen, S., Tager-Flusberg, H., & Cohen, D. (Eds.). (1993b). *Understanding other minds: Perspectives from autism*. Oxford, UK: Oxford University Press.
Baron-Cohen, S., Tager-Flusberg, H., & Cohen, D. J. (2000b). *Understanding other minds: Perspectives from developmental cognitive neuroscience* (2nd ed). Oxford, UK: Oxford University Press.
Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The ''Reading the Mind in the Eyes'' test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry*, *42*(2), 241–251.
Baron-Cohen, S., Wheelwright, S., & Jolliffe, T. (1997). Is there a ''language of the eyes''? Evidence from normal adults and adults with autism or Asperger syndrome. *Visual Cognition*, *4*, 311–331.
Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, *31*(1), 5–17.
Bauman, M., & Kemper, T. (1985). Histoanatomic observation of the brain in early infantile autism. *Neurology*, *35*, 866–874.
Bauman, M., & Kemper, T. (1988). Limbic and cerebellar abnormalities: Consistent findings in infantile autism. *Journal of Neuropathology and Experimental Neurology*, *47*, 369.
Bauman, M., & Kemper, T. (1994). *The neurobiology of autism*. Baltimore, MD: Johns Hopkins University Press.
Benton, A. L., Hamsher, K., Varney, N. R., & Spreen, O. (1983). *Contributions to neuropsychological assessment*. New York: Oxford University Press.
Benuzzi, F., Meletti, S., Zamboni, G., Calandra-Buonaura, G., Serafini, M., Lui, F., et al. (2004). Impaired fear processing in right mesial temporal sclerosis: An fMRI study. *Brain Research Bulletin*, *63*, 269–281.
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 and Developmental Disorders*, *35*, 575–583.
Blair, R. J. R. (2005). Responding to the emotions of others: Dissociating forms of empathy through the study of typical and psychiatric populations. *Consciousness and Cognition, 14*, 698–718.
Bormann-Kischkel, C., Vilsmeier, M., & Baude, B. (1995). The development of emotional concepts in autism. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *36*, 1243–1259.
Boucher, J., Mayes, A., Cowell, P., Broks, P., Farrant, A., & Roberts, N. (2005). A combined clinical, neuropsychological and neuroanatomical study of adults with HFA. *Cognitive Neuropsychiatry*, *10*, 165–214.
Brierley, B., Medford, N., Shaw, P., & David, A. S. (2004). Emotional memory and perception in temporal lobectomy patients with amygdala damage. Journal of Neurology. *Neurosurgery and Psychiatry*, *75*, 593–599.
Broks, P., Young, A. W., Maratos, E. J., Coffey, P. J., Calder, A. J., Isaac, C. L., et al. (1998). Face processing impairments after encephalitis: Amygdala damage and recognition of fear. *Neuropsychologia*, *36*(1), 59–70.

Brothers, L., & Ring, B. (1992). A neuroethological framework for the representation of minds. *Journal of Cognitive Neuroscience*, *4*, 107–118.

Buchanan, T. W., Tranel, D., & Adolphs, R. (2004). Anteromedial temporal lobe damage blocks startle modulation by fear and disgust. *Behavioural Neuroscience*, *118*, 429–437.

Calder, A. J., Young, A. W., Rowland, D., Perrett, D. I., Hodges, J. R., & Etcoff, N. L. (1996). Facial emotion recognition after bilateral amygdala damage: Differentially severe impairment of fear. *Cognitive Neuropsychology*, *13*, 699–745.

Capps, L., Yirmiya, N., & Sigman, M. (1992). Understanding of simple and complex emotions in non-retarded children with autism. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *33*, 1169–1182.

Castelli, F. (2005). Understanding emotions from standardized facial expressions in autism and normal development. *Autism*, *9*, 428–449.

Celani, G., Battacchi, M. W., & Arcidiacono, L. (1999). The understanding of the emotional meaning of facial expressions in people with autism. *Journal of Autism and Developmental Disorders*, *29*(1), 57–66.

Critchley, H. D., Daly, E. M., Bullmore, E. T., Williams, S. C., Van Amelsvoort, T., Robertson, D. M., et al. (2000). The functional neuroanatomy of social behaviour: Changes in cerebral blood flow when people with autistic disorder process facial expressions. *Brain*, *123*(11), 2203–2212.

Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., Goldsmith, H. H., et al. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nature Neuroscience*, *8*(4), 519–526.

Darwin, C. (1965). *The expression of emotions in man and animals*. Chicago: University of Chicago Press. (Original work published 1872)

Davies, S., Bishop, D., Manstead, A. S., & Tantam, D. (1994). Face perception in children with autism and Asperger's syndrome. *Journal of Child Psychology and Psychiatry*, *35*(6), 1033–1057.

