CORTEX 52 (2014) 28–34

Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Note

The role of human basolateral amygdala in ambiguous social threat perception

Beatrice de Gelder[a,b,c,*], *David Terburg*[d,e,1], *Barak Morgan*[f,1], *Ruud Hortensius*[b], *Dan J. Stein*[e] and *Jack van Honk*[d,e]

[a] *Department of Psychology and Neuroscience, Maastricht University, The Netherlands*
[b] *Cognitive and Affective Neuroscience Laboratory, Tilburg University, The Netherlands*
[c] *Brain and Emotion Laboratory Leuven, Department of Neurosciences, Leuven University, Belgium*
[d] *Experimental Psychology, Utrecht University, The Netherlands*
[e] *Department of Psychiatry and Mental Health, University of Cape Town, South Africa*
[f] *MRC Medical Imaging Research Unit, Department of Human Biology, University of Cape Town, South Africa*

ARTICLE INFO

Article history:
Received 22 April 2013
Reviewed 13 September 2013
Revised 14 October 2013
Accepted 19 December 2013
Action editor Alan Sanfey
Published online 31 December 2013

Keywords:
Amygdala
Body emotion expressions
Urbach–Wiethe disease
Emotion
Basolateral amygdala

ABSTRACT

Previous studies have shown that the amygdala (AMG) plays a role in how affective signals are processed. Animal research has allowed this role to be better understood and has assigned to the basolateral amygdala (BLA) an important role in threat perception. Here we show that, when passively exposed to bodily threat signals during a facial expressions recognition task, humans with bilateral BLA damage but with a functional central-medial amygdala (CMA) have a profound deficit in ignoring task-irrelevant bodily threat signals.

1. Introduction

It is a common experience that an angry face feels more menacing when accompanied by a pair of fists, but it is rather unsettling when the fists come with a smile. In that case we experience the overall signal as profoundly ambiguous. When instructed to attend to only the facial expression, the brain notices the conflict between the facial expression and the accompanying bodily expression in a matter of milliseconds (Meeren, van Heijnsbergen, & de Gelder, 2005).

A variety of functions related to affective processes have been attributed to the amygdala (AMG) including immediate perception of affective stimuli, learning and conditioning, as

* *Corresponding author*. Department of Psychology and Neuroscience, Maastricht University, The Netherlands.
E-mail address: b.degelder@maastrichtuniversity.nl (B. de Gelder).

[1] These authors contributed equally to this work.

0010-9452/$ – see front matter
http://dx.doi.org/10.1016/j.cortex.2013.12.010

well as emotional memory (Phelps & LeDoux, 2005). The AMG is also involved in modulating behavioral responses and has multiple connections to brain areas directly involved in behavioral output (Mosher, Zimmerman, & Gothard, 2010). There is also overwhelming evidence that the AMG plays an important role in regulating emotion perception and preparing adapted motor behavior (Phelps & LeDoux, 2005).

Previous research has shown that the AMG plays an important role in face (Costafreda, Brammer, David, & Fu, 2008) and body (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004) expression recognition and is also highly sensitive to ambiguous signals (Kim et al., 2004; Whalen, 1998). But further progress in understanding the AMG will require understanding the specific contribution of the multiple nuclei of the AMG. Functions or loss of functions ascribed to the AMG as a whole may in fact result from activation of AMG nuclei or inter- and intra-amygdala connectivity. For example, facial expression recognition has been attributed to the AMG as a whole (Rutishauser et al., 2011) and consequently it was assumed that AMG damage abolishes this (Adolphs, Tranel, Damasio, & Damasio, 1994, but see Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009). But more recently it was shown that an impairment of one of the AMG nuclei, the basolateral amygdala (BLA), leads to hypersensitivity for facial fear expressions (Terburg et al., 2012).

Similarly, the same complete AMG impairment does not seems to abolish body expression recognition (Atkinson, Heberlein, & Adolphs, 2007). This finding does not rule out that an impairment of a specific nucleus of the AMG does nevertheless have consequences for normal processing of body expressions. In the case of a complex structure like the AMG a functional role attributed to the AMG as a whole cannot be attributed automatically to each of its subnuclei.

