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Superior temporal sulcus and social cognition in dangerous drivers

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ABSTRACT

Understanding the neural systems underpinning social cognition is a primary focus of contemporary social neuroscience. Using functional magnetic resonance imaging (fMRI), the present study asked if brain activity reflecting socio-cognitive processes differs between individuals according to their social behavior; namely, between a group of drivers with frequent traffic offenses and a group with none. Socio-cognitive processing was elicited by employing videos from a traffic awareness campaign, consisting of reckless and anti-social driving behavior ending in tragic consequences, and control videos with analogous driving themes but without such catastrophic endings. We investigated whether relative increases in brain function during the observation of these campaign stimuli compared with control videos differed between these two groups. To develop the results of our previous study we focused our analyses on superior temporal sulcus/gyrus (STS/STG). This revealed a bigger increase in brain activity within this region during the campaign stimuli in safe compared with dangerous drivers. Furthermore, by thematically coding drivers' verbal descriptions of the stimuli, we also demonstrate differences in STS reactivity according to drivers' scores on two indices of socio-cognitive processing: subjects' perceived consequences of actors' actions, and their affective evaluation of the clips. Our results demonstrate the influence of social behavior and socio-cognitive processing on STS reactivity to social stimuli, developing considerably our understanding of the role of this region in social cognition.

Introduction

Interacting successfully with others and generally conducting oneself appropriately within social contexts require a variety of cognitive capacities subsumed under social cognition. Such capacities include an understanding that others hold beliefs and desires independent of our own, the ability to infer others' mental states and emotional experiences (i.e. termed mentalizing and empathy, respectively), and an appreciation of the social consequences of our own and others' actions. Research within the social neuroscience domain has begun to elucidate the neural correlates of many of these cognitive faculties (for a review see Frith and Frith, 2010, 2012). One brain region implicated consistently in social cognition is the superior temporal sulcus (STS; e.g. Bzdok et al., 2012; Moor et al., 2012; Winston et al., 2002), within which brain activity appears to underlie the processing of social cues (e.g. Allison et al., 2000), mentalizing (e.g. Gallagher and Frith, 2003; Krämer et al., 2010; Peelen et al., 2010), and empathy (Müller et al., 2008; Pelphrey et al., 2005; Suda et al., 2011).

Importantly, neuroimaging studies have demonstrated individual differences in STS reactivity to social stimuli. Using blood oxygen level-dependent (BOLD) signal as an index of brain activity, Rauch et al. (2007) discuss a modulation of activity within, among other areas, STS in response to emotional facial expression stimuli according to individuals' coping styles. Likewise, Kaplan et al. (2007) report differential activation of a cortical network encompassing STS during the processing of faces belonging to presidential candidates according to the observers' political allegiance. In a similar vein, Goudriaan et al. (2010) report greater activation of a variety of cortical areas including STS in response to smoking-related images in heavy smokers relative to non-smoking controls. In a similar vein, greater activity within superior temporal gyrus (STG) has been observed in response to stimuli depicting risky or safe actions (Tamura et al., 2012). Such studies suggest that certain social behavioral tendencies – e.g. preferences, risk taking – influence directly STS activity reflecting socio-cognitive processes.

To achieve a comprehensive understanding of the neural mechanisms underlying social cognition, social neuroscience must also explore differences in the neural correlates of pro- and anti-social behavior. Indeed, a number of recent functional neuroimaging studies have focused specifically on antisocial behavior (for reviews see Loomans et al., 2010; Raine and Yang, 2006). This research reveals that antisocial behavior is associated with both atypical brain function and structure, particularly

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within the frontal and the temporal lobes (Blair, 2010; Buckholtz et al., 2008; Crowley et al., 2010; Weissman et al., 2008; Yang et al., 2008). This adds to other factors implicated in anti-social behavior, such as levels of hormones (e.g. cortisol [Freeman and Beer, 2010] and testosterone [Volman et al., 2011]), age (Ernst and Fudge, 2009), specific neurotransmitters and their receptors (e.g. Miczek et al., 2002), and a lack of empathy (Ellis, 1982). Additionally, substance abuse (e.g. alcohol, cannabis) and mental disorders are often involved (Kieling et al., 2011); the results of a recent study show that Attention Deficit Hyperactivity Disorder (ADHD) was associated with a higher number of traffic accidents, and antisocial personality disorder was associated with a greater number of traffic violations (Kieling et al., 2011).

Antisocial behavior often occurs in driving situations, presenting a potential danger to all drivers. For this reason, societies try to prevent antisocial driving behavior by means of public education campaigns. The main aim of these programs is to motivate drivers to avoid antisocial behavior that endangers themselves and others, often with the use of videos that aim to educate drivers on the potential consequences of reckless or irresponsible driving. These campaign videos provide important stimuli for social neuroscience research; by incorporating a wide variety of social cues (e.g. biological motion, social interactions, speech) and moral themes, these videos represent more accurately the complexity of real life social contexts. This allows research to move away from the study of single socio-cognitive functions by comparing two narrow categories of social stimuli (e.g. perception of faces vs. bodies). Importantly, Lahnakoski et al. (2012) demonstrated recently the role of STS during the processing of a wide variety of social cues, including biological motion, social interactions, and speech. As such, these campaign videos provide an opportunity to explore the involvement of STS in high-level socio-cognitive processes, and to investigate whether differences exist in STS reactivity to social stimuli between individuals differing in pro- or anti-social behavior.

