Neural Correlates of Error Awareness

Tilmann A. Klein[1], Tanja Endrass[2], Norbert Kathmann[2], Jane Neumann[1], D. Yves von Cramon[1] & Markus Ullsperger[1],
[1]Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany;
[2] Humboldt -University, Berlin, Germany
email: tklein@cbs.mpg.de

MAX PLANCK INSTITUTE FOR HUMAN COGNITIVE AND BRAIN SCIENCES LEIPZIG

Introduction

- Role of conscious error perception for action outcome optimization
- Event related potentials (ERP; Nieuwenhuis et al., 2001, Endrass et al., 2005): modulation of the error positivity (Pe) by error awareness – a normal Pe was found in case of an aware error, a diminished Pe was observed in case of an unaware error; the error related negativity (ERN) was present on aware and unaware errors
- Behavioural: post-error slowing (PES) only after an aware error
- Rostral cingulate zone (RCZ; most probable generator of the ERN) active on error processing (Debener et al., 2005)

Research questions:

1. Are there sizeable differences in RCZ activity or in the activity of other error processing related brain areas due to error awareness?
2. What are the behavioural correlates of error awareness?

Methods

1

a) Participants and Task

- Thirteen healthy right handed subjects (8 female, mean age = 26,15 years)
- Antisaccade task (Nieuwenhuis et al., 2001; 476 Trials; see Figure 1)
- Brief precue (to increase error rate) was presented at the position where the gaze should be directed to (to reduce predictability in 33% of the trials the precue was presented at the position of the following peripheral stimulus)

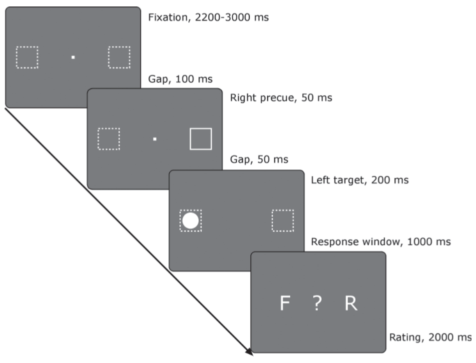

Figure 1. Schematic of the antisaccade task. Average trial duration: 6 s.

b) Data acquisition and Eyetracker

- Data was acquired with a standard fMRI protocol at 3 T
- Data Processing: LIPSIA (Lohmann et al., 2001)
- $z = 2.33$; $\alpha = 0.01$; volume > 81mm³ (Monte Carlo Simulation: 0.05 corrected)
- View Point Eye tracker (infrared light based; Arrington Research)
- Temporal resolution: 60 Hz; spatial resolution: app. 0.15° visual arc

2

c) Region of Interest (ROI)

- Extended metaanalysis of 55 studies on error processing, response conflict, decision uncertainty and negative feedback (based on Ridderinkhof et al., 2004)
- Analysis was based on Activation Likelihood Estimation (ALE; Turkeltaub et al., 2002; see Figure 2 for results)

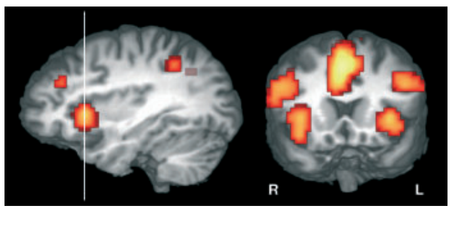

Figure 2. Results of the metaanalysis projected onto a sagittal (x = -32) and a coronal slice (y = 15).

Results

a) Behavioural

- Errors faster than correct responses (see Figure 3 to 6 for details)
- Considerable variance in PES across subjects; PES in 9 out of 13 subjects
- Lower error rate after an aware error
- False alarm rate: 3%; rate of not classifiable trials due to technical problems: 6.1%

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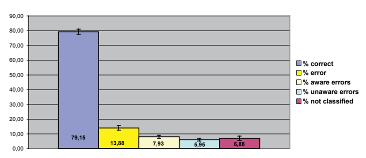

Figure 3. Accuracy in trial N

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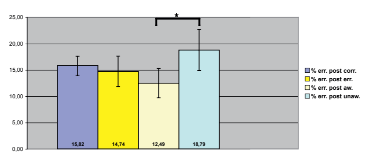

Figure 4. Post error accuracy

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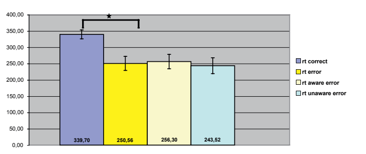

Figure 5. Reaction times in trial N

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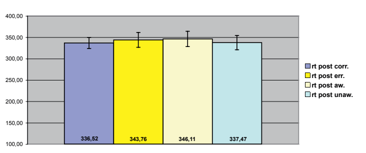

Figure 6. Post error reaction times

Results

b) FMRI

- Error > Correct: Pre-SMA, RCZ and Insula (see Table 1 & Figure 7)
- Aware > Unaware: Left insula (see Table 1 & Figure 7)
- Timecourses: Greater activity in the insular cortex for aware errors, no such difference can be found in RCZ (see Figure 7)
- Parametric second-level analysis with post-error reaction time as a regressor: the more a person slowed down after an aware error, the more activity can be found in the pre-SMA (x = 1, y = 6, z = 48; see Figure 8)

Table 1

Table 1. Brain regions, Brodmann areas, and Talairach coordinates (x, y, z) of voxels co-varying significantly with error processing and error awareness.