We addressed the issue of the functional role of the BLA in ambiguous social threat perception using subjects with Urbach–Wiethe disease (UWD), a rare genetic disorder that in our sample has resulted in bilateral focal calcification of the BLA. We tested three subjects from the South African UWD cohort (Thornton et al., 2008) selected for this specific BLA damage (Morgan, Terburg, Thornton, Stein, & van Honk, 2012) and a group of matched controls on a series of face and body expression recognition tasks. Our goal was first, to investigate the specific role of the BLA in implicit bodily expression recognition and second, the role of the BLA in ambiguity perception. We used angry and fearful Face Body Compounds created by combining a facial expression with either a congruent or incongruent bodily expression. Using convergent evidence from behavior and eye tracking measures, we investigated how BLA damage affects the processing of affective information from body expressions of anger and fear that are, unattended, not task relevant, and presented in the periphery. We conjectured that under these conditions of implicit perception participants with BLA damage would still process the threatening body signals and these signals would be more salient than in normal controls. Therefore we expect an increased effect from threatening bodily expressions on facial expression perception in the UWD group.

2. Methods

2.1. Subjects

Three subjects from the South African UWD cohort (Morgan et al., 2012; Thornton et al., 2008) without any history of secondary psychopathology or epileptic insults and 12 matched controls participated in the experiment. The UWD and control group were all female and matched for age and IQ (see Table 1 for demographic data). All participants were from mountain-desert villages near the Namibian border. Detailed neuropsychological assessment of the UWD group is described elsewhere (Morgan et al., 2012; Terburg et al., 2012). Structural and functional MRI assessment by means of cytoarchitectonic-probability labeling showed that bilateral calcification is restricted to the BLA (see Fig. 1). This study was approved by the Health Sciences Faculty Human Research Ethics Committee of the University of Cape Town. All participants provided written informed consent. We note that all UWD subjects reported here and in previous studies (Adolphs et al., 1994; Morgan et al., 2012; Terburg et al., 2012) are female and we cannot exclude that gender colors past and present results. Resolution of this issue must await availability of male UWD subjects.

2.2. Tasks

2.2.1. Face Body Compound task (FBC)

Congruent and incongruent threatening FBCs (Meeren et al., 2005) were constructed using angry and fearful bodies (de Gelder & Van den Stock, 2011) and angry and fearful faces (MacBrain Face Stimulus Set) (see Fig. 2A). Stimuli (12 per condition, 6 female) were on screen for 350 msec for behavioral testing and 2000 msec for eye tracking. Participants had to recognize the facial expression and ignore the bodily expression while accuracy and reaction time were recorded during behavioral testing.

2.2.2. Sample-to-match task

The Bodily Expressive Action Stimulus Test (BEAST) (de Gelder & Van den Stock, 2011) was used to assess the perception of emotional whole bodily expression. Participants had to match angry, happy, fearful or sad bodily expressions with one of two simultaneously presented bodily expressions (12 per condition, 6 female). Both the target and distracter had different identities, while the distracter had a different

Table 1 – Demographic data.

	UWDs				Controls
	UWD 1	UWD 2	UWD 3	Mean	Mean
Age	24	31	35	32 ± 5.1	32 ± 8.6
VIQ	95	84	93	90.7 ± 5.9	88.1 ± 4.2
PIQ	98	86	85	89.7 ± 7.2	87.1 ± 6.9
FSIQ	97	84	87	89.3 ± 6.8	86.4 ± 4.3

VIQ: verbal IQ, PIQ: performance IQ, FSIQ: full-scale IQ. Means and standard deviations are reported.

