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Intuitive physics ability in systemizers relies on differential use of the internalizing system and long-term spatial representations

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ABSTRACT

According to the Empathizing-Systemizing theory (E-S Theory), individual differences in how people understand the physical world (systemizing) and the social world (empathizing), are two continuums in the general population with several implications, from vocational interests to skills in the social and physical domains. The underlying mechanisms of intuitive physics performance among individuals with a strong systemizing and weak empathizing (systemizers) are, however, unknown. Our results affirm higher intuitive physics skills in healthy adult systemizers (N = 36), and further reveal the brain mechanisms that are characteristic for those individuals in carrying out such tasks. When the participants performed intuitive physics tasks during functional magnetic resonance imaging, combined higher systemizing and lower empathizing was associated with stronger activations in parts of the default mode network (DMN, cuneus and posterior cingulate gyrus), middle occipital gyrus, and parahippocampal region. The posterior cingulate gyrus and parahippocampal gyrus were specifically associated with systemizing "brain type" even after controlling for task performance, while especially in the parietal cortex, the activation changes were simply explained by higher task performance. We therefore suggest that utilization of DMN-parahippocampal complex, suggested to play a role in internalizing and activating long-term spatial memory representations, is the factor that distinguishes systemizers from empathizers with the opposite "brain type" in intuitive physics tasks.

1. Introduction

Human goal-directed behavior is largely based on predictive coding relying on intuitive knowledge of the laws of physics (Fischer et al., 2016; Hegarty, 2004; McCloskey et al., 1983; Sanborn et al., 2013). However, people's basic physical understanding of mechanics varies even across the adult population. For example, people may incorrectly predict the path of a ball released from a curved tube (unlike some presume, it is straight not curved) or fail to envision that a ball will follow a path resembling a parabolic arc when it is dropped from the hand of a walking person (Kaiser et al., 1986; McCloskey et al., 1980, 1983). Some intuitive understanding of basic principles of physics, such as that physical objects are solid, persist over time, and fall to the ground if not physically supported (Bloom, 2009; Spelke, 1994) emerges already during infancy. However, to many of us explicit learning of Newtonian physics and utilizing this knowledge in managing with the real world remains difficult into adulthood (for review see, Sanborn et al., 2013). This suggests that our intuitive understanding of physics deviates from Newtonian physics, although physics and our intuition of it must still share some similarities, as we can learn to deftly interpret the physical world and to use this information in our interaction with it. So far, it has remained unclear what drives the individual differences explaining how well people learn to interpret and interact with the physical world. According to the empathizing-systemizing theory (E-S theory; (Baron-Cohen et al., 2005; Baron-Cohen, 2009)) one possible candidate for individual differences leading to better performance in intuitive physics is systemizing. In this study, we investigate how systemizing might lead to better performance in the intuitive physics tasks and which brain mechanisms could be involved in the better performance.

According to the empathizing-systemizing theory (Baron-Cohen et al., 2005; Baron-Cohen, 2009), systemizing and empathizing traits are normally distributed across the population. Strong empathizers are

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people- and social-world orientated individuals, who have the interest and ability to understand the thoughts and feelings of others and the ability to respond to these with appropriate emotions. Strong systemizers, in turn, have a high interest in physical systems and they understand well how things work (Baron-Cohen, 2002; Baron-Cohen et al., 2005; Baron-Cohen, 2009). Baron-Cohen has suggested that strong systemizers perform well in tasks requiring spatial navigation, map reading, and solving physics problems, and they often choose occupations such as engineering and computers, which are linked to the material world.

Although systemizing and empathizing can be equally developed, among some individuals systemizing can be more developed than empathizing, or empathizing can be more developed than systemizing. In the E-S theory, a cognitive profile with poor empathizing and strong systemizing is called a systemizing "brain type", whereas a profile with strong empathizing and poor systemizing is called an empathizing "brain type" (Wakabayashi et al., 2006). It should be noted that a "brain type" is not assessed with brain measures but with a difference score between self-reported empathizing and systemizing. The "brain type" terminology has its roots in the autism research where an extreme systemizing "brain type" (i.e., extreme male "brain type") has been used to characterize the individual differences associated with the autism spectrum disorders (ASD) and especially the overrepresentation of ASD among males (Baron-Cohen, 2002).