In a previous functional magnetic resonance imaging (fMRI) study we employed videos from one such campaign to explore the neural correlates of social cognition. By contrasting campaign video clips, depicting anti-social driving behavior ending with tragic consequences, with control videos presenting less socially unacceptable driving behavior, we revealed greater STS activity in response to the campaign videos. Importantly, the region of STS exhibiting this preference for the campaign stimuli lay in close proximity to the foci reported by some of the aforementioned studies (Dziobek et al., 2011; Schultz et al., 2005). Moreover, this difference in STS reactivity was particularly pronounced in individuals demonstrating high empathic ability (Zelinková et al., submitted for publication). In the present study we set out to extend these initial findings by investigating whether or not greater STS activation during campaign videos differs between individuals according to their tendency for pro- or anti-social behavior. To do so, we use driving as an index of social behavior, assuming that more pro-social individuals will drive in a manner that is safe and consistent with road regulations, whereas anti-social individuals will drive more dangerously without consideration for others. Specifically, we compared STS reactivity to the complex social stimuli between our previous sample of safe, pro-social drivers and a group of drivers involved regularly in road traffic accidents or the violation of traffic regulations. Such an investigation should help us to understand whether or not STS is associated with an individuals' tendency for a specific form of antisocial behavior. This second aim was to investigate whether greater STS reactivity to the campaign compared with the control videos reflects the degree to which the observer engages in socio-cognitive processing. To this end, we divided our entire sample of drivers into two groups according to their verbal descriptions of the stimuli – under the assumption that subjects would discuss those aspects that are most important and salient to them – and compared relative increases in brain activity within STS between these groups.

We hypothesized that driving behavior would be related to the degree of STS reactivity to campaign videos – as indexed by BOLD signal – with safer, more pro-social drivers engaging this brain region more than dangerous, anti-social drivers. Furthermore, we predicted that relative increases in BOLD STS activity during the campaign relative to the control videos would be greater in individuals who engage in more socio-cognitive processing, such as empathizing and mentalizing.

Materials and methods

Subjects

Functional MRI data were acquired from two different groups of healthy right-handed male volunteer drivers. The first group consisted of 19 drivers who reported at least one incidence of traffic offense (e.g. driving under the influence of alcohol or drugs, high-speed driving) or involvement in road-traffic accident. The mean age of this dangerous driver (DD) group was 24.4 years ($SD = 3.3$ years; range = 19–30 years; median = 24 years). The second group included 25 control subjects with no recorded traffic offenses and who reported no traffic accidents, including but not exclusive to the sample of drivers comprising our previous study. The mean age of this safe driver (SD) group was 23.1 ($SD = 3.0$ years; range = 20–9 years; median = 22 years).

All participants had normal or corrected-to-normal vision. Czech or Slovak was the first language for all subjects. Written informed consent was obtained from each subject prior to the experiment, and the study received the approval of the St. Anne's Hospital Ethics Committee.

Task

During the scanning procedure, all subjects viewed a series of twelve 30-second video clips representing various types of driving situations. Six clips were taken from a national traffic awareness campaign (campaign videos [CV]), each involving a catastrophic and tragic ending by showing various potential consequences of traffic accidents (e.g. resuscitation, death). These video clips, broadcasted widely between 2008 and 2010, were prepared by a professional agency in cooperation with the Ministry of Transport. This Czech road safety campaign – "If you don't think, you will pay!" – was targeted especially at young drivers and the most common causes of traffic accidents, such as alcohol or drug influence, and aggressive or reckless driving. These CV stimuli were presented pseudo-randomly (see below) with 6 control videos (neutral videos [NV]). These NV stimuli, created in our lab by extracting sequences from typical car advertisements involving various traffic situations, followed analogous driving themes but consisted of less anti-social driving behavior and without dramatic endings. The NV stimuli contained no advertisement logos or slogans. All CV and NV clips contained sound, presented binaurally via MRI-compatible headphones. All clips contained an equivalent number of words and lasted identical durations.

No more than two instances of the same stimulus category (CV or NV) succeeded one another. A 26-second pause was inserted between the presented videos, in which a central yellow cross was presented against a black background. Visual stimuli were shown via a back-projection screen onto an overhead mirror. All stimuli subtended 16° visual angle. The subjects were instructed to remain still while in the scanner and to watch the presented video clips. Subjects were informed that some clips would have dramatic endings.

Data acquisition

Imaging was performed on a 1.5 T Siemens Symphony scanner equipped with Numaris 4 System (MRease). The functional scans were obtained using a gradient echo, echoplanar imaging sequence: TR = 3000 ms, TE = 40 ms, FOV = 220 mm, flip angle = 90°, matrix size 64 × 64, in-plane resolution = 3.44 mm × 3.44 mm, slice thickness = 3.5 mm, and 32 transverse slices per scan. Functional scans

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consisted of 220 volumes covering most of the brain, excluding the vertex. Following functional measurements, high-resolution anatomical T1-weighted images were acquired using a 3D sequence that served as a matrix for the functional imaging (160 sagittal slices, resolution 256×256 resampled to 512×512, slice thickness = 1.17 mm, TR = 1700 ms, TE = 3.96 ms, FOV = 246 mm, flip angle = 15°). The overall scanning time was approximately 25 min.

Behavioral examination

Immediately after MRI scanning all subjects completed a short questionnaire concerning their previous knowledge of the campaign clips and their road driving experience. The DD group included subjects who had possessed a driving license for at least 1.5 years (median = 5 years; maximum = 12 years) and drove at least twice a week (median = 5/week). In the SD group, all subjects had possessed a driving license for at least several months (median = 4 years; maximum = 10 years) and drove at least once every other month (median = 1/week).