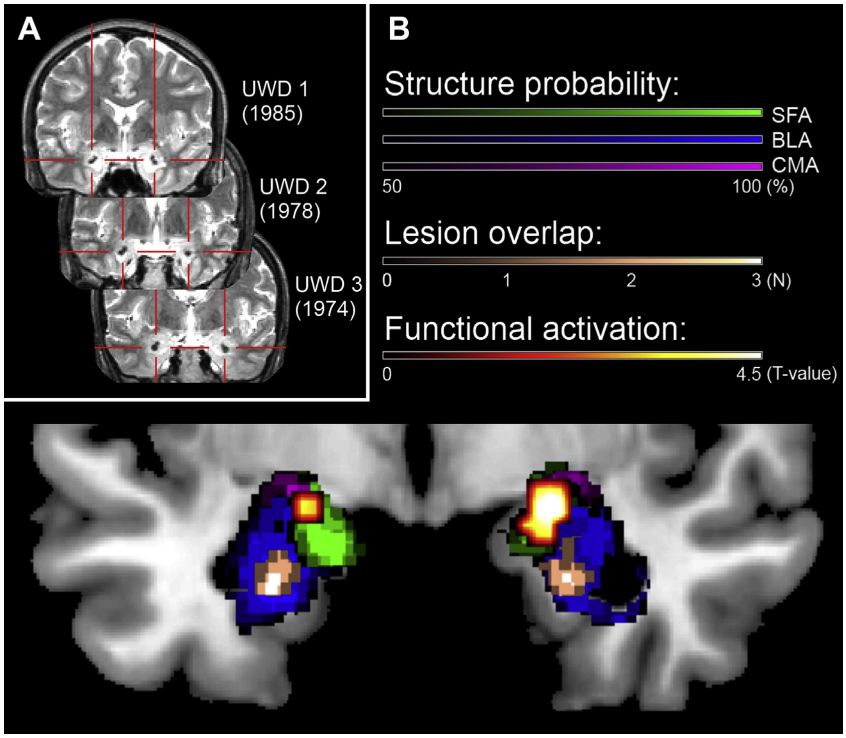

Fig. 1 – adapted with permission from (Morgan et al., 2012). A. T2-weighted MR-images (coronal view) of the three subjects with Urbach–Wiethe disease (UWD), their year of birth and red crosshairs indicating the calcified brain damage. B. Structural and functional assessment of the bilateral amygdala in our group of three UWD subjects. Plotted are the cytoarchitectonic probability-maps of the AMG sub-regions (Amunts et al., 2005), structural lesion overlap, and functional activation during an emotion-matching task (Hariri et al., 2002), all normalized to the Montreal Neurological Institute template brain. The structural method indicates that the lesions of the three subjects are located in the basolateral amygdala (BLA), while the functional method shows activation during emotion matching in the superficial amygdala (SFA) as well as the central-medial amygdala (CMA).

emotional expression. Stimuli were presented on screen until response while reaction time and accuracy were recorded.

2.2.3. *Three-alternative forced choice task*

In a three-alternative forced choice task (3AFC) participants indicated if the expressed emotion of the presented body was angry, happy or fearful. Stimuli were on screen for either 350 msec for behavioral testing or 2000 msec for eye tracking. Stimuli (12 per condition, 6 female) were from the same stimulus database as used in the sample-to-match task, but with different actors. Accuracy was measured for both durations, while reaction time was recorded for the 350 msec task.

2.2.4. *Flanker task*

A modified Erikson flanker task was used to test for interference of non social-emotional information. The task was similar to the one described by Cavanagh and Allen (2008), and involved 300 trials requiring the participants to identify a middle target letter flanked by 4 distractors. Half of the targets were flanked by the same letters (e.g., XXXXX, congruent trial), and half were flanked by a different letter (e.g., XXYXX, incongruent trial). A trial consisted of a blank screen (100 msec), a fixation screen (700 msec), a flanker screen (e.g., XX XX, 135 msec), a target screen (e.g., XXYXX, 265 msec), and a fixation cross screen (600 msec). Participants had to indicate as fast as possible what the middle target letter was by pressing the correct button (2AFC, left-hand or right-hand button). Participants received feedback only after incorrect trials in which the word 'VERKEERD' (Afrikaans for 'wrong') was presented. When participants did not respond within 1000 msec after flanker screen presentation feedback was given by presenting the word 'TE STADIG' (Afrikaans for 'too slow'). The flanker screen preceded the target screen to increase task difficulty (Cavanagh & Allen, 2008). The task was divided in 10 blocks of 30 trials. Within each block 2 target/distractor letters were used, and each target letter was assigned to either the left or right-hand button counterbalanced across blocks (i.e., MN, NM, FE, EF, QO, OQ, VU, UV, TI, IT). Participants first practiced the task using the letter combinations XY and YX, and preceding each block the new target/button combinations were explained. The blocks only commenced after the participants correctly identified the target/button combinations. Accuracy and reaction times were recorded for all trials.