Recent research has provided cumulative empirical evidence supporting the E-S theory, indicating that empathizing and systemizing have wide-ranging influences on cognition, interests, and hobbies in both the physical and social spheres across the typically developing population (Nettle, 2007; Svedholm-Häkkinen and Lindeman, 2016; Wright et al., 2015; Zeyer et al., 2013). Furthermore, behavioral studies have shown associations between intuitive physics abilities and self-reported systemizing in healthy adults (Lindeman and Svedholm-Häkkinen, 2016; Morsanyi et al., 2012). Additionally, at least with children, Asperger Syndrome, which represents a high-functioning form of the ASD and is characterized by high systemizing and low empathizing, is associated with better performance in intuitive physics tasks (Baron-Cohen et al., 2001; Binnie and Williams, 2003; Muth et al., 2014). These findings suggest that these differences may emerge early. Furthermore, there are some brain imagining studies showing that in the healthy population, the systemizing vs. empathizing "brain type" manifests as differences in distributed brain networks involved in cognitive control and social cognition, for instance, the cingulate gyrus, midline parieto-occipital cortex, dorsolateral prefrontal cortex, and medial prefrontal cortex (mPFC; Lai et al., 2012; Sassa et al., 2012; Takeuchi et al., 2014a, 2014b, 2013). Hence, these are candidate regions, some of which may explain how systemizers perform intuitive physics tasks.

Intuitive physics expertise can also be approached from neurocognitive functions directly involved in physical processing, such as processing of mechanistic movement and making causal inferences about moving physical objects. Performance of tasks involving, for example, predicting the direction toward which a shaky tower will fall are associated with activation of the frontoparietal network, as well as specific temporal cortex areas (Blos et al., 2012; Fischer et al., 2016; Fugelsang et al., 2005; Jack et al., 2013; Wende et al., 2013). However, the frontoparietal network is not specific to intuitive physics whatsoever; instead, this domain-independent network is required in almost any task (e.g., Duncan, 2010), and its activity is proportional to cognitive load (Owen et al., 2005). As systemizing is characterized per se by interested in physical world (Baron-Cohen, 2002; Baron-Cohen et al., 2005; Baron-Cohen, 2009) and systemizers are likely to be better in these tasks (Lindeman and Svedholm-Häkkinen, 2016; Morsanyi et al., 2012), higher systemizing could be associated with faster response times and lesser cognitive effort, reflected in activation differences in the frontoparietal network during intuitive physics tasks. Increased activation of the frontoparietal network further relates to decreased activation of the opposite network, the so-called default-mode network (Raichle et al., 2011; Fox et al., 2005; for a review see Buckner et al., 2008). That is, higher activity in this network may result in lower activity in the default-mode network, and vice versa.

However, mechanical reasoning where one must predict and simulate possible outcomes of objects presented in a picture requires also mental simulation or in other words imagining in one's mind how things move (Hegarty, 2004). In line with this argument, there is evidence that high systemizing is associated with better performance in classic mental rotation tasks that require simulation of 3D-rotation of objects in one's mind (Brosnan et al., 2010; Cook and Saucier, 2010; Zheng and Zheng, 2017). Even though there are no studies connecting mental imagery directly with altered brain functioning associated with systemizing, in general the neural mechanisms of mental rotation are well known. Especially mental rotation tasks involving non-bodily/non-biological stimuli elicit activity in the middle occipital gyrus, cuneus, and superior parietal lobule/precuneus (for a review, see Tomasino and Gremese, 2016).

Finally, while the mental simulation skills may contribute to better performance in intuitive physics tasks, success in intuitive physics may also require the use of prior knowledge of object movement (Sanborn et al., 2013) and spatial memory (Burgess et al., 2002) to support visual imagery. Spatial memory, prospection, navigation, sense of three-dimensional space, and constructing contextual situation models of visual stimuli have been associated with the parahippocampal cortex and retrosplenial cortex (Mullally and Maguire, 2011; Ranganath and Ritchey, 2012; Spreng et al., 2009). The parahippocampal system is also functionally and anatomically linked to the mental rotation system, which could explain how long-term memory representations can be utilized in performing ongoing tasks (Vincent et al., 2006; see Buckner et al., 2008 for a review).

This study aimed to resolve how systemizers perform intuitive physics tasks to provide evidence of the brain systems involved in systemizing. We first wanted to confirm that systemizers (high systemizing and low empathizing) indeed performed better in our tasks than empathizers (low systemizing and high empathizing). Then, to reveal the neural basis of differential strategies associated with systemizing and not the effects of higher task performance per se, we controlled for these performance differences in the subsequent analyses.

Converging evidence from studies focusing on systemizing vs. empathizing (Lai et al., 2012; Sassa et al., 2012; Takeuchi et al., 2014a, 2014b, 2013) and those examining intuitive physics tasks in general (Jack et al., 2013; Fischer et al., 2016) suggested that we would observe activation changes especially in the frontoparietal network and default mode network. As domain-general systems (e.g., Duncan et al. 2010) associated with task performance (e.g., Braver et al., 1997; Honey et al., 2000, see also Pessoa et al., 2002; Linden et al., 2003), some of the observed activations, especially in the frontoparietal networks, could simply reflect different cognitive demands. However, there could be also other brain areas in which activation changes are directly related to characteristic way how systemizers perform intuitive physics tasks (Takeuchi et al., 2014a). Due to the important role of the default-mode network in internalizing cognitive functions such as mental rotation (Tomasino and Gremese, 2016) as well as internalizing social information processing (Jack et al., 2013; Lai et al., 2012), we hypothesized that systemizers would rely more on this network during the performance of intuitive physics tasks than empathizers. Because activation in this network is negatively correlated with activation in the frontoparietal network it could, however, also be that lower activation of the default mode network simply reflects higher activation in the frontoparietal network and would thus be related to cognitive effort. To distinguish between these two alternatives, we separately analyzed how much the "brain type" and task performance explain of the individual variance in the frontoparietal and in the default mode network activity during performance of an intuitive physics task. Finally, due to the critical role of spatial representations in successful task performance, we expected that the parahippocampal areas supporting these functions could play a special role among systemizers (Mullally and Maguire, 2011; Spreng et al., 2009; Ranganath and Ritchey, 2012), especially because this network is putatively working together with the mental rotation system (Bucker et al. 2008).