To investigate the relationship between subjective evaluations and brain function, during this post-scanning session, each subject was shown all of the CV and NV videos a second time and asked to evaluate each of them. For the evaluation, participants were required to provide valence and arousal ratings on a scale from 1 to 10 (1 = pleasant/peaceful, 10 = unpleasant/exciting), and a time-unlimited verbal description of the content of each clip. By coding these verbal descriptions according to the frequency with which certain themes (see below) were mentioned, we set out to measure the degree to which certain socio-cognitive processes were elicited by the video content and their relationship with brain function.

In order to capture different aspects of socio-cognitive processing, we scored the transcribed verbal descriptions by analyzing their thematic content. Assuming that people would describe those aspects that are more important to them, we created special thematic categories: (1) Car brands, (2) mental states of the video actors, (3) mental states of the subjects themselves, (4) the positive and (5) negative emotional states of the video actors, and (6) the positive and (7) negative emotional states of the subjects themselves, (8) the perceived consequences of characters' actions, (9) references to oneself, (10) perspective taking, (11) subjects' interpretations of situational aspects — e.g. relationships, car functionality, (12) the subjects' own positive and (13) negative evaluation of the clips, and (14) a meta-level description of the video clips. Since some of these indices are conceivably related very closely or even overlap partially, it was difficult to delineate them — e.g. categories concerning the mental states of the video actors and perspective taking. For this reason, we defined specific criteria with which to distinguish between individual indices. In the example given, mentalizing referred to instances when participants were guessing the actors' mental state but there was no way they could know it for sure (e.g. "the driver is not paying attention"). In contrast, perspective taking referred to those instances when participants are able to take the perspective of the actor easily (e.g. "he cannot see round the corner"). Table 1 summarizes all these thematic content categories and provided examples for each. Three subjects were removed from subsequent analyses because the recording of their verbal description was unavailable.

The descriptive texts were divided into short utterances that were scored according to these individual thematic categories. In doing so we obtained frequencies for each category. To avoid any biases in the analysis, frequencies were then divided by verbal fluency — i.e. the total number of words spoken during the verbal description. This is a standard method used in content analysis (e.g. Pennebaker, 2011). One of the main purposes for using number of words rather than number of utterances is the objectivity of the former; utterances, on the hand, can be created in many ways. It is these ratio values for each category that we refer to as indices. Individual indices were correlated positively but only moderately (range: r = .5–.85), allowing us to treat each independently. Additionally, in an attempt to form more general indices, we summed a selection of these indices according to their mutual relationships, as defined by correlations between them and Principal Component Analysis. This produced seven additional combined indices. Finally, for each index we divided all drivers (combining both DD and SD groups) into two groups on the basis of a median split. We also split the group according to the median for combinations of indices (e.g. positive and negative emotions of actors). Altogether we obtained 21 various divisions.

Table 1 t1.1
Examples of statements according to special thematic categories used in content analyses t1.2
of verbal descriptions. t1.3

Thematic categories	Examples of statements	t1.4
Car brand	A man gets on the orange Fabia. It is Ford brand. Woman goes by black big SUV on the roads.	t1.5
Mental states: others	"The man in the business suit is trying to sell the car to them." "The man and the woman are evidently in a hurry." "The driver is not paying attention to driving because of a distraction by the woman sitting in the back."	t1.6
Mental states: own	"When I am thinking about it …" "I think there is no the reason for …" "I pay attention to this mainly."	t1.7
Positive emotions: others	"They are laughing." "They enjoy their journey." "There is pleasant atmosphere in the car."	t1.8
Negative emotions: others	"He is scared from the traffic accident." "… and the dealer is a bit nervous." "Two women are crying during their visit in hospital."	t1.9
Positive emotions: own	"This point is a really funny." "This humorous video brings a pleasant feeling for me." "The clip is very calming."	t1.10
Negative emotions: own	"That song irritates me." "It was a really scary moment." "Boring clip."	t1.11
Perceived consequences	"They got mortally wounded." "Finally he ends in a prison." "He did not manage to drive during overtaking and the car hit into a tree."	t1.12
Reference to oneself	"I have a personal experience with this." "I know I will not ever buy this car." "I had been driving aggressively."	t1.13
Perspective taking	"He cannot see the view." "They need to get home." "He did it under pressure from passengers."	t1.14
Interpretation	"It was the main idea of the advertisement." "This is about the contrast between their driving." "I guess it should motivate people to follow the traffic regulations."	t1.15
Positive evaluation	"This campaign is useful." "It was a good point." "That car is great."	t1.16
Negative evaluation	"He drives aggressively and inconsiderately." "I do not like it in this context." "It is stupid for me."	t1.17
Metalevel	"At the end here is a comment that …" "The car has a special function." "The clip was overplayed."	t1.18

fMRI data processing

The functional and structural MRI data were analyzed using SPM5 (Functional Imaging Laboratory, Wellcome Department of Imaging Neuroscience, Institute of Neurology, University College London, UK) running under Matlab 7.6 (Mathworks Inc., USA). The following preprocessing steps were applied to each individual's functional time series: (1) realignment to correct for any motion artifacts, (2) normalization to fit into a standard anatomical space (MNI), (3) spatial smoothing using a Gaussian filter with a FWHM of 8 mm, (4) high-pass filter with a cut-off at 128 s, and (5) an autoregressive model to estimate serial

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autocorrelations. The voxel size generated from the above acquisition parameters was resampled to 3 × 3 × 3 mm.

A General Linear Model (GLM) was implemented in SPM5 to identify whether any brain regions expressed greater blood oxygenation level-dependent (BOLD) signal during either of the two active conditions (CV or NV) relative to the fixation baseline. The time series corresponding to each condition was convolved with a canonical hemodynamic response function. In addition, 6 time series of movement parameters derived during motion correction were added to the GLM to regress out any residual head movement. Statistical parametric maps with t-statistics were computed to assess the significance of BOLD signal increases during the CV or NV condition relative to baseline, and to assess differences in BOLD signal between the two conditions. Corresponding contrast files were entered into second-level analyses. We used a random-effect analysis to compare relative changes in BOLD during CV and NV conditions between the DD and SD groups, and between other divisions of drivers based upon their verbal description.

