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Neural correlates of causality judgment in physical and social context—The reversed effects of space and time

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The perception of causal relationships is crucial to understanding and interacting with our physical and social environment. However, whether the same or different neural processes are involved in perceiving physical and social causality is unknown. Therefore, this study is focused on commonalities and differences in the neural correlates of causality perception in both contexts.

During fMRI data-acquisition, participants judged causal relationships of objects in two types of animated video clips (physical/social) with similar manipulations of temporal and spatial stimulus characteristics. Four conditions were analyzed in a two-factorial design [physical causal (PC), physical non-causal (PNC), social causal (SC), social non-causal (SNC)].

We found that higher angles and longer time delays led to decreasing judgments of causality in the physical context, whereas the same manipulations led to increasing judgments in the social context.

Instead of a common network for causal judgments (PC > PNC ∩ SC > SNC), we found a reversed activation pattern for the factors context and judgment. PC and SNC [(PC > PNC) > (SC > SNC)] produced activations in the bilateral insula, the right angular and inferior frontal gyrus and the medial supplementary motor area. PNC and SC [(PC > PNC) < (SC > SNC)] produced activity in medial frontal, left superior temporal and anterior cingulate brain regions.

Our data suggest, that the same brain regions contribute to the impression of physical and social causality. However, they demonstrate a reversed activation pattern that reflects the stimulus characteristics of the respective conditions. Thus, specific stimulus characteristics are crucial for the perception of causality.

Introduction

The ability to detect causal relationships in everyday life is of fundamental importance. Knowledge about the processes in the human brain that lead to causal impressions may be helpful for a better understanding of aberrant inferences of causality in mental disorders like autism (Congiu et al., 2010; Klin and Jones, 2008; Saygin et al., 2010) and schizophrenia (Brune, 2005; Tschacher and Kupper, 2006).

The most common phenomenon investigated in the research on the perception of physical causality in the past decades is probably the "launching effect" (Michotte, 1946/1963; Wagemans et al., 2006). When an object A moves towards a stationary object B, and after a contact B moves on, most people describe this event as causal: A is the reason that B moved. Many variations of this kind of experiment have been used to investigate the key parameters that lead to the perception of causality. Those key parameters include a gap between both objects (Oakes and Kannass, 1999; Saxe and Carey, 2006; Schlottmann and Anderson, 1993; Yela, 1952), time delays before the second object starts to move (Guski and Troje, 2003; Schlottmann and Shanks, 1992; Schlottmann et al., 2006; Young and Sutherland, 2009), and the trajectory of movement (Straube and Chatterjee, 2010; Straube et al., 2011) These studies generally suggest that spatial and temporal manipulations play an important role in this context.

Given that spatial and temporal parameters affect causal inferences in physical contexts, the question arises if they contribute similarly to causal judgments in social contexts. The recognition of social interactions is a highly complex process. To investigate social interactions experimentally, it is necessary to minimize the influencing variables in the stimulus material in order to isolate the social processing (Adolphs, 2010). Heider and Simmel famously showed that, under certain conditions, participants bestow human attributes to moving simple geometric forms (Abell et al., 2000; Castelli et al., 2000; Heider and Simmel, 1944; Rimé et al., 1985; Tremoulet and Feldman, 2006). For this attribution to occur, again spatial and temporal manipulations play a crucial role (Carrozzo et al., 2010; Falmier and Young, 2008; Scholl and Tremoulet, 2000; Tremoulet and Feldman, 2000, 2006). In addition, instructions, prior experience and knowledge of the participants have a strong effect on their ratings (Gemelli and Cappellini, 1958; Gruber et al., 1957; Powesland, 1959; Schlottmann et al., 2006).

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More recent studies also use imaging methods like functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) to characterize the neural correlates of causality. In the physical context, Blakemore et al. found activations in the middle temporal gyrus and the right intraparietal sulcus with launching events (Blakemore et al., 2003). For causal events in contrast to non-causal events they found activations in both medial and superior temporal areas and the left intraparietal sulcus (Blakemore et al., 2001). These findings support the assumption that higher-order perceptual brain regions play a role in the detection of causal relationships. Another study in this context showed activations in both superior frontal gyri and the orbitofrontal gyrus during judgments of causality (Fonlupt, 2003). Fugelsang et al. (2005) also found activations in the right superior and middle frontal cortices and in the right inferior parietal lobule. They suggest that the detection of causality is especially instantiated in the right hemisphere. Straube and Chatterjee (2010) did not find brain activations for causal in contrast to non-causal judged stimuli. However, individuals with a higher sensitivity for spatial properties in the causality judgment task had increased brain activations in the parietal lobe, whereas individual biased to use time information had increased activation in the left basal ganglia. Inconsistencies between studies as well as evidence for individual differences, could suggest a strong influence of top-down processes, which might depend on the conditions of the task and individual differences in sensitivity to, preference for or experience with a respective parameter, stimulus, or task.

In contrast to perceptual causality and the perception of animacy (e.g., Blakemore et al., 2001, 2003; Schlottmann et al., 2006) relatively few fMRI studies have investigated social causality. In many cases this is because different research approaches and alternating terms and definitions of causality are used in a social context (Gao and Scholl, 2011). It has been suggested, that the medial frontal cortex plays an important role to determine future behavior of others (Amodio and Frith, 2006). Tavares et al. showed widespread brain activations for highly animated rated stimuli, including the bilateral frontal gyrus, the right superior temporal sulcus and amygdala (Tavares et al., 2008). They concluded that the perception of social causality does not have to be triggered by perceptual systems.

Santos et al. (2010) used two simple 3D spheres to construct short videos that showed different moving patterns of the spheres (e.g. whether the moving sphere 1 did approach sphere 2 or not ("approach"); whether sphere 2 moved toward the moving sphere 1 ("responsiveness")). The participants had to judge a stimulus as "physical", "rather physical", "rather personal" or "personal". The results revealed significant main effects of approach and responsiveness concerning the judgment for a "personal" attribution of an object.

The neural correlates of experiencing animacy according to Santos et al. were activity in the bilateral insula, extending into the superior temporal gyrus and sulcus, the medial orbitofrontal cortex, extending into the anterior cingulate cortex, and left parahippocampal gyrus extending into the left fusiform gyrus. They concluded that animacy experiences activate this "social neural network" (SNN) (Brothers, 1990). However, since the stimuli were judged on the same scale (physical–personal), this study concentrated on brain activations for increasing or decreasing the experience of animacy and did not reveal specific information about the neural substrate of causality judgments in physical as opposed to social contexts.

In the present study we aimed to investigate the neural correlates of the judgment of causality in a physical and social context. Social causality in context of this study refers to the perception of a social interaction in which one person is perceived to influence the behavior of another person. The two persons were illustrated by neutral objects in this study to keep the social context comparable to the physical context. We compared brain activations of physical and social contexts as well as activations concerning causality judgments. Both contexts used highly comparable stimuli, each including a blue and a red simple object (circle) (see Straube and Chatterjee, 2010; Straube et al., 2011). In the physical context the blue ball collided with the red ball, whereas in the social context the blue ball passed the red ball. Two instructions were used to set up the context, which differed minimally in the stimulus arrangement (see Fig. 1). The participants judged each stimulus event as causal or non-causal, while time delay and angle in movement direction were identically manipulated in the physical and social context. The experiment used many stimuli that varied the perceptual cues parametrically to account for individual differences in perceptual sensitivity and total amount of causality judgments.

Based on previous literature (e.g. Schlottmann et al., 2006) we expected opposite effects of our stimulus manipulations on physical and social causality: Small deviations in the stimulus (small angle and short time delay) lead to causal judgment in the physical task, and non-causal judgment in the social task, whereas large deviations (great angle and long time delay) lead to the opposite judgments. In the fMRI analyses, we expect to find different brain activations during physical and social tasks in brain regions predominantly related to perceptual (e.g., for physical task and spatial effects in the parietal lobe, and temporal effects in the supplementary motor area (SMA) and the basal ganglia (Straube and Chatterjee, 2010; Straube et al., 2011)) and inferential (e.g., for social tasks in the prefrontal cortex (Tavares et al., 2008)) processing mechanisms. The medial prefrontal cortex (MPFC) has previously been described as instantiating several psychological mechanisms (e.g. self-concept, mentalizing and emotional experience) and might more generally compute inexact and internally generated estimates for social phenomena (Mitchell, 2009).

