

Integrity of lateral and feedbackward connections in visual processing in children with pervasive developmental disorder

C. Kemner^{a,b,*}, V.A.F. Lamme^c, I. Kovacs^d, H. van Engeland^a

^a Department of Child and Adolescent Psychiatry, University Medical Center Utrecht & Rudolf Magnus Institute for Neurosciences, Utrecht, The Netherlands

^b Department of Neurocognition, Faculty of Psychology, Maastricht University, Maastricht, The Netherlands

^c Department of Psychology, University of Amsterdam & The Netherlands Ophthalmic Research Institute, Amsterdam, The Netherlands

^d Department of Cognitive Science, Faculty of Economics and Social Sciences, Budapest University of Technology and Economics, Budapest, Hungary

Received 30 March 2006; received in revised form 26 September 2006; accepted 27 September 2006

Available online 13 November 2006

Abstract

Enhanced visual detail processing in subjects with pervasive developmental disorder (PDD) has been related to impairments in feature integration. The functional integrity of two types of neuronal connections involved in visual feature integration, namely horizontal and feedbackward connections, were tested.

Sixteen children with PDD and 17 age- and IQ-matched control children (mean age 13.3 years) were included. In a texture segregation task the difference in ERP response to homogeneous and checkered visual stimuli was determined. Additionally, in a contour integration task subjects had to point out a contour consisting of colinearly aligned Gabor signals in backgrounds increasing in noise.

Children with PDD showed a normal performance on the contour integration task, suggesting that neurons in the primary visual cortex of children with PDD can effectively integrate the activity of local detectors that process different aspects of the same object information by making use of long-range lateral connections. The amplitude of ERP activity related to texture segregation was also not different between the PDD and control groups, indicating functional visual feedback mechanisms between V1 and higher order areas in subjects with PDD. However, a difference in latency of texture-segmentation related activity between the groups was noted. This effect did not reach significance, which could be due to the small N of the study. Therefore, the data need replication in a study with larger samples before more definitive conclusions can be drawn.

© 2006 Elsevier Ltd. All rights reserved.

Keywords: Pervasive developmental disorders; Autistic disorder; Event-related potentials; Visual integration

1. Introduction

Although impairments in the social domain are the best known characteristics of PDD, there is an increasing realization that subjects with PDD show atypical processing that is not restricted to socially relevant stimuli. More specifically, subjects with PDD are usually found to excel in visuo-spatial tasks that require detail processing and neglect of the relationship between details, such as the block design test and Embedded Figures Test (Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1993). There are indications that extensive detail processing also plays a role in

abnormal behavior of autistic subjects in the social domain, such as abnormal face processing (Klin et al., 1999; Schultz et al., 2000). It has been suggested that these findings point to abnormal integration of visual features in subjects with PDD, resulting in an impaired ability to perceive aspects of global stimuli, and this was conceptualized as ‘weak central coherence’ (Frith, 1989). Indeed, several functional studies have been published that provide evidence for impaired integration of information at a large-scale level, i.e. between relatively distant (sub) cortical areas (Castelli, Frith, Happe, & Frith, 2002; Schultz et al., 2000). Additionally, abnormalities in white matter tracts indicate abnormal structural connectivity between cortical areas in subjects with PDD (Barnea-Goraly et al., 2004). However, there is little knowledge on the anatomical base for abnormal visual feature integration in PDD, which relies on processing on a more small-scale level, i.e. within the visual cortex.

* Corresponding author at: Department of Child and Adolescent Psychiatry, University Medical Center Utrecht, B01.324 Heidelberglaan 100, 3514 CX Utrecht, The Netherlands. Tel.: +30 2507462; fax: +30 2505444.

E-mail address: C.Kemner@umcutrecht.nl (C. Kemner).