First we explored whether or not brain function within the STS is modulated by social behavioral tendencies. To this end we compared relative differences in BOLD signal during CV and NV stimuli between the DD and SD groups, first throughout the whole brain and then within regions of interest (ROIs) defined by spheres with diameter of 5 mm centered at local maxima of clusters emerging from our previous study (Zelinková et al., submitted for publication). The mean value from all voxels within these spheres was used for statistical analysis. All ROIs used in the present study are detailed in Table 2.

We then asked if brain function within these same ROIs is modulated by socio-cognitive processes. Mann–Whitney U tests were used to assess differences between groups of drivers defined by median splits on all indices within the ROIs specified in Table 2. The results of these multiple between-group comparisons were Bonferroni corrected ($\alpha = 0.05/22$ divisions [21 median splits as discussed above, plus comparisons between safe and dangerous drivers]).

Results

Due to the multiple comparisons we performed, all statistics are subjected to both Bonferroni and False Discovery Rate corrections (Benjamini and Hochberg, 1995). Fig. 1 presents the results of whole-brain analyses for each group independently, in which brain function during the CV stimuli was contrasted to that during the NV stimuli. Comparing the DD and SD groups with a whole-brain analysis revealed no differences that survived multiple-comparison correction. We did, however, observe a greater difference in BOLD signal change between the CV and NV stimuli in safe drivers within one of the ROIs (cl1, STS/STG, −60, −12, 3; $p_{corr} < 0.05$). Fig. 2 illustrates this group difference. A similar trend was also observed within three additional ROIs (cl. 2, 4 and 5), although these results did not survive Bonferroni correction (Table 3).

As expected, subjective evaluations of valence and arousal differed significantly between CV and NV in both groups. We observed no significant difference between the groups on either dimension, however, nor any interaction ($p > .05$; see Table 4).

Table 2
Brain regions with significantly greater BOLD signal during CV compared with NV stimuli in control subjects (Zelinková et al., submitted for publication). Abbreviations: STG = superior temporal gyrus; STS = superior temporal sulcus; SMG = supramarginal gyrus.

Cluster	VOX number	T in max	Z in max	Max coord	Region	Side
cl1	63	10.97	6.09	−60, −12, 3	STG/STS	L
cl2	15	8.45	5.38	60, 3, −12	STS	R
cl3	7	8.37	5.36	−63, −39, 27	SMG	L
cl4	6	8.30	5.33	63, −24, 15	STG	R
cl5	9	7.64	5.11	63, −21, −6	STS	R
cl6	6	7.36	5.00	63, −9, −6	STS	R

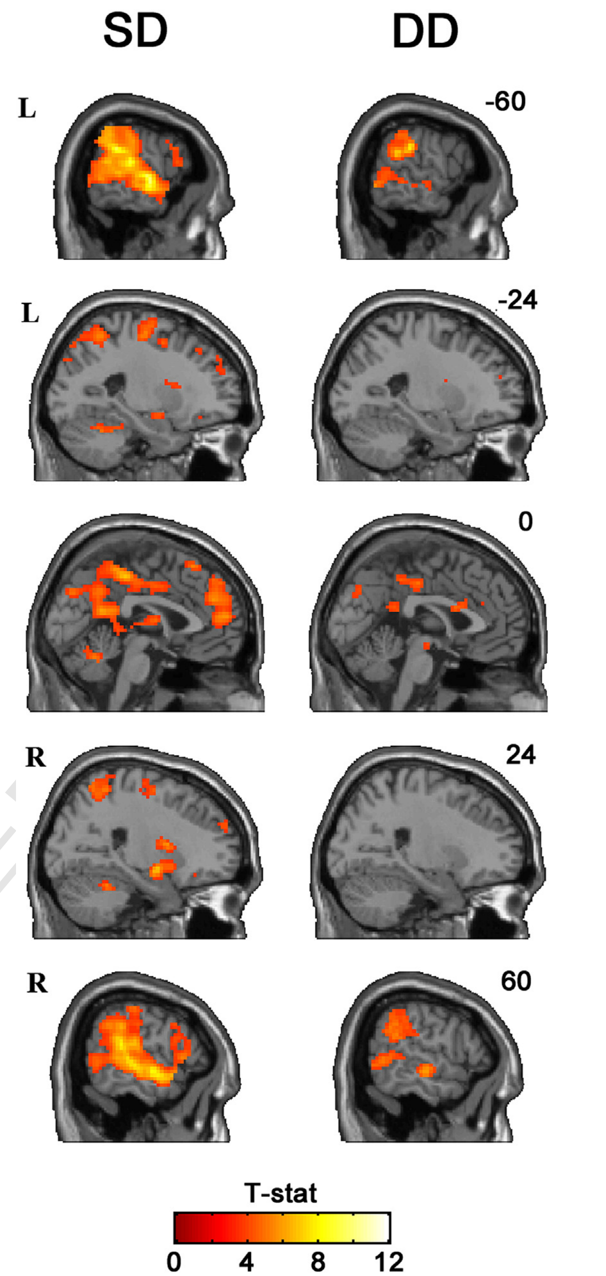

Fig. 1. Whole-brain analysis. The greater relative BOLD signal change between CV and NV stimuli in the safe driver (SD) and the dangerous driver group (DD; p < 0.001 uncorrected; min. cluster extent = 5 voxels).