2. Materials and methods

2.1. Participants

We recruited 38 healthy volunteers (mean age 31, range 20-46 years, 50% female) from a larger population of participants in an earlier study (Lindeman et al., 2015). We measured the participants' systemizing score using the 18-item Systemizing Quotient scale (SQ; Ling et al., 2009) and empathizing using the 15-item Empathy Quotient scale (EQ; Muncer and Ling, 2006). Then, we calculated the difference score by subtracting the SQ scores from the EQ scores and used this difference score as a continuous variable in the analysis. This variable is referred to as "brain type" in the following sections for simplicity. Recruited volunteers were chosen based on this E-S difference score. We recruited participants whose E-S scores were among the upper or lower 25% for their gender (for distribution of the brain-type scores and sex, see Fig. 1). Two participants were discarded from the analysis due to large head movement (> 3 mm) during the imaging, leaving 36 participants (19 = women) in the final sample. Men's average "brain type" was 13.06 (sd = 17.67) and women's -.48 (sd = 21.18).

2.2. Stimuli

We constructed an intuitive physics task with 28 trials and 3 practice trials. Ideas for the tasks were taken from the Intuitive Physics Test (Baron-Cohen et al., 2001) together with other sources (Kaiser et al., 1986; McCloskey et al., 1980, 1983). Every trial had a cue picture and three possible outcome pictures. The cue picture presented a situation with different kinds of objects and an arrow marking the direction of movement of an object. The outcome pictures presented three different possible outcomes of the cue picture after the movement. The task of the participants was to choose the most likely outcome from the three





possible outcome pictures as to where the objects in the pictures will end up. For example trials, see Fig. 2.

2.3. Procedure

Prior to entering the fMRI scanner, participants were briefed about the task and they completed three practice trials similar to the trials that were about to follow during scanning. Participants were notified that not all the necessary information was presented, such as the weight of the objects or the force of the movement and that their task was to deduct the most likely outcome. Trials were presented in random order. Every trial consisted of a fixation cross (1500 ms), followed by the cue picture, which was presented in the upper part of the screen in the middle (cue phase, 3000 ms). After 3000 ms presentation of the cue picture, a response phase started by presenting the three possible outcome pictures (target pictures) below the cue picture, all pictures on the screen at the same time. Immediately after presenting the three outcome options, participants were instructed to respond as soon as possible by pressing a response button corresponding to the right outcome picture. The maximum response time window after presenting the three target pictures was 12 s. Trials with no response were coded as incorrect responses. After the response, the screen went blank and there was a 6-second break (rest phase) before the next trial. To optimize the sampling of the haemodynamic response, scanning was jittered in relation to the trial onsets. The number of correct responses and response times were calculated for each participant.

2.4. fMRI parameters and analyses

Magnetic resonance imaging was done with a MAGNETOM Skyra 3.0 T (Siemens, Erlangen) scanner. Imaging parameters were: echo time 32 ms, repetition time 1.5 s, flip angle 75°, 36 slices aligned along the anterior and posterior commissures axis, slice thickness 4.0 mm and matrix size 64 × 64. Analyses were done with SPM12 software (Statistical Parametric Mapping, Wellcome Trust Center for Neuroimaging, London, UK). Functional images were realigned to the first volume via linear rotation to correct for movement and spatially normalized to Montreal National Institute (MNI) space. Co-registration of the first functional scan to the anatomical images was used and the segmentation of the anatomical pictures was done with tissue segmentation, bias correction, and spatial normalization (Ashburner and Friston, 2005). Spatial smoothing was done with an 8 mm full-width at half-maximum Gaussian kernel.

Functional time series were analyzed using a general linear model. Box-car functions were entered for *cue picture, response,* and *rest* (including the fixation period). Movement parameters were entered as confounding covariates in cases where movements larger than half a



Fig. 2. Example trial. The cue picture (upper row) was first presented alone for 3000 ms. After that, the response phase started, and three possible outcome pictures were presented below the cue picture and the participants' task was to answer which picture depicted the most likely outcome.

voxel occurred during the scanning. The fMRI data were fitted to the model and individual contrast images were calculated for group-level statistical tests. The following contrasts were calculated: cue picture > rest, response > rest, and cue picture > response to study activations during the different phases of the task. We used the difference score of E-S ("brain type"), sex, and average response time as regressors in the models to isolate the related effects and to control for the potential confounding variables.