The integration of visual features in healthy subjects is usually explained in the context of the feedforward model of visual processing. This model builds on the anatomical hierarchy of cortical areas: the neurons of low-level areas represent simple features, which are integrated and transferred via feedforward corticocortical connections toward higher levels of stimulus integration. While the primary cortex is involved in the analysis of elements, the integration of these elements is thought to occur in the temporal and parietal cortices. According to this model, PDD would be associated with an abnormality in feedforward integration systems. However, the feedforward view of visual perception is now being challenged. Feedforward connections are reciprocated by numerous feedback fibers, and there is increasing evidence that these feedback-connections are effective in integrating information. For example, in a recent model of visual processing, reverse hierarchy theory (RHT), feedforward and feedbackward processing are directly associated with the perception of global and local aspects of a stimulus, respectively. According to RHT, feedforward processing occurs first, resulting in a representation of the global aspects of a scene at higher cortical levels. Later recurrent processing to lower areas provides detailed information (Hochstein & Ahissar, 2002). There are indications that in PDD the primary abnormality is not in the processing of global percepts. Several studies have shown that individuals with PDD can respond to the global level of a hierarchical stimulus in the same way as controls, but sometimes respond better to the local level of a stimulus (Mottron, Burack, Iarocci, Belleville, & Enns, 2003; Ozonoff, Strayer, McMahon, & Filloux, 1994; Plaisted, Swettenham, & Reese, 1999). Individuals with PDD also perform visual search tasks better (O’Riordan, Plaisted, Driver, & Baron-Cohen, 2001; Plaisted, O’Riordan, & Baron-Cohen, 1998), and these findings have led to the suggestion that subjects with PDD have a greater awareness of individual features of a stimulus (Mottron & Burack, 2001). Since perceptual awareness of stimulus details is associated with feedbackward activity, an alternative explanation for increased detail processing in PDD is that feedbackward activity is relatively stronger in this group. Abnormal structural cortical connections between several brain areas have been reported in subjects with PDD (Barnea-Goraly et al., 2004). If such deficient wiring would occur between occipital areas in subjects with PDD, this is likely to affect the delicate interaction between visual feedforward and feedbackward processing.

Another important mechanism for visual integration are the horizontal neuronal connections within the visual cortex. Studies have shown the existence of extensive axonal collaterals of pyramidal cells in layers 2 and 3 of the primary visual cortex, which may span several millimeters horizontally across the cortex. It is assumed that these neuronal connections are involved in the integration of the activity beyond the neuron’s receptive field (Kovács & Julesz, 1993; Lamme & Roelfsema, 2000). Recent neuropathological studies demonstrate that subjects with autism have more numerous and more narrow minicolumns than control subjects (Casanova, Buxhoeveden, Switala, & Roy, 2002a; Casanova, Buxhoeveden, Switala, & Roy, 2002b) providing a neuroanatomical base for integration abnormalities within cortical areas.

So, both feedback and horizontal connections are involved in normal visual feature integration. There is increasing attention for the role of such low-level mechanisms in atypical visuo-spatial processing in PDD (Dakin & Frith, 2005). More specifically, two recent studies have related deficient processing in specific visuo-spatial tasks with abnormalities in neurointegrative mechanisms in the visual cortex (Bertone, Mottron, Jelenic, & Faubert, 2003; Bertone, Mottron, Jelenic, & Faubert, 2005). Using first- and second order static stimuli, superior processing of first order stimuli, but decreased processing of second-order stimuli was shown in subjects with PDD. The authors suggested that feedback connections between V1 and higher order visual areas (V2/V3) are necessary for the processing of second order stimuli. The processing of first order stimuli, on the contrary, would rely on V1 only (Bertone et al., 2005). Therefore, the impaired processing of second-order stimuli was interpreted as an indication for abnormal integration of information between brain regions. However, this study was not aimed to test the functional integrity of visual structures involved in feature integration, and provides only indirect evidence for abnormalities in this respect in PDD.