We tested the following alternate hypothesis: firstly, if the perception of causality is a universal function independent of context, we expect the same brain regions to be activated for causal in contrast to non-causal trials in both the physical and the social contexts. However, if the judgment of causality is instantiated through specific context dependent neural networks, we expect significant interaction effects in brain regions previously reported with regard to perception of physical and social causality or animacy (e.g., the bilateral insula, the superior temporal gyrus/sulcus (STG/STS), the medial orbitofrontal cortex, the anterior cingulate cortex (ACC), and left parahippocampal gyrus (Santos et al., 2010), right medial frontal gyrus and in the inferior parietal lobule (Fugelsang et al., 2005); bilateral superior frontal gyri and the orbitofrontal gyrus (Fonlupt, 2003); medial and superior temporal areas and the bilateral intraparietal sulcus (Blakemore et al., 2001, 2003)). Such an interaction of context and judgment would further suggest that brain activity depends on stimulus parameters rather than on judgments, given the expected opposite effects of time and space in the physical and social causality contexts.

Material and methods

Participants

20 subjects were included in the analyses (10 male/female, mean age = 24.3 years). All were right-handed and had a normal or corrected-to-normal vision. None of them reported significant medical treatment because of neurological or psychiatric reasons.

Initially, twenty-two participants took part in the study. However, one male participant was excluded from the fMRI-analysis because of excessive head movement and one female participant was excluded because of technical problems during the behavioral data acquisition. Every participant received 20 Euros for their participation in the study. Written informed consent was obtained prior to the experiment. The ethics committee of the Medical Faculty of the University of Marburg, Germany, approved the study.

Stimulus construction

All the stimuli were created with *Strata 3D CX 6* software. Two types of animated video clips with parametric modulations of spatial

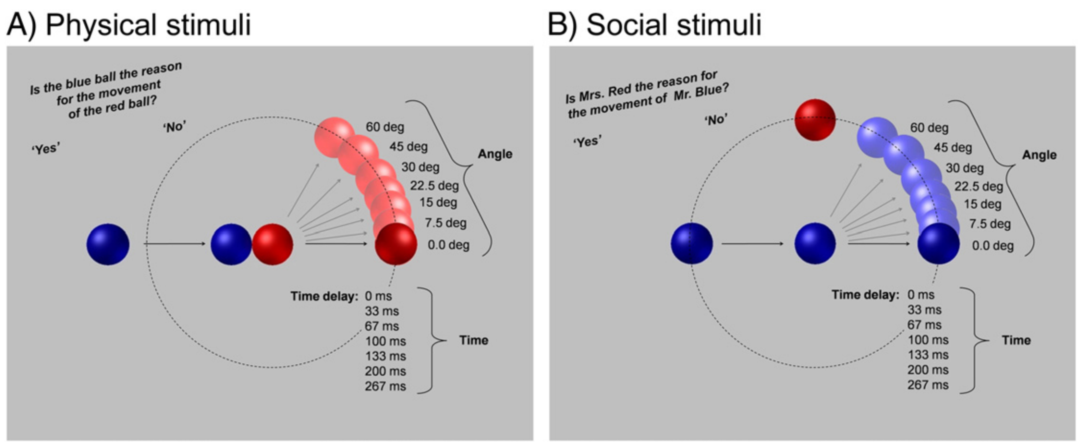

Fig. 1. Stimulus material. Variations of physical and social stimuli: The arrows denote direction of motion. All stimuli were shown in two directions (horizontally flipped). 98 Stimuli for each condition (7 angles × 7 time delays × 2 directions).

and temporal characteristics were used in this study. Each video was two seconds long. The round discs were shaded to give the impression of three dimensional objects. For both stimuli types the first shape (colored blue) began to move 500 ms after video onset, rolled along a horizontal plane and stopped moving 500 ms after animation onset (1000 ms after video onset) in the middle of the screen.

In the physical condition the blue ball always stopped once it made contact with the second ball (colored red). The red ball varied in the direction and the time at which it began to move. The trajectory of the red ball varied by seven different angles (0°, 7.5°, 15°, 22.5°, 30°, 45°, 60°), and by seven different time delays (0, 33, 67, 100, 133, 200, 267 ms) (Fig. 1A). All possible combinations and two directions (moving from left to right and right to left) were used in the experiment with a total of 98 physical stimuli (see Straube and Chatterjee, 2010).

In the social condition the red ball was stationary positioned in the center above the path of the blue ball (Fig. 1B). The blue ball moved horizontally, stopped in the middle of the screen for a varying time delay (0, 33, 67, 100, 133, 200, 267 ms), and then advanced in seven different trajectories (0°, 7.5°, 15°, 22.5°, 30°, 45°, 60°). The balls did not make contact during the video and the red ball did not move. The social videos were presented with the identical variations as the physical videos (98 stimuli = 7 angles × 7 time delays × 2 directions).

Since speed and length of trajectory were the same for both balls in all conditions, the time at the end of each video clip varied in accordance to the time delay between 133 ms (267 ms delay) and 400 ms (no delay). All stimuli were rendered and converted to the Windows Media File format (WMV2/PAL; frame rate = 60 frames per second, resolution = 720 × 576 pixels).

Experimental design

The experiment was conducted in a rapid event-related design. The videos of each condition were shown in randomized order and grouped in six blocks with twelve and two blocks with thirteen stimuli. A small fixation object was shown after each video with a variable duration (main duration 5000 ms, range of 2000 to 8000 ms). The fixation object was different in both conditions in order to avoid any possibility of confusion (see supplement). The blocks of both conditions were presented in alternating order, so the test persons had to switch between both tasks.

In the physical condition the participants were instructed to answer the question 'Is the blue ball the reason for the movement of the red ball?' with 'yes' or 'no'.

In the social condition the participants were instructed to regard the red ball as a 'Mrs. Red' and the blue ball as a 'Mr. Blue' and to judge a possible causal relation between both subjects (Is Mrs. Red the reason for the movement of Mr. Blue? Yes or No).

Before the first block of trials, participants were given detailed instructions and completed several practice trials. For both conditions the participants were instructed to respond by pressing a button (right index finger for [yes] or the right middle finger for [no]) on an fMRI compatible response device. For both contexts, the participants were instructed to respond as soon as they were able to answer the question about causality. They were not instructed to wait for the end of the stimulus or to respond as quickly as possible. For the presentation of the experiment the "Presentation" software was used (Version 14.1, build 09.21.09 Neurobehavioral systems).

After the causality tasks a simple stimulus variation task with a temporal and a spatial questioning was implemented, in order to control that all participants are able to detect different angles and time delays. In the spatial task, the participants had to judge if the angle of the pathway of a moving ball is greater than a reference angle. In the temporal task the participants had to judge if the time-delay that occurred during the movement of the ball was longer than a reference time-delay. These data were not used to model neural activity in the reported analyses.

The fMRI experiment took 45 min. Afterwards the participants were asked to fill in two questionnaires concerning the experimental manipulations (scale 1–7, 1 = minimal agreement, 7 = maximal agreement; Statements: I understood the physical/social task, I could imagine a social situation in the social task, I had problems with switching between both tasks, The fMRI did interfere my answers, I had problems with the response device, I often pressed the wrong button accidentally).

Behavioral pilot study

A behavioral experiment was conducted prior to the fMRI study to test the two causality tasks and whether the instructions were comprehensible. 20 healthy participants (mean age = 24.30, SD = 2.18, 10 male/female) enrolled in the pilot study. In additional to the questionnaire that was used in the fMRI study, a verbal probe was included in which participants judged three different videos of both contexts once again and then were instructed to describe why they decided the way they did. Most participants (70%) mentioned social reasons for their social judgments (for a detailed report of the pretest, see supplemental material).