We observed no significant differences between the DD and SD groups when comparing them on indices derived from the thematic coding of verbal descriptions ($p > 0.05$ on all indices). When combining the DD and SD groups together and then dividing all drivers into two groups according to median splits on all indices, however, revealed two indices of particular importance — i.e. where group differences existed: Within four ROIs there was a greater increase in BOLD signal during CV relative to NV stimuli in drivers scoring higher on perceived consequences of actors' actions (see Table 5); within two other ROIs a similarly greater increase in BOLD signal between CV and NV stimuli was observed in drivers scoring high in positive evaluation (see Table 6). Statistical significance did not exceed Bonferroni correction, however. No significant effect of thematic categories on relative BOLD change was observed in ROIs 3 or 4.

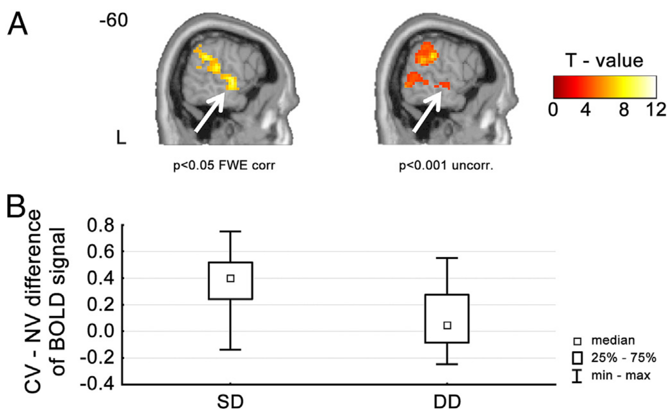

Fig. 2. BOLD signal change between CV and NV stimuli in safe (SD, left) compared with dangerous drivers (DD, right) within cluster 1 (STS/STG: x = −60, y = −12, z = 3). A: Illustration of cluster 1 (indicated with an arrow) in SD (left; p < .05, corrected) and DD (right; p < .001, uncorrected). B: Boxplot of difference in relative BOLD signal change between CV and NV stimuli in SD and DD groups.

Table 4
Means (±SD) of subjective evaluations of valence and arousal for campaign (CV) and neutral video (NV) stimuli, in the dangerous (DD) and safe driver (SD) groups.

Affective reaction	Video category	DD mean	SD mean
Valence	CV	7.45 (±1.83)	7.21 (±2.28)
	NV	2.77 (±1.57)	3.11 (±1.85)
Arousal	CV	7.23 (±1.82)	7.03 (±2.30)
	NV	2.81 (±1.59)	3.12 (±1.85)

Discussion

The purpose of this study was twofold: Firstly, we examined whether or not differences exist in brain response to complex social stimuli between individuals who differ in terms of their proclivity for pro- or anti-social behavior. Secondly, we assessed whether relative changes in brain function within the superior temporal sulcus (STS) during the observation of these social stimuli reflect the degree to which individuals engage in social cognitive processing of the stimuli. We used as stimuli the traffic awareness campaign videos consisting of various complex social stimuli to elicit social cognitive processes, and driving habits as an index of social behavior. We hypothesize that watching such stimuli will elicit psychological processes involved in construing, interpreting, and, more generally, the extraction of meaning; that is, processes engaged during social contexts. These processes are likely to be highly individual, differing according to cognitive and emotional makeup, and also personal experiences. People with a high capacity for mentalizing or empathizing, for example, will rely more often on these processes when construing meaning within social contexts. We suggest, therefore, that comparing groups of individuals differing on measures of social behavior according to the degree of brain function evoked by such stimuli, will help us to understand the relationship between social cognition and social behavior.

In a previous study using the same stimuli, we demonstrated greater activation within STS/STG during the observation of these campaign video clips compared with videos consisting of less socially unacceptable driving behavior (Zelinková et al., submitted for publication). This was true especially for drivers expressing greater empathy with the actors, illustrating a relationship between this facet of social cognition and brain function within a region shown consistently to be involved in social cognition. Our previous sample consisted of safe drivers only, however. In the present study we have developed these initial findings by revealing greater relative BOLD signal change in these safe drivers compared with a new group of dangerous drivers. Moreover, by dividing the entire group of drivers according to a detailed thematic analysis of their verbal descriptions of the stimuli, we revealed a relationship between STS activity and the degree to which individuals engage in socio-cognitive processes; specifically, greater BOLD signal increases within STS during the campaign relative to the control stimuli were observed in subjects who express a greater awareness of the consequences of actors' actions, and who evaluate the videos positively rather than negatively in terms of the emotions they evoke.

Our findings of differences in STS reactivity between safe and dangerous drivers are consistent with a previous study using similar stimuli; Tamura et al. (2012) employed stimuli depicting risky or safe actions (i.e. hand movements with or without a risk of harm) and revealed that risk-taking behavior elicited significantly stronger activation in a number of brain regions that included STG. As discussed above, there have also been other demonstrations of differential brain function between individuals differing in their behavioral tendencies (e.g. Deppe et al., 2005; Goudriaan et al., 2010; Kaplan et al., 2007; Rauch et al., 2007). Sosic-Vasic et al. (2012), for example, reveal that the neural correlates of error detection are related strongly to personality traits. Similarly, Caspers et al. (2012) report dissociated patterns of brain activity during decision making in managers and non-managers. This suggests that professional requirements modulate cognitive decision processing that, in turn, influence brain function during these processes. In the context of the present study, the results of Straube et al. (2010) are particularly interesting; these authors report greater cerebral hypoactivation in high-compared with low sensation seekers during the observation of threatening stimuli, and suggest that this may be compensated by increased sensation-seeking behavior. This leads us to question whether lower activation within STS/STG during campaign videos in dangerous compared with safe drivers is connected to sensation-seeking behavior. This could be something to explore in future research.