The present study is aimed to test as direct as possible the functioning of lateral and feedbackward connections in school age children with PDD by means of a contour integration and a texture segmentation task. In both tasks, lateral as well as feedforward/feedbackward connections are probably important. However, the design of the tasks allows focusing specifically on, respectively, lateral and feedbackward connections. The contour-integration task consists of cards including a closed chain of collinearly aligned Gabor signals (contour), which the subjects have to point out, and a background of randomly oriented and positioned Gabor signals (noise). The cards increase in amount of noise, and at low signal to noise ratios, the subject is forced to rely on horizontal connections in primary visual cortex in integrating the orientation of the Gabor elements, and finding the contour (Kovács, Polat, Norcia, Pennefather, & Chandna, 2000). The second task is aimed to study texture segregation, a prerequisite for the segregation of scenes into objects and background. It involves the pre-attentive processing of certain visual dimensions, such as luminance, color, orientation, or direction of motion, identifying differences between adjoining regions in the visual field. Texture segregation can be studied by presenting visual stimuli containing the same feature presented in two ways, such as lines in different orientations (like the checkerboards used in the present study), and comparing the event-related potentials evoked by these stimuli to the potentials evoked by presentation of the same feature presented in a homogeneous fashion (i.e. lines solely in a horizontal direction or solely vertical). Electrocortical activity in response to textured stimuli is enhanced compared to the activity evoked by homogeneous stimuli at latencies ranging from 100 to 250 ms after stimulus onset (Bach & Meigen, 1997; Fahle, Quenzer, Braun, & Spang, 2003; Lamme, Van Dijk, & Spekreijse, 1992). This EEG activity is directly related to similar modulations of activity that can be recorded in V1 of the awake monkey, and that have been shown to depend on recurrent neural interactions between V1 and higher visual areas; removal of the extra-striate areas abolishes the

feedback induced V1 activity (Lamme, Super, & Spekreijse, 1998). Thus, subtracting activity in response to homogeneous stimuli from activity to checkered (textured) stimuli selectively isolates neural signals related to recurrent processing between V1 and higher visual areas, mediated by feedback and horizontal interactions (see Roelfsema, Lamme, Spekreijse, & Bosch, 2002 for a model). Moreover, these signals have been shown to reflect the integration of individual line segments into the organized percept of a figure overlying a background (Lamme, 1995; Lamme & Roelfsema, 2000; Zipser, Lamme, & Schiller, 1996). The underlying neural mechanisms are thus directly related to texture segregation, and to the process of perceptual organization in general (Lamme & Roelfsema, 2000). This paradigm is therefore ideally suited to study the role of recurrent processing in PDD specifically. These tasks were presented to a group of high functioning children with PDD and a group of age- and IQ matched controls.

2. Methods and materials

2.1. Subjects

Twenty-three control children and 24 children with PDD took part in the study. Clinical subjects were recruited from the Department of Child and Adolescent Psychiatry at the Utrecht Academic Hospital. Control children were recruited from elementary schools in and around Utrecht. In the control group, one child was excluded because she did not finish the testing procedure, two children because of technical problems, and three children were excluded because of matching criteria. Of the PDD subjects, four children were excluded for technical reasons, one child was excluded because he kept his eyes shut for considerable periods of time and three because they did not meet the inclusion criteria. The final clinical and control groups in the texture segmentation task each consisted of 16 and 17 subjects, respectively; each group included one girl. All subjects were administered the Wechsler Intelligence Scale for Children, revised Dutch edition (WISC-RN). There were no significant age or IQ differences between the groups (age, verbal IQ, performatory IQ and total IQ for the control group respectively 13.3, 104, 105, 105, for the PDD group respectively 13.3, 108, 102, 106). In the contour integration task, no information was obtained from one subject with PDD, resulting in a total of 15 subjects in this group. However, this resulted in only slight changes in IQ and age parameters. Again, age and IQ did not differ between groups in this task.

For PDD subjects, all diagnoses (either Autistic Disorder or Asperger Syndrome) were based on DSM-IV criteria and were made by a child psychiatrist. Furthermore, all PDD subjects were administered the Autism Diagnostic Interview Revised (ADI-R) (Lord, Rutter, & Le Couteur, 1994) by a trained rater. Thirteen children with PDD met full ADI-R criteria for autism or autism spectrum disorder. The other three subjects scored two points below cutoff for the subscale stereotypical behavior. Subjects were medication free and had no significant neurological history. The medical ethics committee of the University Medical Center Utrecht approved the study, in accordance with the Declaration of Helsinki, and all parents or caretakers gave written informed consent prior to participation after explanation of the procedure.

2.1.1. Contour integration task

A card-test version (Kovacs, Kozma, Feher, & Benedek, 1999; Kovács et al., 2000) of the contour integration task was used. A contour integration card consists of a closed chain of collinearly aligned Gabor signals (contour), and a background of randomly oriented and positioned Gabor signals (orientation noise). The carrier spatial frequency of the Gabor elements was 5 c/deg at a test distance of 50 cm. Inter-element spacing along the contour was fixed at 8 wavelengths (8λ) of the carrier, center-to-center (1.6°). The task is to identify the path of the contour. To estimate the actual strength of long-range interactions in each observer, relative noise density is varied across the set. Relative noise density (D) is defined as the ratio of average noise spacing over contour spacing.

