A Neural Basis for Identifying Social Contract Violators in Humans

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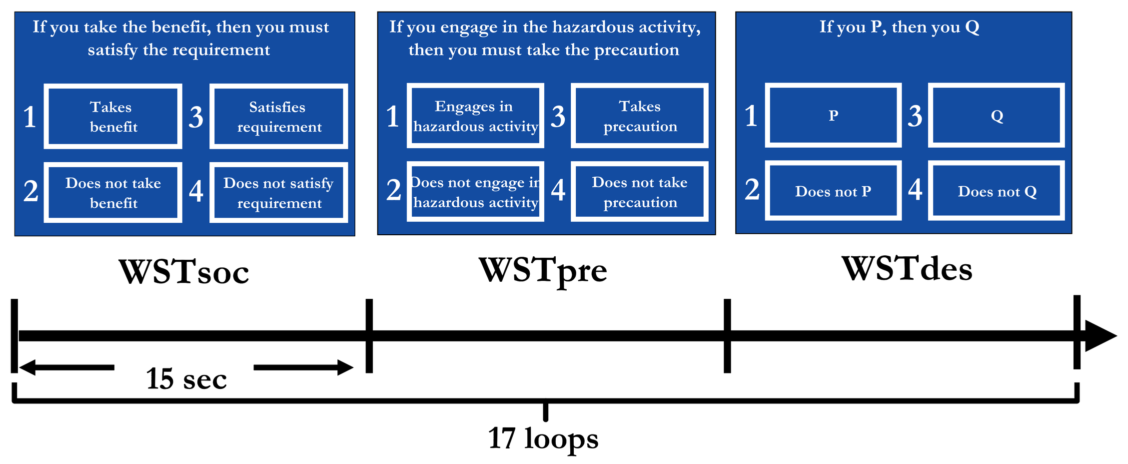
INTRODUCTION

Evolutionary models suggest that developing and maintaining succesfull social exchange within a species requires that individuals are able to successfully identify social non-reciprocators. This has led researchers to hypothesize that an extensively social species such as humans have evolved specialized cognitive mechanisms for identifying social contract violators [1]. A recent lesion-study found neurological support for this hypothesis, indicating that the identification of social contract violators could be selectively impaired compared to the identification of non-social rule (precaution rule) violators in a patient suffering from bilateral damage to the anterior PFC (BA 10/11) and temporal poles (BA 38) extending to more posterior temporal areas in the left hemisphere (BA 20/21/22/27) [2]. Correspondingly, the aim of the present study was to test the hypothesis that some or all of these brain areas are activated in healthy controls during the detection of social contract violators compared to precaution rule violators using a simliar experimental design.