The behavioral results showed a strong influence of spatial and temporal manipulations on the judgment of causality (see supplemental material). Behavioral data of the fMRI experiment replicated these findings from the behavioral pilot study outside the fMRI scanner.

MRI data acquisition

MRI was performed on a 3 T MR Magnetom Trio Trim scanner (Siemens). T1-weighted high resolution anatomical images were acquired for each subject. Functional data were acquired using a T2-weighted echo planar image sequence (repetition time (TR) = 2000 ms; echo time (TE) = 30 ms; flip angle = 90°). The volume included 33 transversal slices (slice thickness = 3.6 mm; interslice gap = 0.36 mm; field of view (FoV) = 230 mm, voxel resolution = 3.6 mm^2). 425 volumes were acquired during each of the two functional runs. To minimize motion, the head of the subjects was fixed with foam pads. Vision correction was necessary for n = 8 participants, 6 of which had MRI-compatible contact lenses. The remaining 2 were equipped with a special MRI-compatible plastic goggle set. All participants reported that they could see the videos without any problems.

MRI data analysis

Preprocessing

Data were analyzed with the statistical parametric mapping method using the standard routines of the SPM8 software. The presentation of the experiment started with the sixth image, so the first five images were discarded. All functional images were realigned to this sixth image and then normalized into standard stereotaxic anatomical space using the transformation matrix (mean image) calculated from the first EPI-scan for each subject and the EPI-template created by the Montreal Neurological Institute (MNI). The normalized data (resliced voxel size: 2 mm^3) were then smoothed with an 8 mm^3 Gaussian kernel in order to compensate for inter-subject variance in brain anatomy.

Statistical analysis of the fMRI data

The onsets were set 1.5 s after the start of the stimulus when the object had changed its trajectory and/or the pause had occurred. A design matrix was modeled with the single-subject BOLD responses of the trials, divided in trials judged as causal and trials judged as non-causal for both conditions. This procedure led to a design matrix with four different conditions [physical causal (PC), physical non-causal (PNC), social causal (SC), social non-causal (SNC)]. The instruction period was included separately as a factor of no interest. The number of trials varied because of individual differences in judging (mean number of trials: PC = 41.80, SD = 12.04, PNC = 55.75, SD = 12.12; SC = 54.80, SD = 17.13; SNC = 42.55, SD = 17.25). To reduce response specific variance within each condition we included the following covariates of no interest as parameters in the single subject analyses: Response time, angle, time-delay and movement direction of the stimulus.

Second level analysis

At group level a flexible-factorial analyses implemented in SPM8 were used compare brain activation with regard to the different conditions. Contrast images of the 20 participants for the four conditions [physical causal (PC), physical non-causal (PNC), social causal (SC), social non-causal (SNC)] were entered into the analyses. For each of the four condition corresponding contrast images from the single-subject analyses were used. Main effects and interactions were calculated using linear contrasts of the corresponding conditions (e.g.: main effect: 1 −1 1 −1; interaction: 1 −1 −1 1). Despite "subject" and "condition" factors were defined in the flexible factorial analyses, only the effects of the "condition" factor have been incorporated in the analyses. However, the additional inclusion of the main effect subject in the analysis (design matrix) would not change the general result pattern (exceptions were noted).

Statistical analyses were performed under a $p < 0.001$ (uncorrected) threshold. In order to correct our results for multiple comparisons, we applied a cluster extend threshold of 60 voxel for all analyses. Thus, all reported cluster of activation are corrected for multiple comparisons applying the SPM cluster threshold ($p < 0.05$, false discovery rate, FDR).

The following contrasts of interest were computed: At first, baseline contrasts were performed (PC > baseline [fixation object]; PNC > baseline [fixation object], SC > baseline [fixation object], SNC > baseline [fixation object], PC ∩ SC > baseline [fixation object], PNC ∩ SNC > baseline [fixation object]) in order to show general activations for physical and social stimuli. For all conjunctional analyses we used the conjunction null, which is based on the minimum statistic approach (see Nichols et al., 2005). Secondly, main effects for context (physical > social; social > physical) were calculated to reveal possible differences in network activations based on perceptual or social contexts. For the third set of analyses, three different contrasts were performed to demonstrate the commonalities and differences with regard to causal judgments in a physical and social context. A conjunction analysis was performed to reveal brain regions commonly involved in the perception of causality (causal > non-causal) regardless of whether it was in a physical or social context [(PC > PNC) ∩ (SC > SNC)]. Then two interaction contrasts were employed [(PC > PNC) > (SC > SNC); (PC > PNC) < (SC > SNC)] to obtain brain regions differentially activated with regard to causality judgments in a physical in contrast to social context.

Parametric analyses modulating the effects of stimulus parameters (time-delay and angle) independent of causality judgments as well as an interaction with causality judgments across conditions were calculated for exploratory reasons and are reported in the supplementary material. These analyses indicate general effects of space and times in primary sensory cortices of the occipital lobe as well as top-down modulations with regard to the judgment of causality in predominantly bilateral temporal and parietal regions (see supplemental material).

Correlation analyses

We expected correlation between brain activity in the parietal lobe and individual sensitivity to spatial parameters, and correlations between SMA and basal ganglia activity and individual sensitivity to temporal parameters. Therefore, we performed correlation analyses primarily for activity found in these regions of interest and the corresponding parameter (see Result section). For this analyses BOLD-Signals were correlated with average angle (respectively average time) and partial corrected for average time (respectively average angle). Additionally we conducted further post-hoc analyses to explore correlations between all other activated brain regions and behavioral data (see supplemental material).

Results

Behavioral results

The participants rated 42.86% (SD = 12.36%, range = 24.49–69.39%) of the physical stimuli and 56.31% (SD = 17.68%, range = 28.57–88.78%) of the social stimuli as causal. Thus, there is a significant difference in the degree of detected causality in both conditions ($t(19) = -2.411$, $p < 0.026$). Furthermore, correlation analyses indicate no significant correlation between causality judgments in both contexts (Correlation coefficient = −0.361, $p > 0.118$).

With a greater angle deviations and time delays the impression of causality in the physical task decreased (Fig. 2A) and increased in the social task (Fig. 2B). In the physical task we found an average angle and time delay of 14.35° (SD = 7.48°) and 81.86 ms (SD = 30.69 ms) for events judged as causal, as well as 33.83° (SD = 6.46°) and 139.26 ms (SD = 26.61 ms) for events judged as non-causal (see Figs. 2C, D).

In the social task we found an average angle and time delay of 35.43° (SD = 8.60°) and 126.98 ms (SD = 13.81 ms) for events judged as causal, as well as 16.21° (SD = 8.02°) and 91.55 ms (SD = 29.01 ms) for events judged as non-causal (see Figs. 2C, D).