D is varied between 0.5 and 1.2 in steps of 0.05, resulting in 15 cards per set. At a D value of 1.2, the contour can be detected on the basis of a first-order texture density cue. Contour detection at D values of 1 or less can only be accomplished through the detection of the relative orientation of elements along the contour. Observers were requested to trace the path of the contour in each card. After familiarizing subjects with the task, cards were presented in an increasing order of difficulty. A simple staircase procedure was used in which threshold was defined by the last correctly identified card. The staircase allowed progression if a card was missed, but when the next card was missed as well, a reversal occurred.

2.1.2. Texture segmentation task

One block consisted of full-screen presentations of 900 stimuli on a 21 in. computer screen (42 cm × 32 cm) approximately 1 m from the subject. The stimuli consisted of homogeneous fields of either 45° or 135° oriented, randomly positioned, line segments (eight different stimuli), or of checkerboards consisting of the same line segments (also eight different stimuli). The homogeneous and checkerboard maps alternated every 550 ms. The basic sequence consisted of the 16 maps presented in a fixed order (see Lamme et al., 1992 for details on stimuli and presentation sequence). During presentation a red dot was shown in the middle. Randomly during the task, Pokemon stimuli were also presented (in total 39 stimuli, 19 of which were targets). Subjects were required to press a button in response to the target Pokemon. Data for the first two trials after each Pokemon presentation were not included in the analysis.

2.2. Data recording and analysis

Electroencephalographic activity was recorded from eight electrode positions (Fz, Cz, Pz, Oz, P3, P4, O1, and O2) by means of a Quickcap (NeuroMedical supplies of Neurosoft Inc.), with subjects sitting in an acoustically shielded room. Scalp electrodes were at standard EEG recording locations of the international 10/20 system. Horizontal EOG was recorded using an electrode attached to the outer cantus of the left eye. Similarly, vertical EOG was recorded from the infra-orbital and supra-orbital electrodes in line with the pupil of the left eye.

Two different EEG systems were used. The first series of subjects were tested with tin electrodes using the Psylab system (Contact Precision Instruments, London). Signals were sampled at a rate of 500 Hz and stored as a continuous signal. A ground electrode was placed at the middle of the forehead and signals were referenced to the left mastoid. EEG signals were filtered online with a high-pass filter of 0.05 Hz and a low-pass of 70 Hz. The second series of subjects were tested with AgAgCl electrodes using the Active Two system (Biosemi, Amsterdam) and the EEG was sampled at a rate of 2048 Hz and stored as a continuous signal. Two electrodes in the electrode cap, the CMS (=common mode sense) and DRL (=driven right leg), provided an 'active ground' in this system. An electrode placed on the left mastoid was used as a reference. Data were resampled at 500 Hz offline.

All data were filtered offline with a high-pass filter of 1 Hz, a low-pass filter of 30 Hz, and a Notch filter of 50 Hz. In order to compute event-related potentials (ERPs), epochs from 100 ms prestimulus until 400 ms poststimulus were extracted offline from the continuous data and corrected for baseline, using the data for the 50 ms prior to stimulus onset. EOG artefacts were removed (Gratton, Coles, & Donchin, 1983). EEG artefacts were removed if they were larger than 100 or $-100 \mu\text{V}$, if there was an amplitude difference per sample point larger than $50 \mu\text{V}$ or if the difference between maximum and minimum amplitudes in a window of 200 ms was smaller than $3 \mu\text{V}$. Signals were averaged across stimulus conditions. In the homogeneous condition, the average number of trials on which the average ERPs were based were 378, and 374 trials for the control and PDD subjects, respectively. In the textured condition on average 384, and 380 trials were included in the average ERPs of the control and PDD subjects, respectively. A minimum of 315 trials was included in each individual average.