Dziobek, I., Fleck, S., Rogers, K., Wolf, O. T., & Convit, A. (2006). The "amygdala theory of autism" revisited: Linking structure to behavior. *Neuropsychologia, 44*, 1891–1899.

Ekman, P. (1982). *Emotion in the human face*. Cambridge, UK: Cambridge University Press.

Ekman, P. (1992). Facial expression of emotion: An old controversy and new findings. *Philosophical Transactions of the Royal Society of London, 335*(1273), 63–69.

Ekman, P. (2003). *Emotions revealed*. London: Weidenfeld & Nicolson.

Ekman, P., & Friesen, W. (1971). Constants across cultures in the face and emotion. *Journal of Personality and Social Psychology*, *17*, 124–129.

Ekman, P., & Friesen, W. (1975). *Unmasking the face: A guide to recognizing emotions from facial cues*. Englewood Cliffs, NJ: Prentice Hall.

Ekman, P., & Friesen, W. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychologists Press.

Ellis, H. D., & Leafhead, K. (1996). Raymond: A study of an adult with Asperger syndrome. In P. W. Halligan & J. C. Marshall (Eds.), *Method in madness: Case studies in cognitive neuropsychiatry*. Hove, UK: Psychology Press.

Field, T. M., Woodson, R., Greenberg, R., & Cohen, D. (1982). Discrimination and imitation of facial expressions by neonates. *Science*, *281*, 179–181.

Frith, C., & Frith, U. (1999). Interacting minds: A biological basis. *Science*, *286*(5445), 1692–1695.

Frith, U. (2001). Mind blindness and the brain in autism. *Neuron*, *32*(6), 969–979.

Giola, J. V., & Brosgole, L. (1988). Visual and auditory affect recognition in singly diagnosed mentally retarded patients, mentally retarded patients with autism and normal young children. *International Journal of Neuroscience*, *43*, 149–163.

Golan, O., & Baron-Cohen, S. (submitted). The Cambridge Mindreading Face–Voice Battery for children (CAM-C): Testing basic and complex emotion recognition in children with and without autism spectrum conditions.

Golan, O., Baron-Cohen, S., & Hill, J. J. (2006). The Cambridge Mindreading (CAM) Face–Voice Battery: Testing complex emotion recognition in adults with and without Asperger syndrome. *Journal of Autism and Developmental Disorders, 36*, 169–183.

Gosselin, P., Kirouac, G., & Dore, F. Y. (1995). Components and recognition of facial expressions in the communication of emotions by actors. *Journal of Personality and Social Psychology*, *68*, 83–96.

Grelotti, D. J., Gauthier, I., & Schultz, R. T. (2002). Social interest and the development of cortical face specialization: What autism teaches us about face processing. *Developmental Psychobiology*, *40*(3), 213–225.

Grelotti, D. J., Klin, A. J., Gauthier, I., Skudlarski, P., Cohen, D. J., Gore, J. C., et al. (2005). fMRI activation of the fusiform gyrus and amygdala to cartoon characters but not to faces in a boy with autism. *Neuropsychologia*, *43*(3), 373–385.

Grice, S. J., Halit, H., Farroni, T., Baron-Cohen, S., Bolton, P., & Johnson, M. H. (2005). Neural correlates of eye-gaze detection in young children with autism. *Cortex*, *41*(3), 342–353.

Grossman, J. B., Klin, A., Carter, A. S., & Volkmar, F. R. (2000). Verbal bias in recognition of facial emotions in children with Asperger syndrome. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *41*, 369–379.

Haan, M. D., & Nelson, C. A. (1998). Discrimination and categorization of facial expressions of emotion during infancy. In A. Slater (Ed.), *Perceptual development: Visual, auditory and language development in infancy* (pp. 287–309). London: UCL Press.

Harris, P. (1989). *Children and emotion*. Oxford, UK: Blackwell Publishing.

Hobson, R. P. (1986). The autistic child's appraisal of expressions of emotion. *Journal of Child Psychology and Psychiatry*, *27*, 321–342.

Hobson, R. P. (1993). *Autism and the development of mind*. Hove, UK: Lawrence Erlbaum Associates Ltd.

Hobson, R. P., Ouston, J., & Lee, A. (1988). Emotion recognition in autism: Coordinating faces and voices. *Psychological Medicine*, *18*, 911–923.

Howard, M. A., Cowell, P. E., Boucher, J., Broks, P., Mayes, A., Farrant, A., et al. (2000). Convergent neuroanatomical and behavioural evidence of an amygdala hypothesis of autism. *Neuroreport*, *11*(13), 2931–2935.