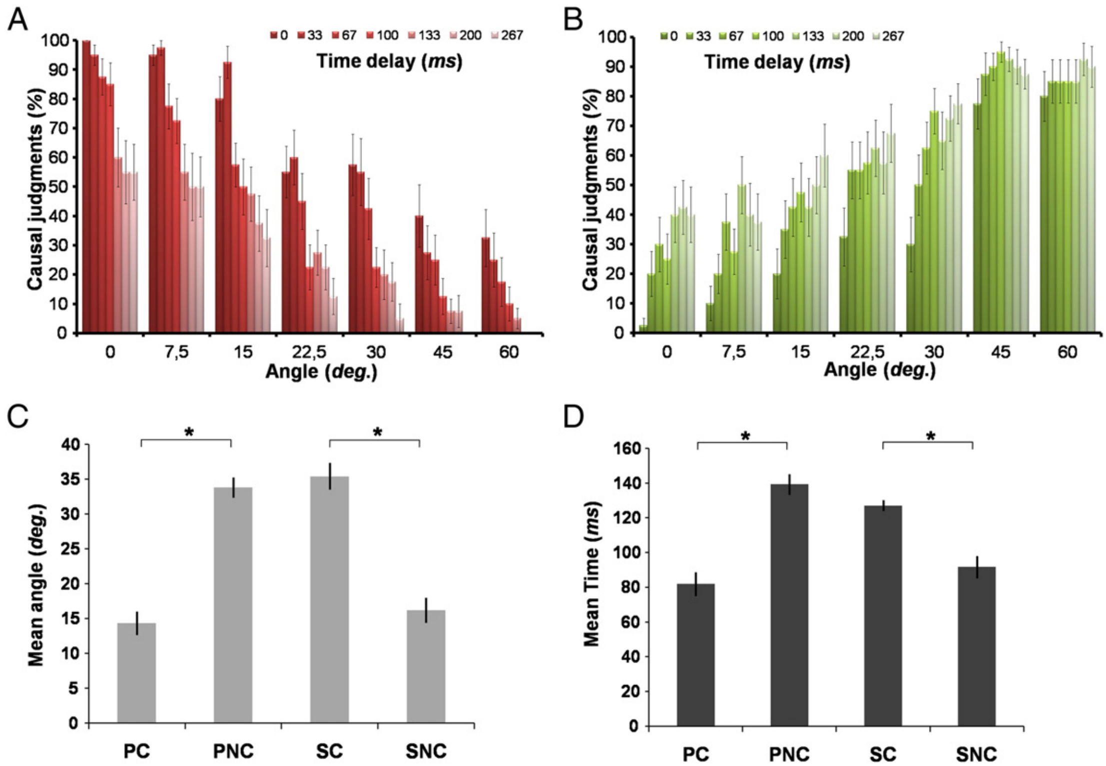

Fig. 2. Behavioral data. (A) Physical causality: Decreasing number of causal judgments for higher angles and time delays in the physical task. (B) Social causality: In contrast increasing causal judgments in the social task. (C) Judged mean angle. (D) Judged mean time delay. (PC = physical causal judged stimuli, PNC = physical non-causal judged stimuli, SC = social causal judged stimuli, SNC = social non-causal judged stimuli, Error bars represent the standard error of the mean, the asterisks represent statistically significant differences).

Thus, for the mean angle as well as for the mean time delay we found a significant interaction of the factors conditions (physical/social) and judgments (causal/non-causal; mean angle: $F(1, 19) = 74.683$, $p < 0.001$, partial eta squared = 0.797; mean time-delay: $F(1, 20) = 31.442$, $p < 0.001$, partial eta squared = 0.623). Post-hoc tests revealed significant lower mean angles and mean time delays for causal in contrast to non-causal trials (causal > non-causal) in the physical context (physical mean angle: $t(19) = -6.977$, $p < 0.001$; physical mean time: $t(19) = -4.670$, $p < 0.001$) and significant higher mean angles and mean time delays for causal in contrast to non-causal trials (causal > non-causal) in the social context (social mean angle: $t(19) = 5.933$, $p < 0.001$; social mean time: $t(19) = 4.086$, $p < 0.001$; see Figs. 2C, D).

There were no significant correlations between parameters (average angle or average time) used in a physical and social context (for all $p > 0.20$; see supplemental material).

Responses in the social task took significantly longer than responses in the physical task (physical task: Mean RT = 2.32 s, SD = 0.28 s; social task: Mean RT = 2.52 s, SD = 0.32 s; $t(19) = -5.373$, $p < 0.001$). The RTs for non-causal judgments were significantly longer than for causal judged events (physical task: Mean RT causal = 2.31 s, SD = 0.31 s; mean RT non-causal = 2.34 s, SD = 0.27 s; social task: Mean RT causal = 2.45 s, SD = 0.29 s; mean RT non-causal = 2.64 s, SD = 0.41 s; $F(1,19) = 24.592$, $p < 0.001$, partial eta squared = 0.564). The post-hoc t-tests revealed only significant longer RTs for non-causal judged events in the social task (physical task: $t(19) = -0.868$, $p < 0.396$; social task: $t(20) = -4.671$, $p < 0.001$), as indicated by a significant interaction (physical/social, causal/non-causal; $F(1, 19) = 7.343$, $p < 0.001$, partial eta squared = 0.279).

The control "stimulus parameter detection task" revealed that all subjects detected time delays and angles with a high accuracy (spatial task: 98.05%, SD = 2.72%; temporal task: Mean 95.15%, SD = 2.03%). Detection rate was not correlated with the actual use of angle or time delay for the judgment of causality in a physical or social context ($p > 0.20$).

Questionnaire results

Answers were given based on a 1 to 7 scale, with 1 representing a minimal agreement and 7 a maximal agreement. Statements concerning the understanding of the physical and social task were both rated with an average of 6.75 (physical: range = 6.00–7.00, SD = 0.44; social: range = 5.00–7.00; SD = 0.55). The statement 'it was easy it was to imagine a social situation in the social task' was answered with an average of 5.35 (range = 3.00–7.00, SD = 1.09). The statement regarding switching between both tasks was rated with an average of 6.70 (range = 5.00–7.00, SD = 0.57). Statements concerning interference generated by the fMRI (mean = 1.50, range = 1.00–4.00, SD = 0.76), problems with the response device (mean = 1.55, range = 1.00–4.00, SD = 0.89) or pressing of the wrong button (mean = 2.30, range = 1.00–7.00, SD = 1.30) were rated low.

fMRI-results

For the physical and social conditions (PC, PNC, SC, SNC) and the conjunctions (PC ∩ PNC, SC ∩ SNC), in contrast to low-level baseline (fixation object) we found highly comparable activation patterns including predominantly bilateral occipital, parietal and frontal lobes (see Fig. 3). The physical condition revealed strongest activation in the left parietal lobe and the social condition in both parietal lobes as well as the right frontal cortex.

For the analysis of the physical context (contrasted to the social context) we found increased activity in the left lingual gyrus, extending to the inferior occipital gyrus and activations in the right inferior occipital gyrus, extending to the calcarine gyrus. Other activated regions were situated in more anterior brain regions, namely the bilateral middle frontal gyri, extending to the superior frontal gyri, the right insula and the left superior temporal gyrus, extending to the left insula and amygdala (see Fig. 4, Table 1).