2.3. Statistical analysis

Contour integration task. An independent sample t -test was used to test for differences between PDD and control groups in number of cards with a correctly detected contour. *Texture segmentation task:* A difference wave was computed by subtracting the ERPs to homogeneous stimuli from the ERPs to checkered (textured) stimuli and the main negativity in this difference wave (texture seg-

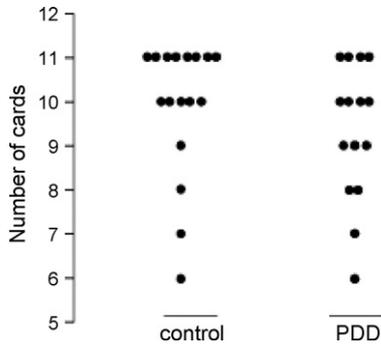


Fig. 1. The number of correctly identified contours for each individual.

regation negativity) was scored between 100 and 220 ms at Oz. Independent samples *t*-tests were done to test for differences between groups in latency or amplitude of the texture segregation negativity. The significance level for all tests was set at $p < 5\%$, two-tailed.

3. Results

Contour integration task. No statistically significant difference between groups was found in number of cards with a correctly detected contour ($t(30) = 0.32, p = 0.55$) (mean number of cards control group 9.9, in the PDD group 9.3) (see Fig. 1). Since more subjects with PDD than controls showed a relatively low score, as compared to an earlier developmental study (Kovács et al., 2000), it was also tested whether there was a correlation between number of cards and scores on the subdomains of the ADI (subdomains Social Interaction, Communication,

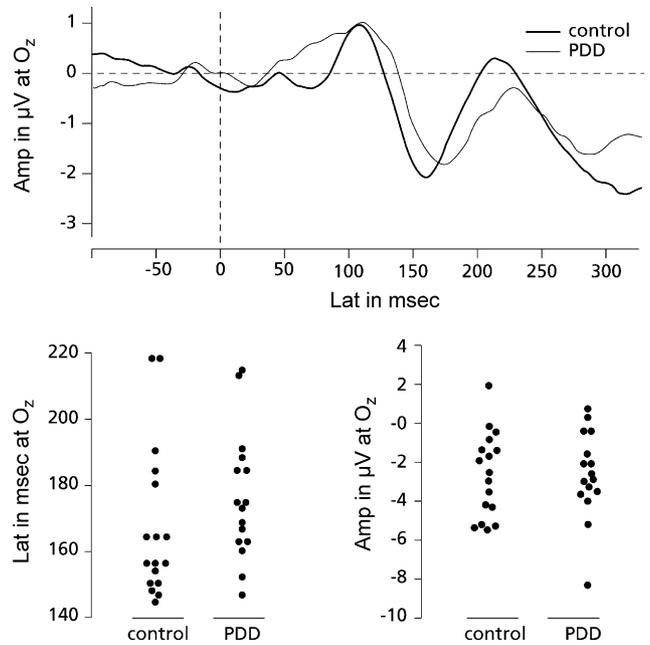


Fig. 3. (Upper panel) Difference waves between ERPs to homogeneous stimuli and ERPs to texture stimuli (i.e. texture segregation related activity) at the Oz electrode. (Lower panel) Amplitude (left) and latency (right) of the texture segregation related negativity at Oz for each individual.

and Stereotypic Behaviors). However, no such correlations were found.

Texture segmentation task. No difference between the two groups was found with relation to either the amplitude ($t(31) = -0.016, p = 0.99$) or the latency ($t(31) = -1.07, p = 0.30$) of the texture segregation negativity (latencies of the normal and PDD group respectively 167 and 175 ms, amplitudes of the normal and control group both $-2.7 \mu V$) (see Fig. 2 for the average ERPs to homogeneous and textured stimuli, and Fig. 3 for the difference wave).

4. Discussion

Recently, several studies have indicated that subjects with PDD might have atypical integration of visual features, resulting in, amongst others, increased detail processing. However, little is known so far on the functioning of neurocognitive mechanisms underlying atypical visual feature integration in this group. In this study we specifically tested the functional integrity of two types of neuronal connections involved in visual feature integration, namely horizontal and feedback connections, in high functioning children with PDD. To this end, we used two tasks that each provide in a relatively precise way information on these integrating mechanisms, namely a contour integration task and a texture segmentation task. In the contour integration tasks the lateral processing strength is related to the number of detected contours. In the texture segmentation task feedback processing to area V1 is reflected in the ERP difference wave between homogeneous and textured stimuli.