ICD-10. (1994). *International classification of diseases* (10th ed.). Geneva, Switzerland: World Health Organization.

Kanner, L. (1943). Autistic disturbance of affective contact. *Nervous Child*, *2*, 217–250.

Kawashima, R., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Ito, K., et al. (1999). The human amygdala plays an important role in gaze monitoring. *Brain*, *122*, 779–783.

Kirita, T., & Endo, M. (1995). Happy face advantage in recognizing facial expressions. *Acta Psychologia*, *89*, 149–163.

Klin, A., Jones, W., Schultz, R., & Volkmar, F. (2003). The enactive mind, or from actions to cognition: Lessons from autism. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences*, *358*(1430), 345–360.

Klin, A., Jones, W., Schultz, R., Volkmar, F., & Cohen, D. (2002a). Defining and quantifying the social phenotype in autism. *American Journal of Psychiatry*, *159*(6), 895–908.

Klin, A., Jones, W., Schultz, R., Volkmar, F., & Cohen, D. (2002b). Visual fixation patterns during viewing of naturalistic social situations as predictors of social competence in individuals with autism. *Archives of General Psychiatry*, *59*(9), 809–816.

Lundqvist, D., Flykt, A., & Ohman, A. (1998). *The Karolinska Directed Emotional Faces (KDEF)* [CD-ROM: ISBN 91-630-7169-9]. Department of Clinical Neuroscience, Psychology section, Karolinska Institute, Stockholm, Sweden.

Meletti, S., Benuzzi, F., Nichelli, P., & Tassinaria, C. A. (2003). Damage to the right hippocampal-amygdala formation during early infancy and recognition of fearful faces: Neuropsychological and fMRI evidence in subjects with temporal lobe epilepsy. *Annals of the New York Academy of Sciences*, *1000*, 385–388.

Meletti, S., Benuzzi, F., Rubboli, G., Cantalupo, G., Stanzani Maserati, M., Nichelli, P., et al. (2003). Impaired facial emotion recognition in early onset right mesial temporal lobe epilepsy. *Neurology*, *60*, 426–431.

Njiokiktjien, C., Verschoor, A., de Sonneville, L., Huyser, C., Op het Veld, V., & Toorenaar, N. (2001). Disordered recognition of facial identity and emotions in three Asperger type autists. *European Journal of Child and Adolescent Psychiatry*, *10*, 79–90.

Ogai, M., Matsumoto, H., Suzuki, K., Ozawa, F., Fukuda, R., Uchiyama, I., et al. (2003). fMRI study of recognition of facial expressions in high-functioning autistic patients. *Neuroreport*, *14*(4), 559–563.

Osterling, J., & Dawson, G. (1994). Early recognition of children with autism: A study of first birthday home videotapes. *Journal of Autism and Developmental Disorders*, *24*, 247–257.

Osterling, J. A., Dawson, G., & Munson, J. A. (2002). Early recognition of 1-year-old infants with autism spectrum disorder versus mental retardation. *Development & Psychopathology*, *14*(2), 239–251.

Ozonoff, S., Pennington, B., & Rogers, S. J. (1990). Are there emotion perception deficits in young autistic children? *Journal of Child Psychology and Psychiatry*, *31*, 343–363.

Pelphrey, K. A., Sasson, N. J., Reznick, J. S., Paul, G., Goldman, B. D., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders*, *32*(4), 249–261.

Phillips, W., Baron-Cohen, S., & Rutter, M. (1992). The role of eye-contact in the detection of goals: Evidence from normal toddlers, and children with autism or mental handicap. *Development and Psychopathology*, *4*, 375–383.

Pierce, K., Haist, F., Sedaghat, F., & Courchesne, E. (2004). The brain response to personally familiar faces in autism: Findings of fusiform activity and beyond. *Brain, 127*, 2703–2716.

Pierce, K., Muller, R. A., Ambrose, J., Allen, G., & Courchesne, E. (2001). Face processing occurs outside the fusiform "face area" in autism: Evidence from functional MRI. *Brain*, *124*(10), 2059–2073.

Prior, M., Dahlstrom, B., & Squires, T. L. (1990). Autistic children's knowledge of thinking and feeling states in other people. *Journal of Child Psychology and Psychiatry*, *31*(4), 587–601.

Rutherford, M., Baron-Cohen, S., & Wheelwright, S. (2002). Reading the mind in the voice: A study with normal adults and adults with Asperger syndrome and high-functioning autism. *Journal of Autism and Developmental Disorders*, *32*, 189–194.