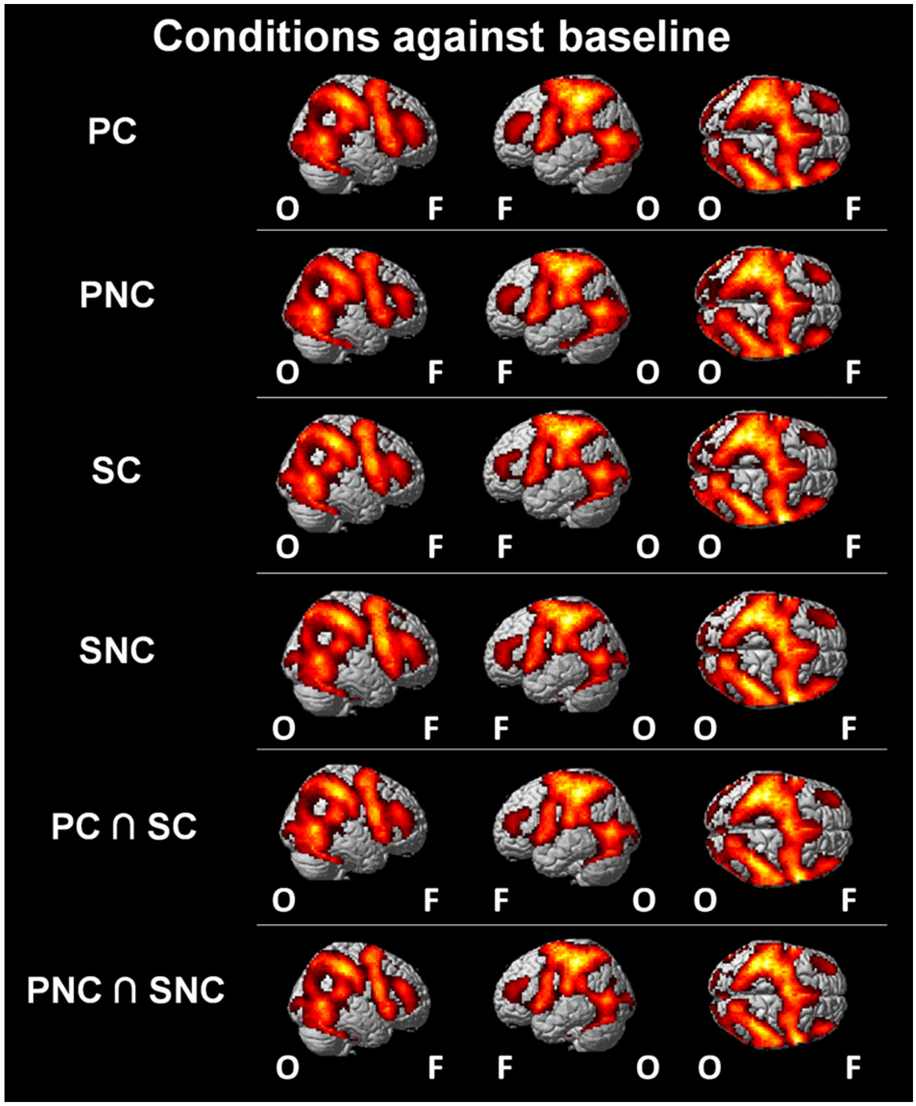

Fig. 3. General brain activations > low-level baseline. General activations of the conditions against low-level baseline (fixation object, $p<0.001$, >60 voxel). Conjunction analyses of causal and non-causal conditions in contrast to low level baseline (fixation object) across contexts (PC ∩ SC; PNC ∩ SNC). Common activations in a large number of brain regions across contexts could be observed. These data indicate several common brain mechanisms between the different conditions. (PC = physical causal judged stimuli, PNC = physical non-causal judged stimuli, SC = social causal judged stimuli, SNC = social non-causal judged stimuli, F = frontal, O = occipital).

For the opposite contrast (social stimuli > physical stimuli) we did not find significant activations. However, at a lower threshold ($p<0.001$, extend > 20 Voxel; without FDR correction), we found activations in the right inferior frontal gyrus (pars triangularis; MNI x, y, z = [51, 23, 16]; t-value = 4.60, cluster extend = 52 voxel), the right superior parietal gyrus (MNI x, y, z = [15, −76, 55]; t-value = 3.95, cluster extend = 32 voxel) and the right medial occipital gyrus (MNI x, y, z = [42, −76, 31]; t-value = 3.94, cluster extend = 39 voxel).

For the main effect of causality (causal > non-causal) we found no significant activation for causal judged stimuli contrasted to non-causal judgments across both contexts. Corresponding to the main effect in the conjunction analysis we found no common network activation for causal judged stimuli contrasted to non-causal judgments in a physical and social context [(PC > PNC) ∩ (SC > SNC)], even at a very low threshold ($p<0.01$, uncorrected).

At the chosen threshold, used in this study ($p<0.001$, cluster extend > 60 voxel), we also did not find activations for physical causal contrasted to physical non-causal, and social causal contrasted to social non-causal stimuli.

In the social context we found two areas at a lower threshold ($p<0.001$, cluster extend > 20 voxel, no FDR correction). The left fusiform gyrus (MNI x, y, z: [−33, −52, −11], $p<0.001$, t-value = 4.00, cluster extend = 23 voxel) and the left medial superior frontal gyrus (MNI x, y, z: [−6, 53, 34], $p<0.001$, t-value = 3.86, cluster extend = 30 voxel).

In the interaction analysis [(PC > PNC) > (SC > SNC)] we found significant activations in the bilateral insula, the right angular gyrus, the inferior frontal gyrus (pars opercularis) and the medial supplementary motor area (Fig. 5). The opposite interaction contrast [(SC > SNC) > (PC > PNC)] revealed activation in the left medial superior frontal gyrus, the right anterior cingulate cortex (ACC; this cluster would not reach the sig. threshold if the main effect subject is included in the analyses; t = 4.46, $p<0.001$ uncorr., 39 voxels; see Section Second level analysis) and the left superior temporal gyrus. Despite the significant interaction effect, contrast estimates indicate general deactivation (baseline > conditions) in the superior MFG (Fig. 6).

Correlation analyses

Based on our hypotheses, we implemented two post-hoc validations to explore correlations between activated brain regions and behavioral data. In the first interaction contrast we found activations in

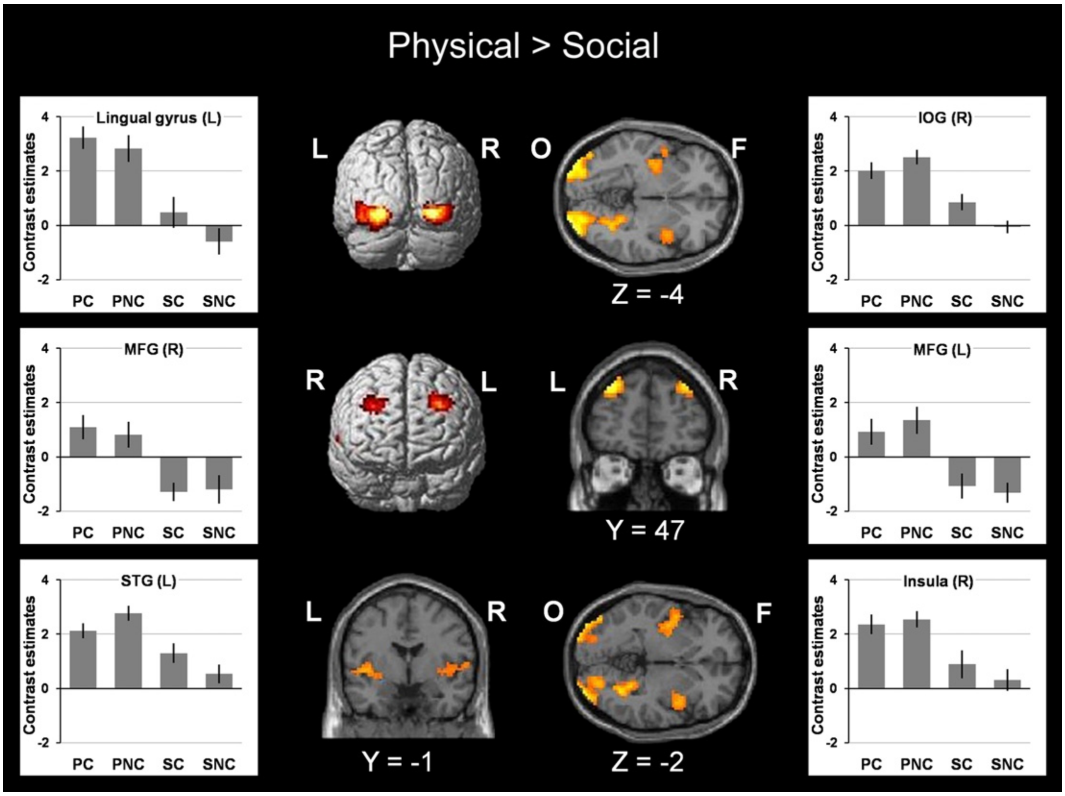

Fig. 4. Brain activations for physical > social stimuli. Physical stimuli contrasted to social stimuli (phys > soc). ($p<0.05$, FDR cluster threshold corrected; IOG = inferior occipital gyrus, MFG = middle frontal gyrus, STG = superior temporal gyrus; L = left, R = right, O = occipital, F = frontal, Phys = physical stimuli, Soc = social stimuli, PC = physical causal judged stimuli, SNC = physical non-causal judged stimuli, SC = social causal judged stimuli, SNC = social non-causal judged stimuli; Error bars represent the standard error of the mean).

the right angular gyrus, driven by the physical causal and the social non-causal condition (see Fig. 5). We expected a negative correlation between the activation in that region (high value means high BOLD signal) and the average angle for the respective condition (low value indicates a strict use of spatial information). We found a significant unilateral correlation, between the brain activations and the average angle, but only in the physical causal condition (correlation coefficient = −0.435, $p<0.031$, partial corrected for judged mean time). However, in the first interaction contrast (Fig. 5) we also found activations in the supplementary motor area. In this case we expected a negative correlation between the activation and the average time for the respective condition (low value indicates a strict use

Table 1
Activations related to different contrasts.