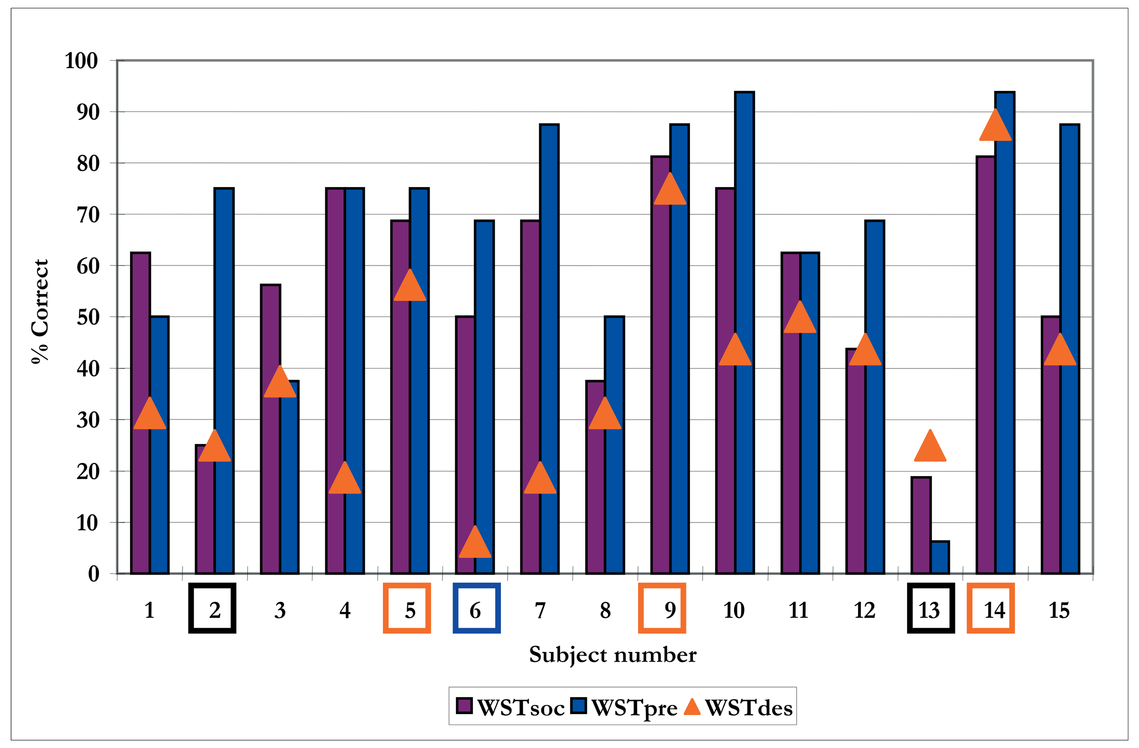
EXPERIMENTAL DESIGN

The social contracts (WSTsoc), the precaution rules (WSTpre) and the descriptional rules (WSTdes) used in this study are logically identical variants of the classic Wason Selection Task (WST) [3]. We compared activity during WSTsoc and WSTpre which were contructed to be equally familiar and difficult. The more difficult WSTdes were included to indicate reasoning strategy. High performance indicate a deductive (“non-intuitive”) strategy and therefore exclusion.

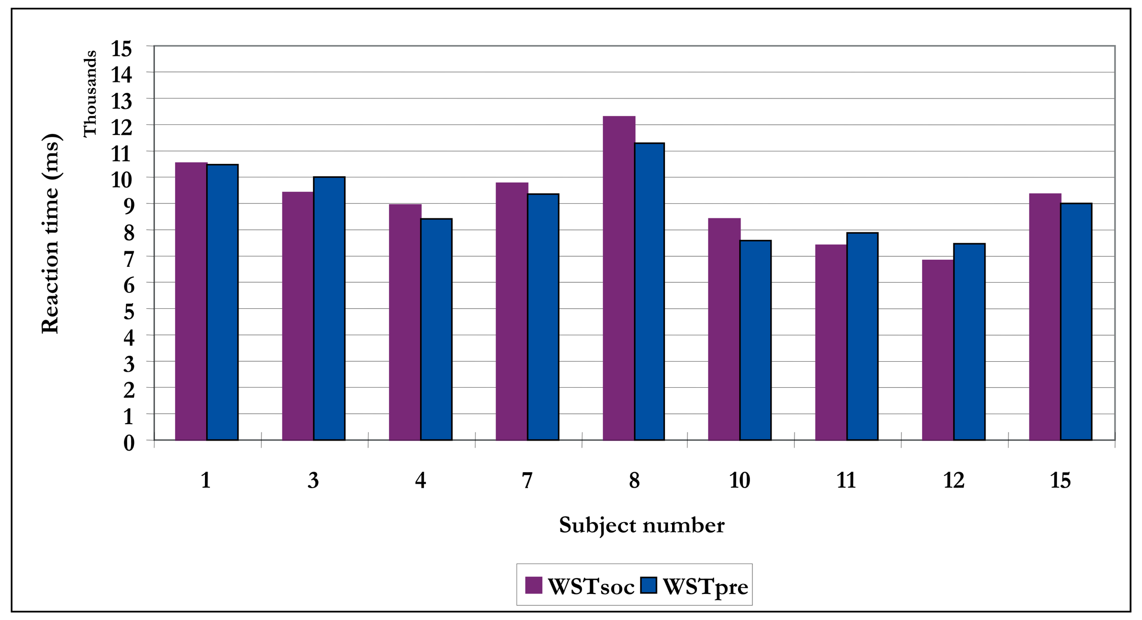


Experimental design. WSTsoc, WSTpre, and WSTdes were presented sequentially in 15 second blocks. The first loop was excluded from further analysis.