The contour integration task showed that most children were able to correctly identify contours of Gabor stimuli in about 10–11 cards out of a set of 15. In this task the relative noise den-

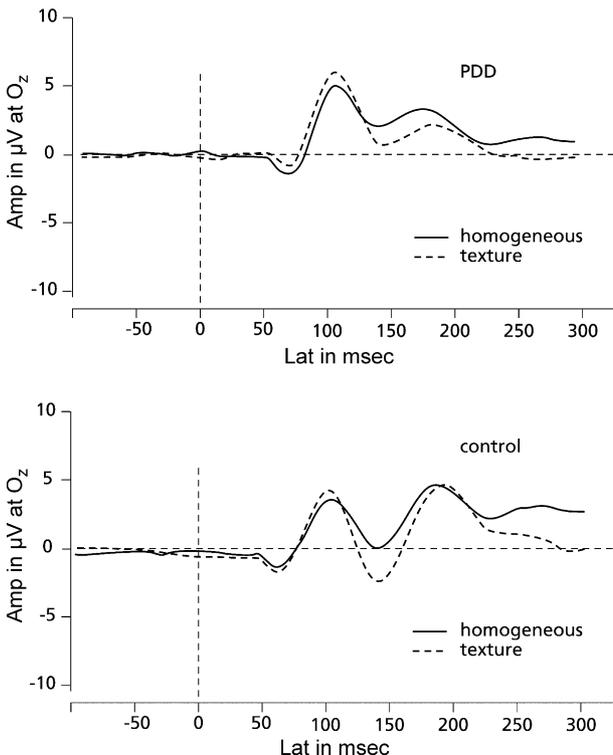


Fig. 2. Grand average ERPs to homogeneous and textured stimuli, at electrode Oz: (upper panel) PDD group; (lower panel) control group.

sity (D) is varied, while keeping contour spacing constant. In the present study, a set of 15 cards was used in which D ranged between 1.20 and 0.50. A D value of 1 (present in card 5) or less implies that the contour can only be detected by using lateral long-range interactions (Kovacs et al., 1999). Since almost all children identified five cards or more, this type of processing occurred in both control and PDD groups. The average number of correctly identified contours was somewhat lower than in an earlier study involving control children in the same age range, but this could be due to different laboratory settings or differences in motivation. Additionally, gender differences might have influenced the results, since the subjects in our study consisted of mainly boys, while in the earlier study more females than males were included (Kovacs et al., 1999). No significant differences between the clinical and the control group were found, indicating that the strength of the lateral interactions was comparable in both groups. These data suggest that PDD in children is not associated with an abnormality in the integration of visual spatial information as needed for contour detection. Apparently, neurons in the primary visual cortex of children with PDD can effectively integrate the activity of local detectors that process different aspects of the same object information by making use of long-range lateral connections.

With respect to the texture segregation task, in both the control group and the clinical group the difference wave between ERPs to textured minus homogeneous stimuli showed significant activity related to texture segregation at about 170 ms. The latency of the peak of activity was earlier than reported in some studies of adults (Bach & Meigen, 1997; Fahle et al., 2003), but not in others (Lamme et al., 1992), and this difference might be related to the age of the participants, or to differences in the experimental set-up. The clinical and control groups showed the same average amplitude of the scored peak of the difference wave, indicating a normal amount of activation related to texture segregation in the children with PDD. Additionally, average values suggested a difference in latency of the recurrent activity between the groups, although this was not statistically significant. Since the N of our groups was relatively small, the fact that the difference did not reach significance could be due to a power problem. The activation pattern suggests re-entrant activity from within the visual cortex in children with PDD, implicating the existence of functioning visual feedback mechanisms between V1 and higher order areas in this group, at least in relation to the relatively simple stimuli that were used in the present study. However, the latency data suggest the possibility of a delay in this recurrent activity in the PDD group that warrants further research.

It has been reported several times that subjects with PDD have a reduced ability to perceive motion (Blake, Turner, Smoski, Pozdol, & Stone, 2003; Milne et al., 2002; Pellicano, Gibson, Maybery, Durkin, & Badcock, 2005; Spencer et al., 2000) and it was suggested that abnormalities in motion processing might be the result of impaired stimulus integration (Bertone et al., 2003). Given the results on the contour integration cards, which specifically manipulated involvement of horizontal processing, the present study indicates that there is no abnormality in integration mechanisms that rely on horizontal connections in V1.