Anatomical region	Cluster extend	Side	Coordinates			No. of voxel	t-Value
			x	y	z		
Physical contrasted to social condition (P > S)							
Lingual gyrus	Inferior occipital gyrus	L	−24	−97	−14	279	6.39
Inferior occipital gyrus	Lingual gyrus, calcarine sulcus	R	33	−94	−11	532	5.83
Middle frontal gyrus	Superior frontal gyrus	L	−30	47	37	93	5.28
Middle frontal gyrus	Superior frontal gyrus	R	33	53	34	85	4.86
Insula		R	42	5	7	159	4.31
Superior temporal gyrus	Insula, Amygdala	L	−48	2	−2	149	4.08
Interaction: (PC > PNC) > (SC > SNC)							
Insula		L	−30	23	1	82	4.84
Insula	Inferior frontal orb., inferior frontal tri.	R	33	29	−5	82	4.68
Angular gyrus		R	45	−61	49	162	4.35
Inferior frontal oper.	Inferior frontal tri.	R	48	8	25	221	4.33
Supp. motor area		L/R	3	20	52	102	3.95
Interaction: (PC > PNC) < (SC > SNC)							
Medial superior frontal gyrus	Superior frontal gyrus	L	−9	59	22	123	5.34
Anterior cingulate cortex[a]	Inferior frontal gyrus tri., medial superior frontal gyrus	R	18	38	4	154	4.84
Superior temporal gyrus	Inferior temporal gyrus	L	−45	−28	10	122	3.87

Brain activation for contrasts employed in this study. ($p<0.001$, cluster extend > 60 voxel, $p<0.05$ FDR corrected; L = left hemisphere, R = right hemisphere, Supp. = supplementary, Orb. = pars orbitalis, Tri. = pars triangularis, oper. = pars opercularis, P = physical, S = social, PC = physical causal judged stimuli, PNC = physical non-causal judged stimuli, SC = social causal judged stimuli, SNC = social non-causal judged stimuli).

[a] Cluster would not reach the sig. threshold, if the main effect subject is included in the analyses ($t=4.46$, $p<.001$ uncorr., 39 voxels; see Section Second level analysis).

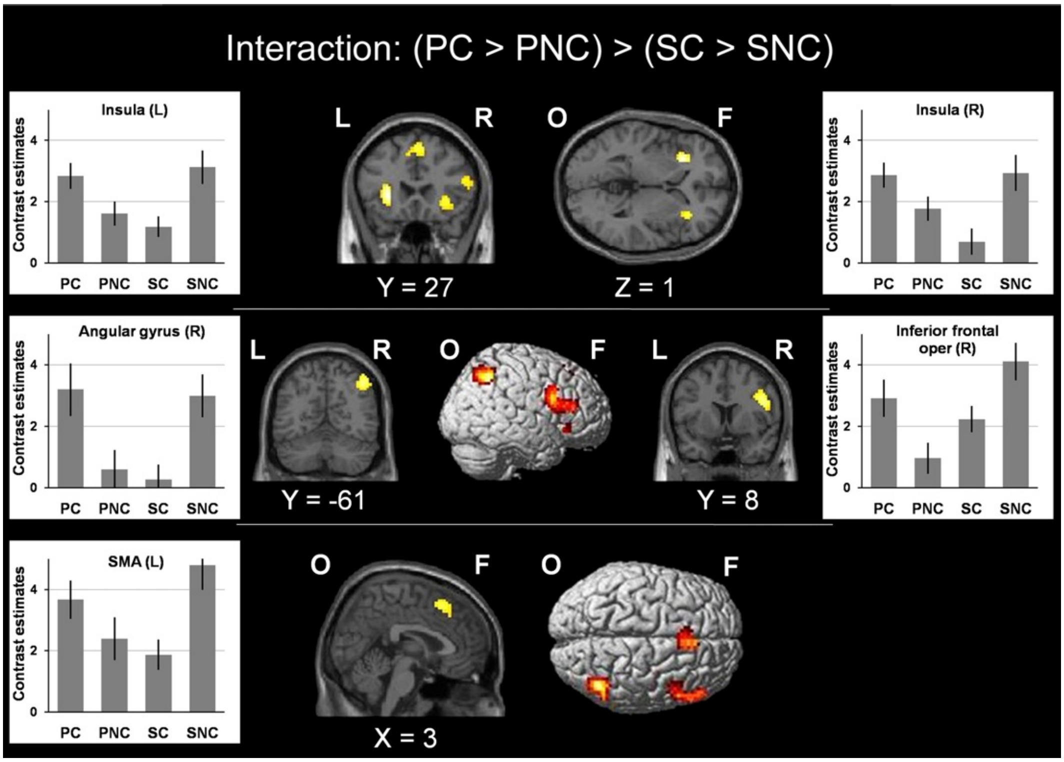

Fig. 5. Brain activations for the first interaction contrast. Brain activations for interaction contrast [(PC>PNC)>(SC>SNC)]. ($p<0.05$, FDR cluster threshold corrected; SMA = supplementary motor area, oper = pars opercularis; L = left, R = right, O = occipital, F = frontal, PC = physical causal judged stimuli, SNC = physical non-causal judged stimuli, SC = social causal judged stimuli, SNC = social non-causal judged stimuli; Error bars represent the standard error mean).

of temporal information). We found significant unilateral correlation between both parameters in the physical causal and in the social non-causal condition (PC: correlation coefficient = −0.446, $p<0.028$; SNC: correlation coefficient = −0.771, $p<0.001$; both partial corrected for judged mean angle). Correlations of other activated brain regions and behavioral data (explorative) are reported in the supplement (Supplementary table S.1).

Discussion

Causal relationships are not restricted to objects and physical forces. They are also inferred in social situations. In the present study we aimed to compare the neural correlates of the perception of causality in physical and social contexts using similar stimuli and manipulations of spatial and temporal parameters.

Behaviorally, we found that spatial and temporal event parameters were important for causality judgments in both contexts. However, whereas violations of spatial continuity and temporal contiguity led to decreasing physical causal judgments, the opposite was true for analogous social judgments.

At the neural level we found highly comparable activation patterns for all conditions in contrast to low-level baseline (fixation cross/object). However, we did not find common networks for the perception of causality (causal>non-causal) in physical and social contexts (conjunction analysis). The absence of a common network suggests that different brain mechanisms instantiate causal perception in physical and social contexts. However, interaction analyses revealed opposite activation patterns with regard to physical in contrast to social condition [(PC>PNC)>(SC>SNC)] in the bilateral insula, the right angular gyrus, the inferior frontal gyrus (pars opercularis) and the left supplementary motor area (see Fig. 5). For the social in contrast to the physical context [(PC>PNC)<(SC>SNC)] we found activation in the left medial superior frontal gyrus, the right anterior cingulate cortex and the left superior temporal gyrus (see Fig. 6). The data of both interaction analyses suggest that the same regions are relevant for the perception of causality in a physical and social context, but demonstrate modulation of activation in opposite directions with regard to the context.

These data provide new evidence about the neural correlates of physical and social causality suggesting that the same brain regions may contribute to the perception of causality in both contexts, but do so with opposite activation patterns.

Behavioral results

Our behavioral findings concerning physical causality are consistent with several previous studies. Longer time delays lead to a decreasing impression of physical causality (e.g. Guski and Troje, 2003; Schlottmann, 2000; Schlottmann and Shanks, 1992; Schlottmann et al., 2006; Young and Sutherland, 2009). Greater angle deviations in the movement path also lead to decreasing impressions of causality (Straube and Chatterjee, 2010; Straube et al., 2011). As shown in Fig. 2 similar manipulations lead to the opposite effects in the social condition. This means that spatial and temporal factors also play important roles in the perception of social causality. Even small differences in the spatial continuity or temporal contiguity can increase/decrease the perception of a causal event in a social context.