In the group-level analysis, we used FWE corrected threshold p <.05 (cluster extend 15). For the regression analyses, we used a priori defined (Tomasino and Gremese, 2016), anatomical ROIs of middle occipital gyrus, cuneus, superior parietal lobule/precuneus, and parahippocampal region that were based on the Automated Anatomical Labeling atlas (Tzourio-Mazoyer et al., 2002). These ROI analyses were FWE corrected with threshold of p < .05 at the voxel-wise level to the volume of ROI. Furthermore, we extracted average signal change in the three main hubs that are sensitive to general physical information processing (Jack et al., 2013) and are part of the frontoparietal network. We extracted the average signal changes from 10 mm spheres centered at each of the peak coordinates of these three areas: superior frontal sulcus, lateral prefrontal cortex, and anterior intraparietal sulcus. The uncorrected average signal change of each of these areas were then correlated to the behavioral measurements of "brain type" and task performance (response time and number of correct answers).

3. Results

3.1. Behavioral results

To study associations of "brain type", reaction time, and correct responses, we used partial correlation analysis controlling for sex. Although men (M = 18.78, SD = 3.30) had more correct responses than women (M = 14.31, SD = 3.70), F(1.35) = 11.01, p = .002, the number of correct responses was strongly associated with "brain type" (r = .47, p = .009) also after controlling for sex. Thus, in line with our hypothesis, systemizing "brain type" was associated with better performance in the intuitive physics task, even after controlling for sex and the average response time. Regarding the response times, there was a trend that men (M = 5.0 s, SD = .96) responded faster than women (M = 5.48 s, SD = .87) F(1.35) = 2.45, p = .126, and after controlling for sex, there was a trend for faster response time for the systemizing "brain type" (r = -.27, p = .112).

4. fMRI results

4.1. Neural basis of intuitive physics task: cue phase > rest and response phase > rest comparisons

To test the activation differences during different phases of the task, we compared the three conditions: (i) the cue phase, where only the cue picture showing the starting situation and direction of movement was presented, (ii) the response phase, when response options were presented together with the cue picture and participants gave answers, and (iii) the rest phase that followed each experimental trial. In the cue phase of the task (*cue picture* > *rest*) activity was enhanced in the frontoparietal network, and in the visual areas, thalamus, left insula, and hippocampus (Table 1, Fig. 3). The inverse comparison (*rest* > *cue picture*, Supplementary Table 1), showed activity in the mPFC, PCC, and bilateral angular gyri, indicating that the activity in these areas was increased during the rest. Similarly to the cue phase, during the response phase (*response* > *rest*), we observed large activation clusters in the

frontoparietal network together with large bilateral activation clusters in the visual areas and cerebellum (Table 1, Fig. 3). The inverse contrast (*rest* > *response*) did not reveal any activations.

4.2. Neural basis of intuitive physics task: cue picture > response phase comparison

Comparison between *cue picture* > *response phase* showed that cues elicited stronger activations in the middle and inferior occipital gyri, lingual, fusiform gyrus, superior parietal gyrus, middle frontal gyrus, and precentral gyrus. In the response phase (*response phase* > *cue picture*) we observed activations spreading from the PCC in posterior axis to the cuneus and precuneus, and anterior axis to the middle cingulum, ACC and to mPFC. There were also activations in the right middle frontal gyrus, thalamus, and superior temporal gyrus (Table 1, Fig. 3).

4.3. Regression analysis with systemizing "brain type" as a covariate (controlling for response time and sex)

During the cue picture (*cue picture* > *rest*) a higher systemizing "brain type" was associated with higher activation of the left parahippocampal region/lingual gyrus spreading towards the hippocampus, posterior cingulate/precuneus, and cuneus (Table 2, Fig. 4). When the cue picture and response phase were compared (*cue picture* > *response phase*), a higher systemizing "brain type" was associated with stronger activations in the bilateral cuneus, right middle occipital gyrus, and left parahippocampal region spreading towards the lingual gyrus and hippocampus (Table 2). There was also a non-significant trend activation in the right parahippocampal region (p = .067), and precuneus (p = .076) that did not survive FWE corrections (Fig. 4). In the response phase > rest comparison lower systemizing was associated with higher activation in the left inferior parietal lobule and left middle frontal gyrus.