2.3. *Procedure*

Session-1 started with the 3AFC task followed by the FBC task. For both tasks the eye tracking session was presented first to ensure eye-movements were not biased by previous exposure

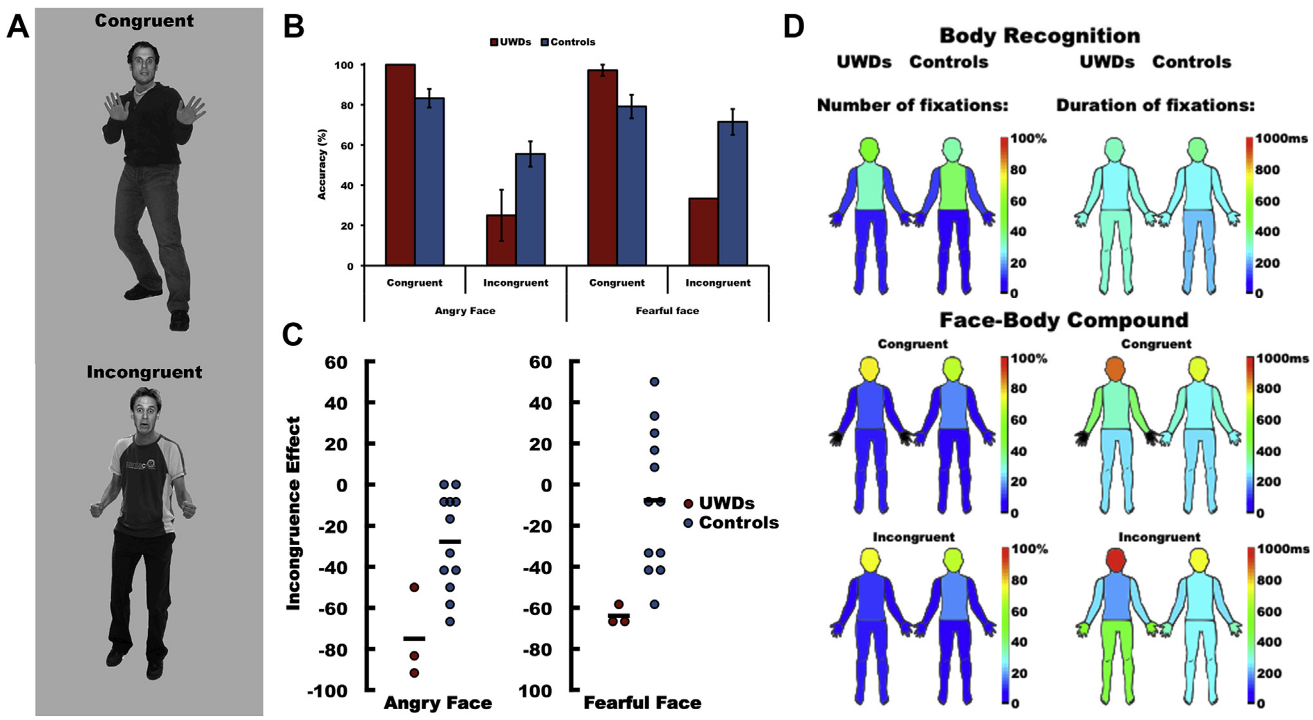

Fig. 2 – A. Examples of a congruent and incongruent Face Body Compounds. B. The UWD group performs worse compared with controls for both fearful and angry facial expressions when paired with an angry or fearful bodily expression respectively, whereas they have similar recognition ability of congruent Face Body Compounds. C. The incongruence effect for both fearful and angry facial expression was larger in the UWD group compared with controls. D. No difference in number and duration of fixations were found between UWD subjects and controls for both the body recognition conditions as well as the congruent and incongruent Face Body Compounds.

to the stimuli. The sample-to-match task was done in session-2. Instructions were presented in Afrikaans. The flanker task was conducted two years earlier than the other experiments, but the same three UWD subjects participated together with ten age (29.9 years old, $SD = 5.8$) and IQ (VIQ: 85.9, $SD = 4.7$; PIQ: 84.8, $SD = 8.0$, FSIQ: 83.7, $SD = 6.1$) matched controls living in the same area as the UWD subjects.

2.4. *Data analysis*

Reaction times <150 msec and >2 SD of the subject's mean were removed from the analysis. Incongruence scores were calculated by subtracting recognition accuracy for congruent from incongruent FBCs for each facial expression (FBC task) and by subtracting average accuracy and reaction time for congruent from incongruent trials (Flanker task). Group differences were tested cell-by-cell with two-tailed non-parametric Mann–Whitney *U* tests.

2.5. *Eye tracking*

The tasks were presented and eye-movements recorded with a Tobii-1750 eye tracker, sampling at 50 Hz, with .5° accuracy. Trials only commenced when subjects fixated gaze somewhere in a rectangle with the exact size and position of the stimuli, which ensures valid eye tracking data without biasing fixation positions. Gaze-fixations were defined as the average location of all subsequent gaze points within 1° visual angle, with a minimal duration of 100 msec (Tobii Technology, Danderyd, Sweden). Gaze-fixations were mapped onto a priori determined areas of interest (AOI); face, torso, arms, hands and legs. For each AOI mean fixation duration (FD) and proportion of number of fixations relative to all fixations (NF) was computed and used for further analysis.