Beside the similarities between conditions, we found differences in the degree of judged causality in both conditions. Participants judged significantly more causal relationships in the social than in the physical condition. This finding is consistent with the fact that more causal relationships are possible in a social context (driven by communication, attractiveness, smell,…) than are possible in a physical context (physical forces). Despite the fact that subjects used time and space for their judgments in both contexts there were no significant correlation between parameters (average angle or average time) used in a physical and social context as well as the number of causality judgments in a physical and social context.

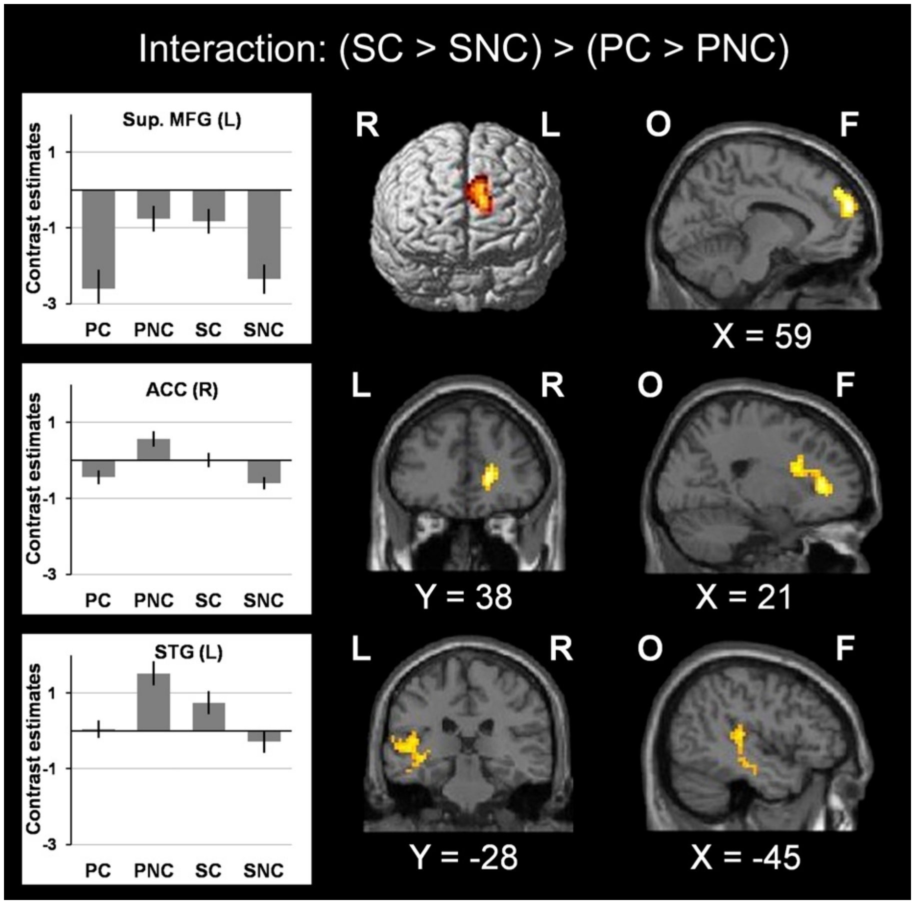

Fig. 6. Brain activations for the second interaction contrast. Brain activations for interaction contrast [(SC > SNC) > (PC > PNC)]. ($p<0.05$, FDR cluster threshold corrected; sup. MFG = medial superior frontal gyrus, ACC = anterior cingulate cortex, STG = superior temporal gyrus, L = left, R = right, O = occipital, F = frontal, PC = physical causal judged stimuli, SNC = physical non-causal judged stimuli, SC = social causal judged stimuli, SNC = social non-causal judged stimuli; Error bars represent the standard error of the mean).

This indicates that participants used different evaluation strategies across both context. Further support for this interpretation comes from the pilot study questionnaires, where subjects described varied reasons for their judgments of social causality (supplemental material).

These data hint at the complexity of mental mechanisms engaged by our participants in response to our highly controlled simple stimuli. Such complexity is true even in the straightforward case of physical causality, where it is obvious that a ball that directly hits another one does not cause spatial deviations of the trajectory of the second ball being hit by the first. Spatial and temporal deviation becomes increasingly inexplicable on physical grounds, but could be explained by unusual physical forces (e.g. magnetic forces or spin on the ball). Causal relations are far more complex in social conditions where abstract, psychological reasons likely contribute (e.g. "social attractiveness": the red ball could also be less attractive and could make the blue ball "escape"). Interestingly, despite the wide range of possible reasons for judging social causality, we observed highly predictable response patterns. We suspect that our pared down schematic stimuli succeeded in focusing attention to the simple manipulations of space and time, even though in real world events many factors contribute to the impression of social causality.

Taken together, our behavioral data show that spatial and temporal factors have a large impact on the perception of physical and social causality. Interestingly, similar manipulations of space and time lead to opposite impressions of causality. This means, that while the perception of causality is influenced by elementary perceptual (temporal/spatial) processes, the actual judgment of causality is extracted by top-down contextual effects.

General brain activations against baseline

At the neural level we found highly comparable activation patterns for all conditions in contrast to low-level baseline (fixation cross/object) as indicated by conjunctional analyses. These data indicate that differences between conditions identified below are most likely just based on subtle differences between conditions, which are relevant to the differences in the perception and judgment of causality in both contexts.

Brain activations for physical > social causality

For the physical in contrast to the social condition we found activations in the bilateral inferior occipital gyri, the insulae/STG and the middle frontal gyri. The activations of the occipital brain regions suggest increased perceptual processing mechanisms activated during the physical in contrast to social context. This interpretation is in line with studies showing that increased visual perceptual effort produces greater occipital lobe activation (Brown, 2009; Kravitz et al., 2011).

The finding of bilateral insula and left STG activation suggest further an involvement of higher order processing in physical in contrast to the social conditions, as found for example for the detection of biological motion (Frith and Frith, 2003, 2010), the identification of moving geometrical figures, independent of a social context (Kawawaki et al., 2006; Schultz et al., 2004, 2005) and have also been found in previous causality studies with similar stimulus material (Blakemore et al., 2001, 2003).

Interestingly, we also found activations of both middle frontal gyri, extending to the superior frontal gyrus. The same areas are also known for visospatial processing of moving objects, together with the posterior parietal cortex (de Graaf et al., 2010; Wu et al., 2008).

Together, differences between conditions independent of causal judgments suggest increased effort of the perceptual system during the physical in contrast to the social causality task. However, activation of the middle frontal cortex were also modulated by condition, suggesting at least some top-down processes relevant for the distinction of physical and social context information.

Brain activations for social > physical causality

For the social task contrasted to the physical task we found activations at a lower threshold ($p < 0.001$, cluster extend > 20 voxel, no FDR correction) in the right inferior frontal gyrus (pars triangularis; MNI x, y, z = [51, 23, 16]), the right superior parietal gyrus (MNI x, y, z = [15, −76, 55]), and the right medial occipital gyrus (MNI x, y, z = [42, −76, 31]). Those areas in the parietal and occipital lobe are known for perceptual processing, e.g. spatial orientation (Beudel et al., 2009; Billino et al., 2009; Keehner et al., 2006; Shulman et al., 1999). However, the inferior frontal activation might also indicate top-down processes, as for example, involved with action observation networks (Billino et al., 2009) or biological motion detection (Saygin, 2007). But these findings have to be interpreted with caution because of the weakness of the activations. One explanation for the weak effects for the social task is the higher variability among all subjects in the social task. Whereas in the physical task, the stimuli were more realistic (more comparable to real billiard balls), the social task was more open to different interpretations of the stimulus (e.g. different environments of Mr. Blue and Mrs. Red, different relationships, etc.). At the group level this variability between interpretations might be responsible for the weak effects in the social, compared to the physical conditions. It is also possible that the social task was easier to judge for the subjects even though they had to imagine a social situation. However, longer reaction times for the SNC condition speak against this possibility. But the longer reaction times could also reflect the fact that social interaction can occur during the whole stimulus period, whereas the physical interaction is clear after the collision. It might be the case, that it is easier for human beings, to get an overview over a social every-day life situation, than to evaluate a physical setting.