Likewise, in an earlier study (Spencer et al., 2000) evidence for normal global form perception was found in subjects with PDD and it has been argued before that the global form task used in this study relies on the integration in V1 (Pellicano et al., 2005). Alternatively, as an explanation for decreased processing of second- but not first-order stimuli, it has been suggested that subjects with PDD have problems in the integration of information between V1 and higher-order areas V2/V3 (Bertone et al., 2005). In the texture segmentation task feedback activity was specifically measured. However, clinical subjects did not differ from controls in with respect to ERP activity related to feedback processing, indicating normal integration of information between V1 and V2/V3 in this group.

The results of this study should be interpreted with caution because the subjects with PDD included in this study were high functioning and therefore are not representative of the PDD population. Another potential problem concerns the power of the study. It is well possible that, due to the low N , potentially significant differences between groups are statistically unnoted. This problem seems especially present for the latency data of the texture related difference wave. Therefore, this study should be regarded as a first attempt to determine the functioning of horizontal and feedback connections related visual processing in subjects with PDD. Although the present study shows no evidence for abnormal integrating mechanisms related to visual processing in children with PDD, either within or between visual cortical areas, there is a need for replication of the data with larger groups.

Acknowledgements

The work described was supported by a VIDI-NWO grant (no. 402-01-094) and a Cure Autism Now grant to Chantal Kemner. We thank Renate Simons and Emmie Schaffelaar for recruitment and testing of the subjects, and Gert Camfferman for technical assistance.

References

- Bach, M., & Meigen, T. (1997). Similar electrophysiological correlates of texture segregation induced by luminance, orientation, motion and stereo. *Vision Research*, 7, 1409–1414.
- Barnea-Goraly, N., Kwon, H., Menon, V., Eliez, S., Lotspeich, L., & Reiss, A. L. (2004). White matter structure in autism: Preliminary evidence from diffusion tensor imaging. *Biological Psychiatry*, 55, 323–326.
- Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2003). Motion perception in autism: A “complex” issue. *Journal of Cognitive Neuroscience*, 15, 218–225.
- Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2005). Enhanced and diminished visuo-spatial information processing in autism depends on stimulus complexity. *Brain*, 128, 2430–2441.
- Blake, R., Turner, L. M., Smoski, M. J., Pozdol, S. L., & Stone, W. L. (2003). Visual recognition of biological motion is impaired in children with autism. *Psychological Science*, 14, 151–157.
- Casanova, M. F., Buxhoeveden, D. P., Switala, A. E., & Roy, E. (2002a). Asperger’s syndrome and cortical neuropathology. *Journal of Child Neurology*, 17, 142–145.
- Casanova, M. F., Buxhoeveden, D. P., Switala, A. E., & Roy, E. (2002b). Minicolumnar pathology in autism. *Neurology*, 58, 428–432.
- Castelli, F., Frith, C., Happé, F., & Frith, U. (2002). Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. *Brain*, 125, 1839–1849.