3. Results

In line with previous results (Terburg et al., 2012), UWD participants performed as well as the controls in recognizing congruent fearful and angry Face Body Compounds ($U = 7$, $p = .14$ and $U = 6$, $p = .13$, respectively). However, recognition of fearful ($U = 1.5$, $p = .02$, $r = -.62$) and angry faces ($U = 5$, $p = .06$, $r = -.49$) was impaired when a face was combined with an incongruent bodily expression (see Fig. 2B). This incongruence effect was significantly larger in the UWD group compared to the control group for fearful as well as for angry faces, $U = .5$, $p = .007$, $r = -.66$ and $U = 2.5$, $p = .02$, $r = -.58$ respectively (see Fig. 2C). No differences in reaction times were found between the UWD and control group (p's $< .37$).

Importantly, the groups were not different in gaze behavior. Consistent with the task instructions, both the UWD and control group predominantly looked at the faces (76%

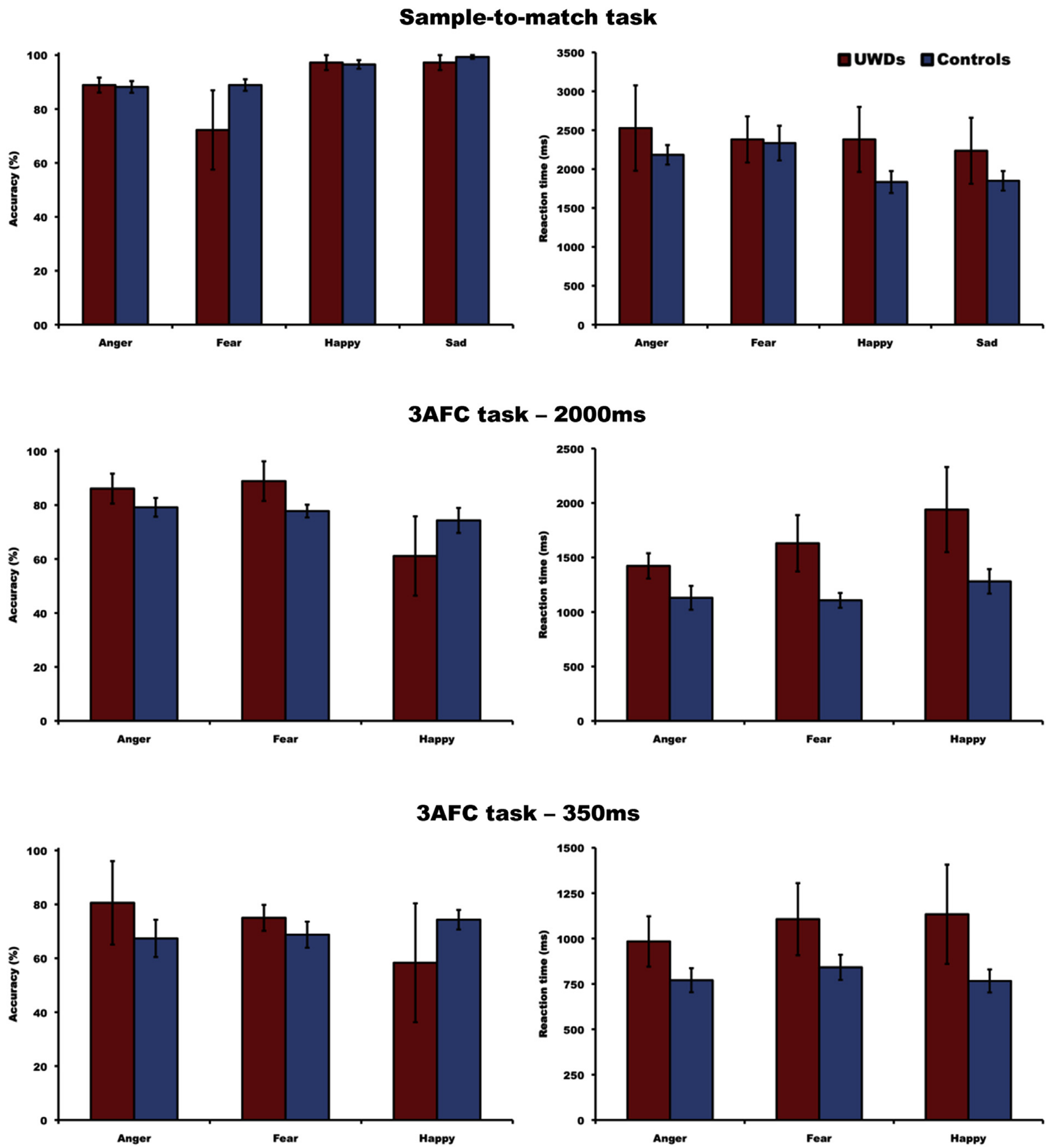

Fig. 3 – Recognition accuracy and reaction times for the sample-to-match task (top), the 3AFC task with 2000 msec (middle) and 350 msec stimulus duration (bottom). No differences were found between the UWD and control group.

vs 65%) (see Fig. 2D), which rules out a possible attention deficit underlying the current finding.

As revealed by the control experiments, recognition of bodily expressions, including fear, was intact in the UWD group. No differences in accuracy and reaction time were found in recognizing whole body expressions in either a sample-to-match (p's > .14) or the 3AFC task (long stimulus duration; p's > .18, short stimulus duration; p's > .18, see Fig. 3). Eye tracking data also showed no abnormalities in terms of gaze duration or fixation patterns. No group differences were found on the eye-track measures NF or FD in the 3AFC or in the congruent and incongruent conditions of the FBC task (all p's > .1, see also Fig. 2D). Crucially, visual attention in the FBC task was predominantly directed to the face compared to the other AOI's on both measures (all p's < .05), and compared to the 3AFC task, visual attention in the FBC task was longer and more often directed to the face part of the stimuli (all p's < .001). These results confirm that the subjects' visual attention was increasingly directed to the faces when they were asked to judge the facial emotion, and that this was not different for UWD subjects and the controls. Furthermore, no significant correlation between recognition accuracy on congruent and incongruent FBC trials were found for both fearful (r_{rho} (15) = −.36, p = .19) and angry faces (r_{rho} (15) = −.12, p = .68), which confirms that task instructions to recognize the facial emotion were followed.