To reveal the effect of judgment (causal vs. non-causal) for both conditions, we implemented a conjunction and two interaction contrast analyses.

No common network for causal-judged stimuli

In this study we did not find general activations for causal judged stimuli contrasted to non-causal judged stimuli at the chosen threshold. In other words, no common network was activated for 'Yes' (causal) judgments contrasted to 'No' (non-causal) judgments across contexts. One explanation for this finding might be the fact that both contexts trigger two very different psychological processes, which do not have much in common. However, conjunction analyses of the baseline contrasts as well as the behavioral data (e.g., importance of space and time) indicate that there are at least some common processes between contexts and conditions. Our data suggest, that the perception of causality is not a universal cognitive process that is implemented in the same brain regions independent of contextual (physical/social) characteristics.

Interaction contrasts

Using interaction contrasts we found differences in activations during the physical and social context, dependent of the judgments [(PC > PNC) > (SC > SNC)]. We found activations in the bilateral insula, the right angular gyrus and inferior frontal cortex (pars opercularis), and the left supplementary motor area (SMA).

Thus, different brain regions were activated with regard to the judgments of causality depending on the physical or social context. In line with our alternate hypothesis, the significant interaction effect suggest that perception of causality depends on stimulus characteristics that are modulated by the specific context in brain regions previously reported for perception of physical and social causality or animacy (e.g., the bilateral insula (Santos et al., 2010); right inferior parietal lobule (Fugelsang et al., 2005); bilateral intraparietal sulcus (Blakemore et al., 2001, 2003)).

The contrast estimates (Fig. 5) of these different activations indicate opposite activation patterns in corresponding brain regions. For example, activation of the left insula increased for causal trials in physical contexts and for non-causal trials in social contexts. Correspondingly, non-causal trial in a physical context and causal trials in a social context show similar lower activations. This activation pattern is also present for all other regions of this contrast. The fact, that activation is modulated by both contexts with regard to causal judgments indicate that the same brain areas are involved in the causality processing in a physical and social context, but with an opposite activation pattern.

This opposite activation pattern might reflect the opposite response pattern with regard to space and time in the physical and social context (see Figs. 2C, D). Physical causal (PC) and social non-causal (SNC) trials have smaller angles and smaller time delays than trials that were judged as physical non-causal (PNC), and social causal (SC). Therefore in this contrast we also compared brain activation related to the processing of stimuli with small angles and small time delays with stimuli with high angles and high time delays. The bilateral insula, especially the anterior-dorsal part, plays an important role for the integration of external information (Kurth et al., 2010; Mayer et al., 2007; Singer et al., 2009; Soros et al., 2007). In the present study, stronger activations occur when small deviations in the stimulus material were processed, whereas high deviations lead to a decreasing activation. Thus, integration processes reflected in insula activation might just occur with small deviation of spatial and temporal contiguity. One speculative explanation of our finding would be that integration processes of the bilateral anterior insula might be an indicator for causal perception in the physical context and for non-causal perception in the social context. In line with this interpretation right parietal and frontal activation in this contrast might be involved in providing perceptual input (e.g. Straube and Chatterjee, 2010) for the integration processes.

Support for this interpretation comes from the correlation analyses, indicating that the activation of the right angular gyrus specifically correlated with individual sensitivity to spatial manipulations in the PC context. Subjects who are sensitive to spatial manipulations showed higher activation in this region than those who are less sensitive. This correlation is not significant in the SNC condition, indicating that a high sensitivity to spatial manipulations by itself does not necessary lead to an increased activity in the right angular gyrus. The activation appears to depend on the context. However, another explanation for the absent correlation in the SNC condition could be the higher variability in the social task (see Section Brain activations for social > physical causality).

Correspondingly activity in the supplementary motor area, which has been previously found to play a role in time perception (Beudel et al., 2009; Coull et al., 2008; Wiener et al., 2010), is additionally correlated with individual sensitivity to time manipulations in the PC and SNC condition. Thus, the different regions found in the interaction analyses might be related to the processing of specific spatial and temporal information relevant for the perception of causality.

In the opposite interaction contrast [(SC > SNC) > (PC > PNC)] we found activations in the left medial superior frontal gyrus, the right anterior cingulate cortex (ACC) and the left superior temporal gyrus. In this second interaction contrast we found high activations for trials judged as non-causal in a physical context and trials judged as causal in a social context (Fig. 6).

The medial frontal gyrus has been shown to be involved in earlier causality studies (Fonlupt, 2003), whereas the anterior cingulate cortex plays an important role in decision making (Shad et al., 2011). The

STG appears to be involved in detection of biological motion and geometrical figures (Frith and Frith, 2003, 2010; Schultz et al., 2004, 2005). However, the anterior cingulate cortex (ACC) is part of the social neural network (SNN) (Burnett et al., 2011; Frith, 2007), as well as the STG. In this contrast, high deviations of space and time are contrasted to small manipulations. Thus, again, we found a common network with regard to similar stimulus characteristics in both contexts. In conclusion, high manipulations of space and time led to an activation of areas known for social processing which influenced the causality judgment.

Taken together, the interaction contrasts revealed different brain areas activated for causal judgments in both tasks. This activation could be triggered by the degree of spatial and temporal manipulation. The first interaction contrast emphasizes the integrative role of the insula for small deviations in the stimulus material. In the second interaction contrast, high manipulations led to an activation of areas known for social processing.

Limitations of the experiment

Concerning the structure of our experiment, several limitations are relevant. The specific stimuli characteristics across both tasks are not exactly identical. The focus was to hold the manipulations of space and time constant and still convey the impression of a social situation in the second task. But in the social condition angle manipulation is now confounded with the distance between the red and the blue ball. However, distance is at least a spatial variable, too, and the behavioral data do not suggest a stronger effect of space in contrast to time in the social condition.

With regard to the fMRI results, some of these findings have to be interpreted with caution because they did not exceed baseline levels (Fig. 6). However, since there might also be activations in the baseline phases, these can be responsible for deactivations in the task condition. Thus, it makes still sense to interpret stimulus driven findings, than trying to interpret differences due to an uncontrollable baseline (Morcom and Fletcher, 2007).

An insufficient capability to imagine a social situation cannot be precluded completely even though subject ratings in the questionnaires speak against this possibility. Moreover, the behavioral results suggest that subjects performed the task adequately. But it might be the case that the schematic structure of the stimulus induced weaker impressions of a social situation, than social situations in every-day life. This was also reported in previous studies (Schlottmann et al., 2006). The nature of the physical stimulus might be more realistic than the social stimulus, where subjects had to think themselves into a social situation. Future research has to find a balance between a simple stimulus in order to isolate the social processing and a more complex and realistic approach to extend the working definition of social causality (applied in the current study) to more naturalistic concepts with a higher external validity.

Within this study only active tasks were implemented to investigate the perception of causality in physical and social contexts. Thus, our study the perception of causality always involved the goal to judge the impression of causality with an accompanying motor response related to button press. Even if this is true for all presented trial, we cannot rule out interactions of perceptual and task or response effects in our study. To disentangle task-related top down processes from stimulus triggered bottom-up effects the implementation of a low-level baseline task (e.g. direction judgments) would be helpful. Future studies are necessary to clearly differentiate perceptual and inferential contribution on the perception of causality.

Conclusions

Spatial and temporal manipulations have a high impact on the judgment of causality. Whereas high angles and time delays led to decreasing judgments of causality in the physical context and increasing judgments in the social context and the other way around. The physical causality task strongly activated areas known for perceptual processing as well as areas known for top-down processes. We did not find a common network for stimuli judged as 'causal' contrasted to stimuli judged as 'non-causal'. However, in line with the interaction pattern in the stimulus characteristics for causal vs. non-causal trials in a physical vs. social context, we found an interaction in brain activations for both tasks in several areas, strongest in the bilateral insula. These data indicate that spatial and temporal manipulations are crucial for the perception of causality. Thus, the same brain regions and spatial and temporal parameters seem to be involved in the process of causal inference, but they contribute to different judgments, depending on the context. Future work will have to differentiate perceptual and inferential processes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2012.07.028.

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