Alternatively, one of the differences between safe and dangerous drivers that might result in differential patterns of brain activity may be the capacity for behavioral inhibition; it is conceivable that dangerous driving stems from a lack of self-control. Interestingly, within the domain of developmental social neuroscience, Perner and Lang (1999) propose a link between ToM – a core aspect of social cognition – and self-control, due to their related neuroanatomical correlates. Likewise, lower empathy is likely related to impaired executive function (e.g. behavioral inhibition) and the capacity for self control (Perner and Lang, 1999). Further, it has been shown that behavioral inhibition is reflected in brain activity; Guyer et al. (2006) revealed greater striatal activation to monetary incentives in behaviorally inhibited adolescents than in

Table 3
Clusters expressing greater BOLD signal change between CV and NV stimuli in safe compared with dangerous drivers; p < 0.05.

CLUSTER	Max coord	Region	Side	p value	p value (Bonferroni-corrected)	FDR
cl1	−60, −12, 3	STG/ STS	L	p < 0.000138	p < 0.003036	q < 0.05
cl2	60, 3, −12	STS	R	p < 0.009483	p < 0,208626	q < 0.05
cl4	63, −24, 15	STG	R	p < 0.008808	p < 0.193776	q < 0.05
cl5	63, −21, −6	STS	R	p < 0.033987	p < 0.747714	N.S.

Table 5
The effect of the thematic category perceived consequences of characters' actions, within clusters exhibiting significant (p < 0.05) differences in BOLD signal for the CV–NV contrast.

CLUSTER	Max coord	Region	Side	p value	p value (Bonferroni-corrected)	FDR
cl1	−60, −12, 3	STG/STS	L	p < 0.010536	p < 0.231792	q < 0.05
cl2	60, 3, −12	STS	R	p < 0.008247	p < 0.181434	q < 0.05
cl5	63, −21, −6	STS	R	p < 0.036674	p < 0.806828	N.S.
cl6	63, −9, −6	STS	R	p < 0.036674	p < 0.806828	N.S.

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Table 6
The effect of the thematic category positive evaluation, within clusters exhibiting significant ($p < 0.05$) differences in BOLD signal for the CV–NV contrast.

CLUSTER	Max coord	Region	Side	p value	p value (Bonferroni-corrected)	FDR
cl2	60, 3, −12	STS	R	p < 0.015847	p < 0.348634	q < 0.05
cl5	63, −21, −6	STS	R	p < 0.042358	p < 0.931876	N.S.

non-inhibited adolescents. Together this suggests that different patterns of brain activity within STS between our DD and SD groups might result from differences in the capacity for behavioral inhibition.

Behaving appropriately within social contexts requires us to modulate our own behavior according to that of others. In particular, we are required to inhibit certain behavioral preferences and tendencies on the basis of our awareness of others' mental and emotional states. Given the aforementioned evidence for the role of STS in empathizing and mentalising, such behavioral modulation/inhibition in social contexts likely involves the STS. Therefore, we interpret less STS reactivity during our complex social stimuli in dangerous drivers to reflect less engagement of these psychological processes. In other words, we suggest that dangerous drivers are less considerate of others in the situations comprising the videos. This proposal is supported indirectly by the results of our thematic analyses: We observed greater increases in BOLD signal within STS during the campaign videos in subjects with higher scores on the thematic category perceived consequences of characters' actions. This index measured the frequency with which subjects described the impact of the depicted traffic accidents from the perspective of the actors. Together with our previous work (Zelinková et al., submitted for publication), we suggest that this index is linked intimately with empathic and mentalizing abilities. In this light, greater STS activity indexes a greater interest in others rather than a self-focus. This may also explain the relationship between STS activity and scores on the thematic category positive evaluation: Greater BOLD signal during the campaign relative to the neutral stimuli was associated with more frequent positive evaluations. We suggest that those rating the videos more positively were those engaged more in socio-cognitive processes, leading to a better appreciation for the purpose of the stimuli. In other words, those adopting more of an external focus, with greater consideration of others, will appreciate the intentions behind the stimuli — e.g. the campaign stimuli as an attempt to prevent the negative outcomes experienced by the actors from happening to others.

There is accumulating evidence from neuroimaging and neurophysiological studies that criminal and psychotic behavior is associated with, among other things, functional abnormalities in the medial and anterior lateral aspects of the temporal lobe (Kiehl et al., 2006), and with thinner cortex in the temporal lobes (e.g. Howner et al., 2012; Müller et al., 2008). Consistent with this, Sato et al. (2011) discuss specifically the bilateral STG/STG as a region of the brain differentiating psychopaths from healthy controls. While the findings of the present study lend support to this proposition, it remains unknown whether reduced activation in STS is the antecedent of antisocial behavior. More importantly, although we have revealed a relationship between reduced STS reactivity and a particular form of antisocial behavior, it is likely that the integrity of multiple brain networks and the communication between them is more important than functioning of any one distinct brain structure (for review see Loomans et al., 2010). Moreover, understanding the specific role played by STS in social behavior is made difficult by the wide variety of social stimuli for which these brain regions are responsive (for a review see Hein and Knight, 2008).

It is important to acknowledge some potential shortcomings of this study. Firstly, no attempt was made to capture such individual differences. Furthermore, our subjects were instructed simply to view passively the video clips and no attempt was made to measure their attention to the stimuli. Despite these potential shortcomings, however, our data provides strong evidence for a connection between different activation of the left STS/STG and differences in social behavior. This research does not only help better understand the neural underpinnings of human antisocial behavior, but also provides important insights on STS function.