BEHAVIORAL RESULTS



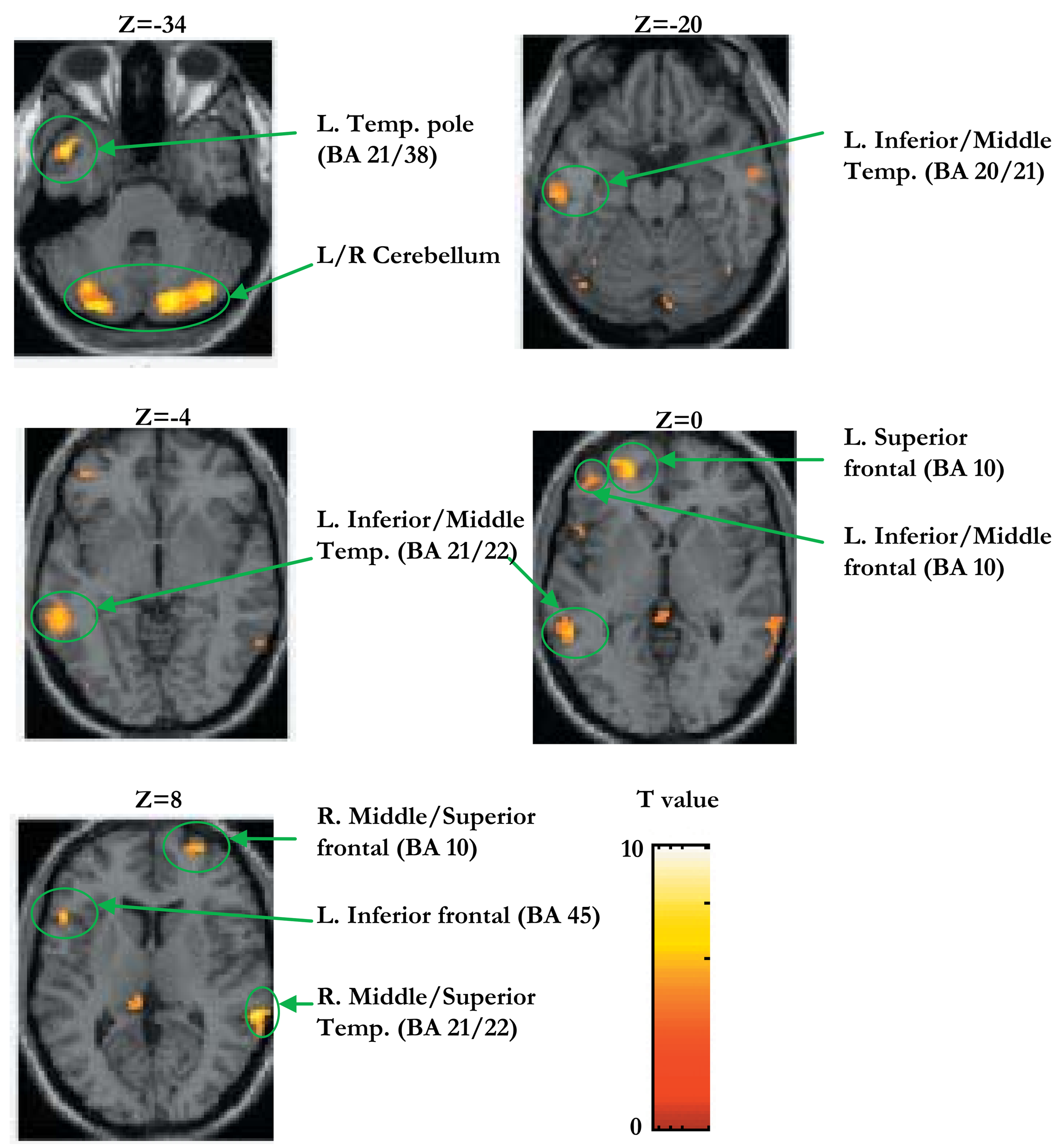
Mean accuracy in reasoning about WSTsoc, WSTpre and WSTdes of all subjects (n=15). Black rectangles specify subjects excluded due to very low performance (below 35% accuracy on WSTsoc and/or WSTpre), and orange rectangles specify subjects excluded due to a deductive strategy (above 50% accuracy on WSTdes), and blue rectangle specify a subject excluded due to technical difficulties. No rectangle represents subjects assigned to the normal group.