Average reaction times and error-rates in the flanker task are summarized in Table 2. As expected the error-rate was significantly (Z = −2.8, p = .005) higher, and reaction time significantly (Z = −3.1, p = .002) slower, in the incongruent compared to congruent trials. The congruency effect on error-rate was not significantly (U = 11, p = .57) different between groups, which was also the case when error-rates were tested separately for congruent (U = 12, p = .69) and incongruent (U = 12, p = .69) conditions. The congruency effect on reaction time was also not significantly (U = 6, p = .16) different between groups, which was also the case when tested separately for congruent (U = 15, p = 1) and incongruent (U = 10, p = .47) conditions. In sum, the flankers successfully evoked interference, but this was not different between the UWD and control groups.

4. Discussion

Our main result shows a strong and selective effect of unattended body signals on facial expression recognition in UWD subjects. This means that BLA damage leads to a stronger interference in a simple facial expression recognition task when the target face is paired with a bodily expression shown in the periphery that is not attended to. In other words, ignoring the role of the task-irrelevant stimulus part appears harder for UWD subjects and their impaired facial expression judgments reflect this. Importantly, this effect was obtained in the UWD group while their gaze behavior was not different from that of the controls. The results from the flanker task show that this effect is specific for affective stimuli and thereby underscore that the AMG is at the core of this process. Future research needs to clarify whether these data reflect heightened threat value of bodily expressions, heightened sensitivity to ambiguous affective signals or a combination of both.

Previous studies of a UWD subject have reported that AMG impairment has only implications for facial (Adolphs et al., 1994, but see Tsuchiya et al., 2009) and not for bodily expressions (Atkinson et al., 2007). The strong effect of bodily expressions on facial expression recognition seen here indicates that as in the case of faces, the AMG is important for processing affective expressions of bodies and this is consistent with similar AMG activation to facial and bodily expressions in normal subjects (de Gelder et al., 2004; de Gelder, Hortensius, & Tamietto, 2012). Fearful bodily expressions are known to trigger automatic action preparation (de Gelder et al., 2004) and the AMG is known to play a role in triggering adaptive emotional reactions (Pessoa, 2010). Rather than illustrating that the AMG is not needed for body expression processing, the present findings are compatible with a role of the BLA in generating hypervigilance for threat signals as previously argued for fearful facial expressions (Terburg et al., 2012). Conversely, our results show that the ambiguity of the emotional signal created by incongruent Face Body Compounds is fully noticed by the UWD subjects. The effects of this stimulus ambiguity and thus of the threatening body expressions are much stronger in the UWD subjects than in the controls. This excessive effect of ambiguity is also consistent with earlier studies on the role of the AMG in ambiguous decision-making (Brand, Grabenhorst, Starcke, Vandekerckhove, & Markowitsch, 2007), ambiguous affect perception (Kim et al., 2004; Whalen, 1998) and conflict resolution (Etkin, Egner, Peraza, Kandel, & Hirsch, 2006; Etkin et al., 2004).