Conclusions

In the present study, we found a significant difference in brain activation between dangerous drivers in comparison with a group of safe drivers; specifically, we reveal reduced activation of the left STS/STG in dangerous drivers during traffic awareness campaign videos. Moreover, we observed a significant relationship between two thematic categories (perceived consequences of characters' actions and positive evaluation of clips) and the reactivity of the STS to these stimuli. Our work provides important insights on STS/STG function. It is entirely likely that the same brain area can support multiple functions depending on task-dependent network connections. These findings raise questions that can be addressed in future research using a similar methodology. A more accurate specification of the function of STS requires further investigation to determine exactly how activity within this brain region differs between individuals with different levels of risk-taking behavior during the perception of different social inputs.

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Conflict of interest

No potential conflict of interest relevant to this article was reported.

References

Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn. Sci. 4 (7), 267–278.
Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. J. R. Stat. Soc. Ser. B Methodol. 289–300.
Blair, R.J., 2010. Neuroimaging of psychopathy and antisocial behavior: a targeted review. Curr. Psychiatry Rep. 12 (1), 76–82.
Buckholtz, J.W., Callicott, J.H., Kolachana, B., Hariri, A.R., Goldberg, T.E., Genderson, M., Egan, M.F., Mattay, V.S., Weinberger, D.R., Meyer-Lindenberg, A., 2008. Genetic variation in MAOA modulates ventromedial prefrontal circuitry mediating individual differences in human personality. Mol. Psychiatry 13 (3), 313–324.
Bzdok, D., Langner, R., Hoffstaedter, F., Turetsky, B.I., Zilles, K., Eickhoff, S.B., 2012. The modular neuroarchitecture of social judgments on faces. Cereb. Cortex 22 (4), 951–961.
Caspers, S., Heim, S., Lucas, M.G., Stephan, E., Fischer, L., Amunts, K., Zilles, K., 2012. Dissociated neural processing for decisions in managers and non-managers. PLoS One 7 (8), e43537. http://dx.doi.org/10.1371/journal.pone.0043537.
Crowley, T.J., Dalwani, M.S., Mikulich-Gilbertson, S.K., Du, Y.P., Lejuez, C.W., Raymond, K.M., Banich, M.T., 2010. Risky decisions and their consequences: neural processing by boys with antisocial substance disorder. PLoS One 5 (9).
Deppe, M., Schwind, W., Krämer, J., Kugel, H., Plassmann, H., Kenning, P., Ringelstein, E.B., 2005. Evidence for a neural correlate of a framing effect: bias-specific activity in the ventromedial prefrontal cortex during credibility judgments. Brain Res. Bull. 67 (5), 413–421.
Dziobek, I., Preissler, S., Grozdanovic, Z., Heuser, I., Heekeren, H.R., Roepke, S., 2011. Neuronal correlates of altered empathy and social cognition in borderline personality disorder. NeuroImage 57 (2), 539–548.
Ellis, P.L., 1982. Empathy: a factor in antisocial behavior. J. Abnorm. Child Psychol. 10 (1), 123–134.
Ernst, M., Fudge, J.L., 2009. A developmental neurobiological model of motivated behavior: anatomy, connectivity and ontogeny of the triadic nodes. Neurosci. Biobehav. Rev. 33 (3), 367–382.
Freeman, H.D., Beer, J.S., 2010. Frontal lobe activation mediates the relation between sensation seeking and cortisol increases. J. Personal. 78 (5), 1497–1528.
Frith, C.D., Frith, U., 2010. The social brain: allowing humans to boldly go where no other species has been. Phil. Trans. R. Soc. B 365 (1537), 165–176.
Frith, C.D., Frith, U., 2012. Mechanisms of social cognition. Annu. Rev. Psychol. 63, 287–313.
Gallagher, H.L., Frith, C.H.D., 2003. Functional imaging of 'theory of mind'. Trends Cogn. Sci. 7 (2).

Goudriaan, A.E., de Ruiter, M.B., van den Brink, W., Oosterlaan, J., Veltman, D.J., 2010. Brain activation patterns associated with cue reactivity and craving in abstinent problem gamblers, heavy smokers and healthy controls: an fMRI study. Addict. Biol. 15 (4), 491–503.

Guyer, A.E., Nelson, E.E., Perez-Edgar, K., Hardin, M.G., Roberson-Nay, R., Monk, C.S., Bjork, J.M., Henderson, H.A., Pine, D., Fox, N.A., Ernst, M., 2006. Striatal functional alteration in adolescents characterized by early childhood behavioral inhibition. J. Neurosci. 26 (24), 6399–6405.

Hein, G., Knight, R.T., 2008. Superior temporal sulcus — it's my area: or is it? J. Cogn. Neurosci. 20 (12), 2125–2136.

Howner, K., Eskildsen, S.F., Fischer, H., Dierks, T., Wahlund, L.O., Jonsson, T., Wiberg, M.K., Kristiansson, M., 2012. Thinner cortex in the frontal lobes in mentally disordered offenders. Psychiatry Res. 203 (2–3), 126–131.

Kaplan, J.T., Freedman, J., Iacoboni, M., 2007. Us versus them: political attitudes and party affiliation influence neural response to faces of presidential candidates. Neuropsychologia 45 (1), 55–64.

Kiehl, K.A., Bates, A.T., Laurens, K.R., Hare, R.D., Liddle, P.F., 2006. Brain potentials implicate temporal lobe abnormalities in criminal psychopaths. J. Abnorm. Psychol. 115 (3), 443–453.

Kieling, R.R., Szobot, C.M., Matte, B., Coelho, R.S., Kieling, C., Pechansky, F., Rohde, L.A., 2011. Mental disorders and delivery motorcycle drivers (motoboys): a dangerous association. Eur. Psychiatry 26 (1), 23–27.