- Dakin, S., & Frith, U. (2005). Vagaries of visual perception in autism. *Neuron*, 48, 497–507.
- Fahle, M., Quenzer, T., Braun, C., & Spang, K. (2003). Feature-specific electrophysiological correlates of texture segregation. *Vision Research*, 43, 7–19.
- Frith, U. (1989). *Autism: Explaining the enigma*. Blackwell Science.
- Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artefact. *Electroencephalography and Clinical Neurophysiology*, 55, 468–484.
- Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, 36, 791–804.
- Jolliffe, T., & Baron-Cohen, S. (1997). Are people with autism and Asperger syndrome faster than normal on the Embedded Figures Test? *Journal of Child Psychology and Psychiatry*, 38, 527–534.
- Klin, A., Sparrow, S. S., de Bildt, A., Cicchetti, D. V., Cohen, D. J., & Volkmar, F. R. (1999). A normed study of face recognition in autism and related disorders. *Journal of Autism and Developmental Disorders*, 29, 450–499.
- Kovács, I., & Julesz, B. (1993). A closed curve is much more than an incomplete one: Effect of closure in figure-ground segmentation. *Proceedings of the National Academy of Sciences*, 90, 7495–7497.
- Kovács, I., Kozma, P., Feher, A., & Benedek, G. (1999). Late maturation of visual spatial integration in humans. *Proceedings of the National Academy of Sciences*, 96, 12204–12209.
- Kovács, U., Polat, A. M., Norcia, P., Pennefather, M., & Chandna, A. (2000). A new test of contour integration deficits in patients with a history of disrupted binocular experience during visual development. *Vision Research*, 40, 1775–1783.
- Lamme, V. A. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *Journal of Neuroscience*, 15, 1605–1615.
- Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neuroscience*, 23, 571–579.
- Lamme, V. A., Super, H., & Spekreijse, H. (1998). Feedforward, horizontal, and feedback processing in the visual cortex. *Current Opinions in Neurobiology*, 8, 529–535.
- Lamme, V. A., Van Dijk, B. W., & Spekreijse, H. (1992). Texture segregation is processed by primary visual cortex in man and monkey. Evidence from VEP experiments. *Vision Research*, 32, 797–807.
- 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*, 2, 659–685.
- Milne, E., Swettenham, J., Hansen, P., Campbell, R., Jeffries, H., & Plaisted, K. (2002). High motion coherence thresholds in children with autism. *Journal of Child Psychology and Psychiatry*, 43, 255–263.
- Mottron, L., & Burack, J. A. (2001). Enhanced perceptual functioning in the development of autism. In J. A. Burack, T. Charman, N. Yirmiya, & P. R. Zelazo (Eds.), *The development of autism: Perspectives from theory and research* (pp. 131–148). Mahwah, NJ: Lawrence Erlbaum.
- Mottron, L., Burack, J. A., Iarocci, G., Belleville, S., & Enns, J. T. (2003). Locally oriented perception with intact global processing among adolescents with high-functioning autism: Evidence from multiple paradigms. *Journal of Child Psychology and Psychiatry*, 44, 904–913.
- O’Riordan, M. A., Plaisted, K. C., Driver, J., & Baron-Cohen, S. (2001). Superior visual search in autism. *Journal of Experimental Psychology: Human Perception and Performance*, 27, 719–730.
- Ozonoff, S., Strayer, D. L., McMahon, W. M., & Filloux, F. (1994). Executive function abilities in autism and Tourette syndrome: An information processing approach. *Journal of Child Psychology and Psychiatry*, 35, 1015–1032.
- Pellicano, E., Gibson, L., Maybery, M., Durkin, K., & Badcock, D. R. (2005). Abnormal global processing along the dorsal visual pathway in autism: A possible mechanism for weak visuospatial coherence? *Neuropsychologia*, 43, 1044–1053.
- Plaisted, K., O’Riordan, M., & Baron-Cohen, S. (1998). Enhanced visual search for a conjunctive target in autism: A research note. *Journal of Child Psychology and Psychiatry*, 39, 777–783.
- Plaisted, K., Swettenham, J., & Reese, L. (1999). Children with autism show local precedence in a divided attention task and global precedence in a selective attention task. *Journal of Child Psychology and Psychiatry*, 40, 733–742.
- Roelfsema, P. R., Lamme, V. A., Spekreijse, H., & Bosch, H. (2002). Figure-ground segregation in a recurrent network architecture. *Journal of Cognitive Neuroscience*, 14, 525–537.
- Schultz, R. T., Gauthier, I., Klin, A., Fulbright, R. K., Anderson, A. W., Volkmar, F., et al. (2000). Ventral temporal cortical activity during face discrimination among individuals with autism and Asperger syndrome. *Archives of General Psychiatry*, 57, 331–340.
- Shah, A., & Frith, U. (1993). Why do autistic individuals show superior performance on the block design task? *Journal of Child Psychology and Psychiatry*, 34, 1351–1364.
- Spencer, J., O’Brien, J., Riggs, K., Braddick, O., Atkinson, J., & Wattam-Bell, J. (2000). Motion processing in autism: Evidence for a dorsal stream deficiency. *Neuroreport*, 11, 2765–2767.
- Zipser, K., Lamme, V. A., & Schiller, P. H. (1996). Contextual modulation in primary visual cortex. *Journal of Neuroscience*, 16, 7376–7389.