There are thus two possible explanations for the finding of more ambiguity sensitivity in the UWD group. The body expressions have a stronger impact because in the absence of the BLA, they are experienced as more salient. This may be for example because the central-medial amygdala (CMA) is not controlled by the BLA and affective signals are over-represented, similar to the explanation of hypervigilance in Terburg et al. (2012). Furthermore, it may be that without BLA there is a heightened sensitivity to the ambiguous meaning of the compound stimuli. The latter presupposes that at the level of perception of the face and of the body expressions there is no difference between the UWD subjects and controls but that the difference is generated once the face and the body percept are combined in later integration processing stages. One may then argue that the BLA deficit creates this heightened sensitivity to ambiguity.

While there were no significant differences in terms of gaze duration or fixation, indicating that both the UWD and control group followed task instructions and looked at the faces, we cannot discard the possibility that there might be small differences in gaze behavior (e.g., scan-paths) between groups that would underlie the found effect. Thus, the UWD group could still pay more attention to the irrelevant bodies. However, while not significant the number of fixations on the face was higher in the UWD group compared with the control group. This is in line with the notion that the distracting threatening body has a stronger impact or heightened sensitivity to the ambiguous threat signal due to BLA deficits.

The present report represents therefore significant theoretical and methodological advances. Methodologically, the present cases are unique in the AMG literature because they have focal damage involving only the basolateral nucleus. Our study combines behavioral methods with spontaneous eye movement recordings. Finally, we use facial expressions but also whole body expressions and face and body combinations that make for highly ambiguous signals and we use implicit perception measures.

Table 2 – Average reaction times and error-rates (with their range) in the flanker task.

	UWD	Control
Average reaction time (ms)		
Congruent trials	430 (387–493)	421 (366–532)
Incongruent trials	443 (401–523)	455 (405–562)
Average error-rate (%)		
Congruent trials	15 (4–25)	11 (8–19)
Incongruent trials	18 (9–25)	17 (8–24)

To conclude, we show that the BLA is important for processing ambiguous social information. In addition to focusing on specific emotions (e.g., fear) or specific categories (e.g., facial expressions) or specific attributes of emotional stimuli (e.g., salience), AMG research would benefit from concentrating on the interplay between the affective context, the different AMG subnuclei, and their connectivity.

Role of funding source

B.d.G. and R.H. were partly funded by the project TANGO. The project TANGO acknowledges the financial support of the Future and Emerging Technologies (FET) programme within the Seventh Framework Programme for Research of the European Commission, under FET-Open grant number: 249858. B.d.G. has also received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013)/ERC grant agreement number 295673. The work in this paper was supported by grants from the Hope For Depression Research Foundation (HDRF: RGA #9-015), the Netherlands Society of Scientific Research (Brain and Cognition: #056 24-010), the South African MRC/DST Professional Development Program, and the University of Cape Town (Brain Behavior Initiative). Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at tott0006@tc.umn.edu for more information concerning the stimulus set.

Conflict of interest

None.

REFERENCES

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*, 669–672.

Amunts, K., Kedo, O., Kindler, M., Pieperhoff, P., Mohlberg, H., Shah, N. J., et al. (2005). Cytoarchitectonic mapping of the human amygdala, hippocampal region and entorhinal cortex: intersubject variability and probability maps. *Anatomy and Embryology, 210*, 343–352.

Atkinson, A. P., Heberlein, A. S., & Adolphs, R. (2007). Spared ability to recognise fear from static and moving whole-body cues following bilateral amygdala damage. *Neuropsychologia, 45*, 2772–2782.

Brand, M., Grabenhorst, F., Starcke, K., Vandekerckhove, M. M. P., & Markowitsch, H. J. (2007). Role of the amygdala in decisions under ambiguity and decisions under risk: evidence from patients with Urbach–Wiethe disease. *Neuropsychologia, 45*, 1305–1317.