Brain region	Brodmann area	z-value	mm≥	Talairach coordinates x	y	z
error processing (incorrect vs. correct response)						
Pre-SMA	8	2.92	756	1	18	51
RCZ	32	3.00	540	-2	30	27
pFMC	8/9	2.93	189	4	30	42
R Insula	13	2.91	108	37	21	-6
L Insula	13	3.64	621	-41	12	0
conscious error awareness (aware vs. unaware errors)						
L Insula	13	3.01	324	-38	11	0

Note: Pre-SMA = pre-supplementary motor area, pFMC = posterior frontomedian cortex, RCZ = rostral cingulate zone, R/L = right/left.

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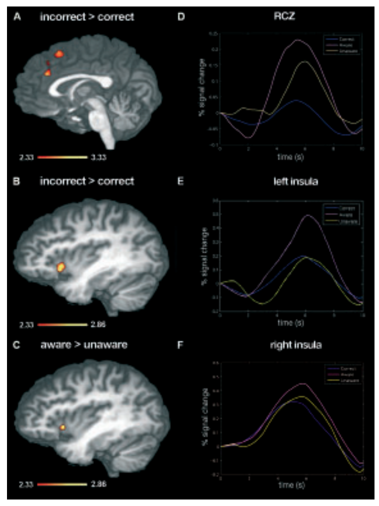

Figure 7. fMRI results. A and B: general error-related brain activity revealed by the contrast error vs. correct response (sagittal slices at x = -2 and -41, respectively). C: activations related to conscious error perception revealed by the contrast aware vs. unaware error (sagittal slice at x = -38). D, E and F: averaged time series of the BOLD response for aware and unaware errors in the RCZ (D; x = -2, y = 30, z = 27), the left anterior insula (E; x = -38, y = 11, z = 0), and in the right anterior insula (F; x = 31, y = 15, z = 0).

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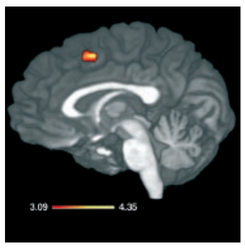

Figure 8. Results of the parametric second-level analysis of brain activity related to aware errors using post-error slowing as a regressor, revealing a significant correlation in the pre-SMA (x = 1, y = 6, z = 48).

Discussion

RCZ

- Active on both error types (aware & unaware) - in line with previous findings, showing no modulation of the ERN by error awareness
- Differences in Pe not generated in RCZ
- Error related RCZ activity is not sufficient for conscious error awareness
- Errors may be detected by RCZ without being consciously perceived

Insular Cortex

- Interoceptive awareness (Critchley et al., 2004) and regulation of autonomic responses
- Enhanced awareness of the autonomic reaction to an error or higher autonomic response itself (direction of relationship cannot be revealed by this study)
- Feeling of having committed an error via visceral reactions to the erroneous event
- Insula by itself unlikely to generate directly the Pe; but maybe via interactions with other cortical areas involved in generating the Pe

Positive correlation between pre-SMA and post-error slowing after an aware error

- Posterior medial frontal cortex (pMFC) involved in signalling the need for performance adjustments
- Post-error slowing more likely when errors are consciously perceived
- Increased RCZ activity alone is insufficient to initiate post-error speed-accuracy adjustments (only on aware errors while RCZ activity is the same for aware and unaware errors)
- Additional processes must co-occur with RCZ activity to enable performance adjustments in N+1

Conclusion

- RCZ and the anterior, inferior insular cortex around the polus insulae seem both important constituents of the performance monitoring system
- RCZ/pFMC activity seems to signal the need for post-error adjustments, it can fulfil this function only when additional conditions – most likely a sufficiently strong general error signal in the cognitive system – are met
- Activity in the anterior inferior insular cortex covaries with error awareness and seems to reflect the awareness of the autonomic response to the error and/or the implementation of this autonomic response itself

LITERATURE:

- Critchley, H. D., Wiens, S., Rotshtein, P., Öhman, A. & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. Nature Neuroscience, 7, 189-195.
- Debener S., Ullsperger M., Siegel M., Fiehler K., von Cramon D.Y. & Engel, A.K. (2005). Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. Journal of Neuroscience, 25, 11730-11737.
- Endrass, T., Franke, C. & Kathmann, N. (2005). Error Awareness in a Saccade Countermanding Task. Journal of Psychophysiology, 19, 275–280.
- Friston, K., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D. & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. Human Brain Mapping, 2, 189–210.
- Lohmann, G., Müller, K., Bosch, V., Mentzel, H., Hessler, S., Chen, L., & von Cramon, D. Y. (2001). Lipsia—A new software system for the evaluation of functional magnetic resonance images of the human brain. Computerized medical imaging and graphics : the official journal of the Computerized Medical Imaging Society, 25, 449-457.
- Nieuwenhuis, S., Ridderinkhof, K. R., Blom, J., Band, G. & Kok, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: Evidence from an antisaccade task. Psychophysiology, 38, 752–760.
- Ridderinkhof, K. R., Ullsperger, M., Crone, E. A. & Nieuwenhuis, S. (2004). The Role of the Medial Frontal Cortex in Cognitive Control. Science, 306, 443 – 447.
- Turkeltaub, P. E., Eden, G. F., Jones, K. M. & Zeffiro, T. A. (2002). Meta-Analysis of the Functional Neuroanatomy of Single-Word Reading: Method and Validation. NeuroImage, 16, 765–780.
- Worsley, K. & Friston, K. (1995). Analysis of fMRI time-series revisited - Again. NeuroImage, 2, 359–365.

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