Krämer, U.M., Mohammadi, B., Doñamayor, N., Samii, A., Münte, T.F., 2010. Emotional and cognitive aspects of empathy and their relation to social cognition — an fMRI-study. Brain Res. 1311, 110–120.

Lahnakoski, J.M., Glerean, E., Salmi, J., Jääskeläinen, I.P., Sams, M., Hari, R., Nummenmaa, L., 2012. Naturalistic fMRI mapping reveals superior temporal sulcus as the hub for the distributed brain network for social perception. Front. Hum. Neurosci. 6 (233), 1–14.

Loomans, M.M., Tulen, J.H., van Marle, H.J., 2010. The neurobiology of antisocial behaviour. Tijdschr. Psychiatr. 52 (6), 387–396.

Miczek, K.A., Fish, E.W., De Bold, J.F., De Almeida, R.M., 2002. Social and neural determinants of aggressive behavior: pharmacotherapeutic targets at serotonin, dopamine and gamma-aminobutyric acid systems. Psychopharmacology 163 (3–4), 434–458.

Moor, B.G., Güroğlu, B., Op de Macks, Z.A., Rombouts, S., Van der Molen, M.W., Crone, E.A., 2012. Social exclusion and punishment of excluders: neural correlates and developmental trajectories. NeuroImage 59 (1), 708–717.

Müller, J.L., Gänssbauer, S., Sommer, M., Döhnel, K., Weber, T., Schmidt-Wilcke, T., Hajak, G., 2008. Gray matter changes in right superior temporal gyrus in criminal psychopaths. Evidence from voxel-based morphometry. Psychiatry Res. 163 (3), 213–222.

Peelen, M.V., Atkinson, A.P., Vuilleumier, P., 2010. Supramodal representations of perceived emotions in the human brain. J. Neurosci. 30 (30), 10127–10134.

Pelphrey, K.A., Morris, J.P., McCarthy, G., 2005. Neural basis of eye gaze processing deficits in autism. Brain 128 (Pt 5), 1038–1048.

Pennebaker, J.W., 2011. The Secret Life of Pronouns: What Our Words Say About Us. Bloomsbury Press, New York.

Perner, J., Lang, B., 1999. Development of theory of mind and executive control. Trends Cogn. Sci. 3 (9), 337–344.

Raine, A., Yang, Y., 2006. Neural foundations to moral reasoning and antisocial behavior. Soc. Cogn. Affect. Neurosci. 1 (3), 203–213.

Rauch, A.V., Ohrmann, P., Bauer, J., Kugel, H., Engelien, A., Arolt, V., Heindel, W., Suslow, T., 2007. Cognitive coping style modulates neural responses to emotional faces in healthy humans: a 3-T fMRI study. Cereb. Cortex 17 (11), 2526–2535.

Sato, J.R., de Oliveira-Souza, R., Thomaz, C.E., Basílio, R., Bramati, I.E., Amaro Jr., E., Tovar-Moll, F., Hare, R.D., Moll, J., 2011. Identification of psychopathic individuals using pattern classification of MRI images. Soc. Neurosci. 6 (5–6), 627–639.

Schultz, J., Friston, K.J., O'Doherty, J., Wolpert, D.M., Frith, C.D., 2005. Activation in posterior superior temporal sulcus parallels parameter inducing the perception of animacy. Neuron 45 (4), 625–635.

Sosic-Vasic, Z., Ulrich, M., Ruchsow, M., Vasic, N., Grön, G., 2012. The modulating effect of personality traits on neural error monitoring: evidence from event-related FMRI. PLoS One 7 (8), e42930. http://dx.doi.org/10.1371/journal.pone.0042930.

Straube, T., Preissler, S., Lipka, J., Hewig, J., Mentzel, H.J., Miltner, W.H., 2010. Neural representation of anxiety and personality during exposure to anxiety-provoking and neutral scenes from scary movies. Hum. Brain Mapp. 31 (1), 36–47.

Suda, M., Takei, Y., Aoyama, Y., Narita, K., Sakurai, N., Fukuda, M., Mikuni, M., 2011. Autistic traits and brain activation during face-to-face conversations in typically developed adults. PLoS One 6 (5), e20021.

Tamura, M., Moriguchi, Y., Higuchi, S., Hida, A., Enomoto, M., Umezawa, J., Mishima, K., 2012. Neural network development in late adolescents during observation of risk-taking action. PLoS One 7 (6), e39527. http://dx.doi.org/10.1371/journal.pone.0039527.

Volman, I., Toni, I., Verhagen, L., Roelofs, K., 2011. Endogenous testosterone modulates prefrontal–amygdala connectivity during social emotional behavior. Cereb. Cortex 21 (10), 2282–2290.

Weissman, D.H., Perkins, A.S., Woldorff, M.G., 2008. Cognitive control in social situations: a role for the dorsolateral prefrontal cortex. NeuroImage 40 (2), 955–962.

Winston, J.S., Strange, B.A., O'Doherty, J., Dolan, R.J., 2002. Automatic and intentional brain responses during evaluation of trustworthiness of faces. Nat. Neurosci. 5 (3), 277–283.

Yang, Y., Glenn, A.L., Raine, A., 2008. Brain abnormalities in antisocial individuals: implications for the law. Behav. Sci. Law 26 (1), 65–83.

Zelinková, J., Mareček, R., Mikl, M., Urbánek, T., Shaw, D.J., Havlíčková, D., Zámečník, P., Haitová, P., Brázdil, M., 2013. Traffic Awareness Campaign Selectively Engages Superior Temporal Sulcus (submitted for publication). Q3

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