To further examine the associations of the observed activations and task performance, we extracted the average activations of the peak voxels of these clusters (no FWE-correction, controlling for sex). Then, we studied the associations between the systemizing "brain type", the peak voxel activations and two aspects of the task performance (the number of correct answers and response time) with partial correlations. Comparison of the cue picture > rest showed that activations of PCC (r = .44, p= .009), parahippocampal region (r = .34 p = .049), and cuneus (r =.39, p = .023) were associated with the higher systemizing even after controlling for both, response time and the number of correct answers. In contrast, when "brain type" was controlled, there was no association between the number of correct answers nor the response time with the peak voxel activations in these areas. Similarly, in the cue > response comparison, the activations of PCC (r = .44, p = .009), parahippocampal region (r = .34 p = .047), middle occipital gyrus (r = .38, p =.026), and cuneus (r = .43, p = .011) were associated with the systemizing "brain type" after controlling for response time and number of correct answers. In contrast, when "brain type" was controlled, there was only one significant association between brain activity and task performance: higher activation in the middle occipital gyrus was associated with faster response time (r = .-34, p = .048). In the response phase > rest comparison, after controlling for response time and number of correct answers, lower systemizing was associated with both, activation of the left middle frontal gyrus (r = .-63 p < .001) and activation of the left inferior parietal lobule (r = .-57 p < .001). Neither reaction times nor numbers of correct answers were associated with these activations when "brain type" was controlled.

Table 1

Activations during the cue phase and response phase contrasted with each other or with the rest condition.

Anatomical region	х	У	Z	t-value	n of voxels	p-value
$Cue \ picture > rest$						
Lingual gyrus (left)	-8	-82	-10	18.01	32,548	>.000 ^a
Inferior temporal gyrus (left)	-42	-70	-4	17.00	*	>.000 ^a
Inferior parietal Lobule (right)	34	- 46	54	16.91	*	>.000 ^a
Putamen (right)	28	20	4	12.30	186	>.000 ^a
Superior frontal gyrus (left)	-36	52	18	11.20	51	>.000 ^a
Thalamus/hippocampus (left)	-22	-30	0	10.53	150	>.000 ^a
Posterior cingulate (left)	-12	- 22	8	9.01	*	$> 000^{a}$
Thalamus (right)	10	-16	4	10.05	120	$> 000^{a}$
Thalamus (right)	16	- 28	0	9.73	*	> 000 ^a
Middle frontal gyrus (right)	48	36	24	9.84	249	> 000 ^a
Middle frontal gyrus (right)	36	26	32	8.31	*	> 000 ^a
Middle frontal gyrus (left)	-40	50	2	9 79	46	> 000 ^a
Insula (left)	- 30	20	2	9.45	124	> 000 ^a
Putamen (left)	-14	2	10	916	36	$> 000^{a}$
Putamen (right)	14	2	8	8 71	33	$> 000^{a}$
Response phase $>$ rest	11	-	0	017 1		- 1000
Cupeus (right)	10	- 86	8	10.49	8641	> 000ª
Cuncus (right)	4	- 98	-2	10.15	*	> 000 ^a
Cerebellum (right)	8	-70	-12	10.04	*	> 000 ^a
Inferior Parietal Lobule (right)	50	- 48	46	9.20	3645	$> 000^{a}$
Postcentral gyrus (right)	50	- 32	56	8 97	*	> 000 ^a
Angular ovrus (right)	40	-68	32	7 20	*	$> 000^{a}$
Insula (right)	38	20	-12	8 97	679	> 000 ^a
Inferior frontal operculum (right)	56	14	2	7.02	*	$> 000^{a}$
Incula (right)	30 46	14	2	6.14	*	> 000 ^a
Inferior temporal gurus (right)	52	-54	-16	8 10	618	> 000 ^a
Dosterior Cingulate (right)	28	- 59	e 10	8.03	*	> 000 ^a
Superior temporal gurus (right)	20 56	-08	-10	0.03 7.19	*	>.000
Dostcentral gyrus (left)	- 38	-40	58	7.10	2440	$> 000^{a}$
Inferior parietal lobule (left)	- 46	-48	50	7.94	*	> 000 ^a
Superior parietal lobule (left)	- 32	-50	62	7.18	*	≥.000 001ª
Middle frontal gyrus (right)	44	32	32	7.10	840	$> 000^{a}$
Middle frontal gyrus (right)	40	54	2	7.60	*	> 000 ^a
Middle frontal gyrus (right)	40	42	26	7.00	*	>.000
Post central gyrus (left)	- 50	-20	18	7.03	410	$> 000^{a}$
Post central gyrus (left)	- 50	- 20	22	7.71	*	> 000 ^a
Middle operinital gyrus (left)	-02	-20	10	7.47	205	> 000ª
Middle occipital gyris (left)	- 20	-54	12	7.47	*	>.000
Fusiform gurus (left)	- 39	- 42	2 	5.00	*	.001 011a
Middle frontal group (left)	- 38	42	16	7.49	215	$> 000^{a}$
Middle frontal gyrus (left)	- 34	54	16	6.65	*	>.000
Middle frontal gyrus (left)	- 36	50	-4	6.25	*	.002 005ª
Middle frontal gyrus (left)	-44	-32	30	6.77	215	> 000 ^a
Middle frontal gyrus (left)	-34	54	16	6.65	*	>.000
Middle frontal gyrus (left)	- 36	50	-4	6.25	*	.002 005 ^a
Middle frontal gyrus (left)	-44	32	30	6.77	199	001 ^a
Middle frontal gyrus (left)	- 44	26	38	6.49	*	003 ^a
Cingulate gyrus	2	-10	50	6.48	133	003 ^a
Insula (left)	-34	20	-6	6.27	172	.005 ^a
Insula (left)	-44	14	-4	5.98	*	009 ^a
Insula (left)	- 32	12	4	5.75	*	016 ^a
Paracentral lobule (right)	2	- 26	78	5.94	39	010 ^a
Superior medial frontal gyrus (right)	2	26	40	5.61	40	023 ^a
Cingulate gyrus (right)	6	18	34	5.36	*	041 ^a
Cue picture > response phase	0	10	01	0.00		1011
Lingual gyrus (left)	-8	- 82	-8	18.38	46.378	>.000 ^a
Superior occipital gyrus (left) / cuneus	-14	- 88	10	16.28	*	>.000 ^a
Inferior temporal gyrus (left)	- 42	- 68	-4	15.86	*	$> 000^{a}$
Insula (right)	30	20	4	8 66	146	$> 000^{a}$
Thalamus (right)	16	- 28	4	8 57	132	> 000 ^a
Thalamus (right)	10	-16	4	6.38	*	.005 ^a
Thalamus (right)	14	-20	10	5.89	*	.017 ^a
Thalamus (left)	-22	- 30	0	8.44	174	>.000 ^a
Thalamus (left)	-14	-24	6	6.43	*	.005 ^a
Thalamus (left)	-12	-14	8	6.13	*	.010 ^a
Middle frontal gyrus (left)	-40	50	2	5.80	150	>.000 ^a
Middle frontal gyrus (left)	-34	52	16	7.43	*	>.000 ^a
Inferior frontal syrus (left)	- 46	40	12	6.28	22	007 ^a
Response phase $>$ cue picture	10	10		0.20		
Cerebellum (left)	-36	-56	- 30	15.16	47.040	>.000 ^a
	**	**				