Mean reaction times on correct responses to WSTsoc and WSTpre within subjects assigned to the normal group (n=9). No significant difference in reaction time was observed.

No significant differences on reaction times between WSTsoc and WSTpre were observed within subjects, or across subjects, indicating similar familiarity and difficulty. During post scan interviews none of the subjects reported perceiving any systematic difference in the presented WSTs, indicating that the systematic difference in content between WSTsoc and WSTpre was cognitively impenetrable. Only time-series until the second correct response on WSTsoc and WSTpre, were included in the imaging analysis.

IMAGING RESULTS
[WSTsoc > WSTpre]



In agreement with our hypothesis, we observed higher activity in bilateral anterior prefrontal cortex, left temporal pole, and more posterior left temporal areas during the detection of social contract violators relative to precaution rule violators [WSTsoc > WSTpre]. Exploratively, we observed higher activation in left posterior temporal area, left lateral prefrontal areas, right posterior temporal areas, and cerebellum bilaterally. No increased activation was observed during the detection of precaution rule violators compared to social contract violators [WSTpre > WSTsoc].

CONCLUSION

Our findings indicate that the detection of social contract violators activates a network of areas implicated in social reasoning. Thus, temporal areas included in this network were activated in ToM tasks [4], while anterior PFC were activated in altruistic punishment [5], and in the observation of intentional social norm violations [6].

DETAILED IMAGING RESULTS
[WSTsoc > WSTpre]

STATISTICS: p-values adjusted for search volume. p(FDR)<=0.01; Extent threshold=10 voxels.

Extent	p(FDR)	T	Z	x,y,z {mm}	L/R	Anatomical area(s)	Brodmann Area(s)
1193	0.001	10.14	5.59	34 -74 -44	R	Cerebellum	--
209	0.001	9.06	5.31	64 -38 8	R	Middle/Superior temporal	BA 21/22
125	0.001	8.94	5.28	-46 10 -36	L	Middle/Superior temporal	BA 21/38
840	0.001	7.98	5.00	-2 10 74	L	Interhemispheric	--
826	0.001	7.51	4.85	-32 -70 -32	L	Posterior/Occipital junction	--
169	0.001	6.72	4.57	-28 -74 -12	L	Lingual/Fusiform	BA 18/19
91	0.002	6.56	4.51	-20 52 0	L	Superior frontal	BA 10
275	0.002	6.39	4.44	-58 -40 -2	L	Inferior/Middle temporal	BA 21/22
102	0.002	6.32	4.41	-60 -18 -22	L	Inferior/Middle temporal	BA 20/21
146	0.002	6.07	4.31	26 60 6	R	Middle/Superior frontal	BA 10
82	0.002	6.06	4.31	-52 18 6	L	Inferior frontal	BA 45
25	0.002	6.03	4.30	-54 -36 -26	L	Fusiform/Inferior temporal	BA 20
271	0.002	6.02	4.29	-4 -52 20	L	Interhemispheric	--
66	0.003	5.65	4.13	-56 -62 20	L	Middle/Superior temporal	BA 22/39
50	0.003	5.62	4.12	56 -4 -24	R	Inferior/Middle temporal	BA 20/21
57	0.003	5.55	4.09	-46 28 -8	L	Inferior frontal	BA 47
65	0.003	5.51	4.07	-42 48 -2	L	Inferior/middle frontal	BA 10
81	0.004	5.27	3.96	-8 -34 6	L	Midbrain	--
31	0.005	5.06	3.86	6 -52 -46	R	Cerebellum	--
12	0.006	4.85	3.75	-44 -2 54	L	Middle frontal	BA 6
12	0.006	4.75	3.70	-62 -22 -10	L	Middle temporal	BA 21

Table shows 3 local maxima more than 8.0mm apart. Expected voxels per cluster, <k> = 11.180; Expected number of clusters, <c> = 1.78; Degrees of freedom = [1.0, 24.0]; Smoothness FWHM = 11.8 11.4 11.0 {mm} = 5.9 5.7 5.5 {voxels}; Search vol: 1305856 cmm; 163232 voxels; 811.1 resels; Voxel size: [2.0, 2.0, 2.0] mm (1 resel = 185.55 voxels).