Cavanagh, J. F., & Allen, J. J. (2008). Multiple aspects of the stress response under social evaluative threat: an electrophysiological investigation. *Psychoneuroendocrinology, 33*, 41–53.

Costafreda, S. G., Brammer, M. J., David, A. S., & Fu, C. H. (2008). Predictors of amygdala activation during the processing of emotional stimuli: a meta-analysis of 385 PET and fMRI studies. *Brain Research Reviews, 58*, 57–70.

Etkin, A., Egner, T., Peraza, D. M., Kandel, E. R., & Hirsch, J. (2006). Resolving emotional conflict: a role for the rostral anterior cingulate cortex in modulating activity in the amygdala. *Neuron, 51*, 871–882.

Etkin, A., Klemenhagen, K. C., Dudman, J. T., Rogan, M. T., Hen, R., Kandel, E. R., et al. (2004). Individual differences in trait anxiety predict the response of the basolateral amygdala to unconsciously processed fearful faces. *Neuron, 44*, 1043–1055.

de Gelder, B., Hortensius, R., & Tamietto, M. (2012). Attention and awareness each influence amygdala activity for dynamic bodily expressions—a short review. *Frontiers in Integrative Neuroscience, 6*, 54. http://dx.doi.org/10.3389/fnint.2012.00054.

de Gelder, B., Snyder, J., Greve, D., Gerard, G., & Hadjikhani, N. (2004). Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proceedings of the National Academy of Sciences, USA, 101*, 16701–16706.

de Gelder, B., & Van den Stock, J. (2011). The Bodily Expressive Action Stimulus Test (BEAST). Construction and validation of a stimulus basis for measuring perception of whole body expression of emotions. *Frontiers in Psychology, 2*, 181.

Hariri, A. R., Mattay, V. S., Tessitore, A., Kolachana, B., Fera, F., Goldman, D., et al. (2002). Serotonin transporter genetic variation and the response of the human amygdala. *Science, 297*, 400–403.

Kim, H., Somerville, L. H., Johnstone, T., Polis, S., Alexander, A. L., Shin, L. M., et al. (2004). Contextual modulation of amygdala responsivity to surprised faces. *Journal of Cognitive Neuroscience, 16*, 1730–1745.

Meeren, H. K., van Heijnsbergen, C. C., & de Gelder, B. (2005). Rapid perceptual integration of facial expression and emotional body language. *Proceedings of the National Academy of Sciences, USA, 102*, 16518–16523.

Morgan, B., Terburg, D., Thornton, H. B., Stein, D. J., & van Honk, J. (2012). Paradoxical facilitation of working memory after basolateral amygdala damage. *PLoS ONE, 7*(6), e38116. http://dx.doi.org/10.1371/journal.pone.0038116.

Mosher, C. P., Zimmerman, P. E., & Gothard, K. M. (2010). Response characteristics of basolateral and centromedial neurons in the primate amygdala. *Journal of Neuroscience, 30*, 16197–16207.

Pessoa, L. (2010). Emotion and cognition and the amygdala: from "What is it?" to "What's to be done?". *Neuropsychologia, 48*, 3416–3429.

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: from animal models to human behavior. *Neuron, 48*, 175–187.

Rutishauser, U., Tudusciuc, O., Neumann, D., Mamelak, A. N., Heller, A. C., Ross, I. B., et al. (2011). Single-unit responses selective for whole faces in the human amygdala. *Current Biology, 21*, 1654–1660.

Terburg, D., Morgan, B. E., Montoya, E. R., Hooge, I. T., Thornton, H. B., Hariri, A. R., et al. (2012). Hyper-vigilance for fear after basolateral amygdala damage in humans. *Translational Psychiatry, 2*, e115.

Thornton, H. B., Nel, D., Thornton, D., van Honk, J., Baker, G. A., & Stein, D. J. (2008). The neuropsychiatry and neuropsychology of lipoid proteinosis. *Journal of Neuropsychiatry and Clinical Neuroscience, 20*, 86–92.

Tsuchiya, N., Moradi, F., Felsen, C., Yamazaki, M., & Adolphs, R. (2009). Intact rapid detection of fearful faces in the absence of the amygdala. *Nature Neuroscience, 12*, 1224–1225.

Whalen, P. J. (1998). Fear, vigilance, and ambiguity: initial neuroimaging studies of the human amygdala. *Current Directions in Psychological Science, 7*, 177–188.