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Table 1 (Continued)

Anatomical region	x	у	Z	t-value	n of voxels	p-value
Fusiform gyrus (left) Lingual gyrus (right) Cuneus (left) Thalamus (left)	-46 6 -14	-50 -68 -10	-20 -10 10 0	15.14 15.08 9.17 8.70	* * 142 75	$>.000^{a}$ $>.000^{a}$ $>.000^{a}$
Middle frontal gyrus (right) Caudate nucleus (right) Thalamus (right) Superior temporal gyrus (right)	26 12 16 44	- 24 44 - 6 - 6 - 22	-10 16 6 10	8.79 8.45 7.90 7.47 7.82	73 18 39 * 34	>.000 ^a >.000 ^a >.000 ^a >.000 ^a

* Peak activation voxel part of the above cluster.

^a FWE-corrected to the whole brain volume (p = .05).



Fig. 3. Upper row: A and B = cue picture > rest comparison, C and D = response phase > rest comparison. Both the cue picture > rest and response phase > rest comparisons activated large-scale frontoparietal networks and areas in the occipital/temporal cortex. In the rest > cue picture (pictures A and B) the rest phase showed stronger activations in PCC, mPFC, and bilateral angular gyri (p = .001 unc. for visualization). **Lower row**: The cue picture > response phase comparison (red) showed activations in the visual areas, superior parietal gyrus, middle frontal gyrus, and in the left precentral gyrus bilaterally. In the response phase, in contrast to cue picture (blue), there were activations in the PCC, mPFC, and bilateral angular gyri (p = .001 unc. for visualization). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

4.4. Correlations between the average signal changes in the areas involved in physical processing, the systemizing "brain type", and task performance

During the cue phase (*cue picture* > *rest*), there was an association between slower response time and higher activation of the intraparietal sulcus ($r - .41 \ p = .008$, controlling for "brain type"). No association between the "brain type" and activations of the frontoparietal network were found in this comparison when we controlled the task performance (response time and number of correct answers).

During the response phase (*response phase* > *rest*) the higher average signal change in the intraparietal sulcus was associated with lower systemizing (r = -.46, p = .006), and there was a negative trend between this activation and the number of correct answers (r = -.33, p = .051). When task performance (response time and number of correct answers) was controlled, the association between "brain type" and intraparietal sulcus activation was no longer quite significant (r = -.32, p = .064). However, also the trend between the number of correct answers and activation of intraparietal sulcus dropped to non-significant when "brain type" was controlled (p = .776).

In the comparison between the cue picture and response phase (*cue picture* > *response phase*) controlling for the "brain type", higher activation of the intraparietal sulcus was associated with slower response time (r = -.44, p = .008). When response time and number of right answers were controlled for, "brain type" had no significant associations. However, lower systemizing was associated with higher activation in the intraparietal sulcus when controlling only for response time (r = -.42, p = .011).