METHODS

15 subjects (six female) with a mean age of 24.4 years (SD=3.7), ranging from 21 to 34 years, participated in the study. All subjects were healthy, had no history of psychiatric diseases, and were right-handed. Subjects were undergraduate students except for two subjects who graduated recently. Written informed consent was obtained. The study was approved by the Danish Ethical Committee ((KF) 01-131/03).

Behavioural acquisition and analysis

Prior to scanning, while in the scanner-room, each subject was presented with three printed WST examples. Two WSTsoc and one WSTpre were presented while guiding the subjects to choose the options that represented a potential cheater of the rule. The instructor made sure that all subjects selected the correct options on all three WST examples before the scanning session started. 17 WSTsoc, 17 WSTpre, and 17 WSTdes were presented in a WTsoc-WSTpre-WSTdes loop. Behavioral and imaging data acquired during the first three WST of the scanning session was excluded from analysis. Immediately after the scanning session, each subject underwent a short interview with open questions as to (1) their thoughts during the tasks, (2) how they selected among the options, and (3) if they perceived any systematic differences among the tasks. To assess reading abilities subjects performed the DART reading test (Dalsgaard 1998), a Danish version of the National Adult Reading Test (NART) (Nelson and O’Connell 1978, Nelson and Willison 1991) The behavioural paradigm was programmed in E-Prime 1.1 (Psychology Software Tools, USA) and was visible to the subject through a small mirror attached to the head coil that reflected the images from a back-projected screen placed at the end of the scanning tube. Behavioural data were collected using a five-button response box. Collection of behavioural data and time-synchronisation with the scanner were controlled by the IFIS SA system (MRI Device Corporation, USA).
Accuracy and reaction times on a total of 16 WSTsoc, 16 WSTpre and 16 WSTdes, were assessed independently. Reaction times were defined as second correct button press on correct performance on WSTs.

Imaging acquisition and analysis

Images were acquired on a Siemens 3T Trio Magnetom scanner at Copenhagen University Hospital Hvidovre, utilizing a Siemens iPAT (integrated Parralel Imaging Techniques) head-coil. Following acquisition of a scout and a T1-weighted anatomical scan (256 x 256 matrix, 1 mm. sagittal slices), subjects performed the behavioural task while functional images were acquired using an anterior PFC optimized axial T2*-weighted EPI sequence (TR=3000 ms, TE=30 ms, 64 x 64 matrix, field of view=192mm, voxel size=3x3x3mm, 40 slices positioned at approx. -35° relative to the AC/PC line and extra +1 mT z- gradient (adapted from Deichmann et al. 2003). All imaging data were pre-processed and analyzed using the SPM2 (Wellcome, London, UK) software package running in Matlab 6.5 (MathWorks Inc., Sherborn, MA, USA). Images were spatially normalized to the MNI template (Montréal Neurological Institute) using 12 parameter linear and non-linear transformation and smoothed with a 8 mm full width at half maximum Gaussian kernel. Images obtained during incorrect responses and after the second correct response was made on each task, were excluded from analysis. Images obtained during correct performance on WSTsoc, WSTpre, and WSTdes, respectively, were convolved with a hemodynamic response function and specified as regressors for each subject in a first level design matrix. In each block, time series obtained after the second correct response was excluded from analysis. Image analysis included a 128 second high-pass filter for time series and adjusted for temporal auto-correlations using AR(1)+w. A second level mixed-effects analysis was applied and the statistical map was thresholded at (p<=0.01, corrected for the False Discovery Rate). Coordinates are MNI coordinates (Montreal Neurological Institute).

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