Salmond, C. H., de Haan, M., Friston, K. J., Gadian, D. G., & Vargha-Khadem, F. (2003). Investigating individual differences in brain abnormalities in autism. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences*, *358*(1430), 405–413.

Saxe, R. (2006). Uniquely human social cognition. *Current Opinion in Neurobiology*, *16*, 235–239.

Schmolck, H., & Squire, L. R. (2001). Impaired perception of facial emotions following bilateral damage to the anterior temporal lobe. *Neuropsychology*, *15*, 30–38.

Schultz, R., Romanski, L. M., & Tsatsanis, K. D. (2000). Neurofunctional models of autistic disorder and Asperger syndrome. In A. Klin, F. R. Volkmar, & S. S. Sparrow (Eds.), *Asperger syndrome* (pp. 172–209). New York: Guilford Press.

Schultz, R. T. (2005). Developmental deficits in social perception in autism: The role of the amygdala and fusiform face area. *International Journal of Developmental Neuroscience*, *23*(2–3), 125–141.

Schumann, C. M., Hamstra, J., Goodlin-Jones, B. L., Lotspeich, L. J., Kwon, H., Buonocore, M. H., et al. (2004). The amygdala is enlarged in children but not adolescents with autism: The hippocampus is enlarged at all ages. *Journal of Neuroscience*, *24*(28), 6392–6401.

Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding recognition from the use of visual information. *Psychological Science*, *13*, 402–409.

Senju, A., Tojo, Y., Yaguchi, K., & Hasegawa, T. (2005). Deviant gaze processing in children with autism: An ERP study. *Neuropsychologia*, *43*(9), 1297–1306.

Senju, A., Yaguchi, K., Tojo, Y., & Hasegawa, T. (2003). Eye contact does not facilitate detection in children with autism. *Cognition*, *89*(1), B43–51.

Sparks, B. F., Friedman, S. D., Shaw, D. W., Aylward, E. H., Echelard, D., Artru, A. A., et al. (2002). Brain structural abnormalities in young children with autism spectrum disorder. *Neurology*, *59*(2), 184–192.

Stone, V. E. (2005). Theory of mind and the evolution of social intelligence. In J. Cacciopo (Ed.), *Social neuroscience: People thinking about people* (pp. 103–130). Boston: MIT Press.

Stone, V. E., & Gerrans, P. (2005). Does the normal brain have a theory of mind? *Trends in Cognitive Sciences*, *10*(1), 3–4.

Teunisse, J.-P., & de Gelder, B. (1994). Do autistics have a generalised face processing deficit? *International Journal of Neuroscience*, *77*, 1–10.

Teunisse, J. P., & de Gelder, B. (2001). Impaired categorical perception of facial expressions in high-functioning adolescents with autism. *Child Neuropsychology*, *7*(1), 1–14.

Volkmar, F. R., Lord, C., Bailey, A., Schultz, R. T., & Klin, A. (2004). Autism and pervasive developmental disorders. *Journal of Child Psychology and Psychiatry*, *45*(1), 135–170.

Volkmar, F. R., Paul, R., Klin, A., & Cohen, D. (Eds.). (2005). *Handbook of autism and pervasive developmental disorders* (3rd ed.). New York: Wiley.

Walker, A. S. (1982). Intermodal perception of expressive behaviours by human infants. *Journal of Experimental Child Psychology*, *33*, 514–535.

Walker-Andrews, A. S. (1997). Infants perception of expressive behaviours: Differentiation of multimodal information. *Psychological Bulletin*, *121*, 437–456.

Wang, A. T., Dapretto, M., Hariri, A. R., Sigman, M., & Bookheimer, S. Y. (2004). Neural correlates of facial affect processing in children and adolescents with autism spectrum disorder. *Journal of the American Academy of Child and Adolescent Psychiatry*, *43*(4), 481–490.

Wechsler, D. (1999). *Wechsler Abbreviated Scale of Intelligence*. San Antonio, TX: The Psychological Corporation.

Welchew, D., Ashwin, C., Berkouk, K., Salvador, R., Suckling, J., Baron-Cohen, S., et al. (2005). Functional dysconnectivity of the medial temporal lobe in autism. *Biological Psychiatry*, *57*(9), 991–998.

Winston, J. S., Strange, B. A., O'Doherty, J., & Dolan, R. J. (2002). Automatic and intentional brain responses during evaluation of trustworthiness of faces. *Nature Neuroscience*, *5*, 277–283.

Young, A. W. (1998). *Face and mind*. Oxford, UK: Oxford University Press.

Young, A. W., Aggleton, J. P., Hellawell, D. J., Johnson, M., Broks, P., & Hanley, J. R. (1995). Face processing impairments after amygdalotomy. *Brain*, *118*(1), 15–24.