Finally, we examined the associations between the found peak activations of the PCC, parahippocampal region, middle occipital gyrus, and cuneus and the average activations of the frontoparietal ROIs to clarify the potential anti-correlations of the activations related to the DMN-network and the frontoparietal network. In the *cue picture* > *rest* comparison only one positive association was found between the lateral prefrontal activation and the parahippocampal region activation (r = .44, p = .007). Similarly, in the *response phase* > *rest* comparison, the only found association was between the lateral prefrontal cortex activation and the parahippocampal region (r = .42, p = .010).

4.5. Regression analysis with sex and response time as covariates

In addition to analyses controlling for sex and response time, we performed separate analyses where we isolated the effects of sex and response time by controlling for the systemizing "brain type" and the other measure (either response time or sex, respectively). These results can be found in Table 2.

5. Discussion

In the current study, we investigated how individual differences in systemizing and empathizing "brain types" reflect on brain activity during the performance of intuitive physics tasks. The intuitive physics task, dealing with various objects and different kinds of movement, activated the frontoparietal network, which has also previously been linked to the processing of physical information (Fischer et al., 2016; Fugelsang et al., 2015; Jack et al., 2013). However, the activation

Table 2

Results of the regression analysis when systemizing "brain type" was used as a covariate (controlling for sex and response time) and regression analysis with sex and response time controlling for each other and the systemizing "brain type".

Anatomical region	x	У	Z	t-value	n of voxels	p-value			
Systemizing brain type as a covariate: cue picture > rest									
Higher activations associated with higher systemizing brain type									
Cuneus (left)	-6	-80	22	4.10	154	.017 ^b			
Parahippocampal region (left)	-18	-40	-8	4.88	206	.005 ^b			
Lingual guris (left)	-14	-44	-10	4.64	*	.010 ^b			
Posterior cingulate (left)	-4	-52	12	4.35	151	.037 ^b			
Precuneus (right)	12	-50	14	4.25	88	.047 ^b			
Systemizing brain type as a covariate: cue picture > response	se phase								
Higher activations associated with higher systemizing brain type									
Cuneus (right)	16	-84	18	4.03	346	.033 ^b			
Cuneus (left)	-6	-80	22	3.96	*	.038 ^b			
Middle occipital gyrus (right)	20	-82	18	3.88	37	.043 ^b			
Parahippocampal gyrus (left)	-18	-48	-10	5.10	511	.002 ^b			
Systemizing brain type as a covariate: response phase > rest									
Higher activations associated with lower systemizing brain type									
Middle frontal gyrus (left)	- 46	12	46	5.68	354	.001 ^a			
Supramarginal gyrus (left)	- 40	-48	34	5.63	1209	.021 ^a			
Inferior parietal lobule (left)	- 44	-54	56	5.43	*	.035 ^a			
Sex as a covariate (higher activation for women): Cue pictur	re > response phase								
Superior parietal lobule (right)	32	-50	60	5.98	687	.009 ^a			
Sex as a covariate (higher activation for men): Cue picture > response phase									
Cuneus (left)	-16	-82	38	4.04	22	.032 ^a			
Sex as a covariate (higher activation for men): Cue picture > rest									
Cuneus (left)	-14	-80	38	5.02	73	.004 ^b			
Precuneus (left)	-10	-76	40	4.28	21	.044 ^b			
Response time as a covariate (higher activation for faster response)									
Cue picture > rest									
Supplementary motor area (left)	-8	8	58	6.46	2684	.004 ^a			
Inferior frontal gyrus (right)	46	16	4	5.63	570	.029 ^a			
Response time as a covariate (higher activation for faster response): Cue picture > response phase									
Supplementary motor area (left)	-12	4	62	6.64	2043	.002 ^a			
Middle frontal gyrus (left)	-32	-4	44	5.86	*	.012 ^a			
Inferior parietal lobule (right)	32	-48	54	5.52	549	.028 ^b			
Cuneus (left)	-24	-90	28	3.86	41	.045 ^b			
Cuneus (right)	22	-92	24	3.83	157	.048 ^b			
Precuneus	-16	- 48	58	4.13	130	.049 ^b			

* Peak activation voxel part of the above cluster.

^a FWE-corrected to the whole brain volume (p = 0.05).

^b FWE-corrected to the volume of ROI (p = 0.05).



Fig. 4. Brain activity resulting from regression analysis with the "brain type" as a covariate. In the cue picture > rest comparison (red) higher systemizing "brain type" was associated with higher activation of the cuneus/precuneus, and left parahippocampal region. The latter activation cluster was spread from lingual gyrus and parahippocampal region to hippocampus. In the cue picture > response phase comparison (yellow) higher systemizing "brain type" was associated with higher activations in the cuneus, middle occipital gyrus, and left lingual/parahippocampal area spreading to hippocampus. (p = .005 unc. for visualization). The mPFC activations did not survive FWE-corrections. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

changes in these circuitries during task performance were not specifically associated with systemizing. Instead, the higher activation of the frontoparietal network was associated mostly with task performance and to some extent with lower systemizing. This suggests that for higher systemizers, the task may have required less cognitive effort than for lower systemizers. We also found that systemizing was associated with higher activation in the areas related to default mode network (PCC, cuneus) and in the parahippocampal region. Even though the task performance may have explained some of the variance of these activations, these associations were statistically non-significant. Thus, these areas were clearly more strongly related to higher systemizing "brain type" than mere task performance. This was also supported by the finding showing no negative associations between DMN-regions and the activations in the frontoparietal network. This indicates that systemizers not only performed better, but also used a characteristic way of performing the intuitive physics task. Both the nature of our tasks, as well as extensive evidence on the functional roles of the regions specifically associated with systemizing "brain type" support that this distinguishing feature could be related to utilizing mental imagery as well as long-term spatial representations during the task. In addition, the results hint how systemizers may use these different cognitive brain functions at different stages of the task, suggesting possible mechanisms of *why* systemizers are able to perform so well in intuitive physics tasks and *how* they perform the tasks.

5.1. Altered function of the internalizing system during intuitive physics task and cognitive effort

Higher systemizing was associated with higher task-related brain activity in the cuneus, middle occipital gyrus and precuneus/PCC. As these regions partly belong to the DMN (Buckner et al., 2008) and their activations could simply reflect lower effort related to task performance, we separately analyzed activations in these regions in relation to systemizing "brain type" by controlling for task performance. Our results clearly showed that in each of these regions, brain activation during the task was associated with systemizing when task performance differences were accounted for. To be more precise, in the precuneus/PCC, systemizing explained about four times more of the variance in brain activation than task performance. We therefore interpret that our results clearly indicate a different way of processing associated with systemizing that goes beyond the higher task performance. This argument is further supported by the finding that there were no anti-correlations between these DMN-regions and the frontoparietal network. Previous studies have demonstrated that greater cuneal and precuneal activity predicts vividness of mental imagery and individual performance in a mental rotation task (Logie et al., 2011). Cuneus and middle occipital gyrus activations contribute, among other visual processing, especially to mental rotation of non-bodily/non-biological stimuli (Tomasino and Gremese, 2016). Hence, our findings together with these earlier findings suggest that performance of the intuitive physics task among systemizers may rely more on mental imagery than among empathizers.

The altered activity in the cuneus/precuneus was observed already during the cue phase of the task before any information about the possible solutions was given. This could mean that the systemizers began to simulate potential outcomes immediately after the presentation of the cue picture. This interpretation is supported by the finding that, in the analysis across all participants, the precuneus activity was weaker during the cue phase, followed by increased activity during the response phase. Furthermore, in addition to systemizing, cuneal/precuneal activity was modulated by response time suggesting that faster responses could have been associated with the use of mental simulation in the earlier stage of the task.

Even though the current results indicate altered function of the precuneus and cuneus during the intuitive physics task, this study cannot fully distinguish between the various functions associated with these regions. Future studies could aim to segregate in greater detail among the strategies or subfunctions utilized in the intuitive physics tasks and examine role of cognitive effort in even greater detail. Even though the default-mode network activations were not associated with task performance in the present study, the strong functional connection between these areas (e.g., Fox et al., 2005) suggests that the observed DMN activity is likely to reflect some functions associated with frontoparietal networks that we are not able to define more accurately without knowing exactly what strategies the participants have used. Disentangling the functional roles of the frontoparietal and default-mode networks could have also benefited of a baseline obtained from a separate resting state measurement or from more detailed analysis of the activation-deactivation cycles that could have been done if the length of the resting period had been varying. The interest for studying the role of precuneus/cuneus in relation to systemizing in greater detail is further enhanced by the several studies linking these areas directly to systemizing (Sassa et al., 2012; Lai et al., 2012; Takeuchi et al., 2013, 2014a, 2014b) and because of the suggestions that the precuneus/cuneus is a potential neural marker of autism that is closely related to extreme systemizing (Just et al., 2014).

5.2. Activity in areas supporting long-term memory representation

Together with activations in the cuneus and precuneus, systemizing was also associated with activations in the parahippocampal region. As part of the hippocampal system, this area plays a key role in several functions relying on long-term memory representations. Some examples of functions relevant to intuitive physics include making gist-based contextual associations (Bar, 2004; Bar and Aminoff, 2003), retrieval of spatial-location information, recognition of objects previously presented in a scene (Hayes et al., 2007, 2004), and episodic autobiographical imagery (Gardini et al., 2006). Similarly to the activations in the default-mode network, the parahippocampal activations were not associated with task performance, but to systemizing brain type specifically. We therefore suggest that the enhanced parahippocampal activity among systemizers during the intuitive physics task may reflect utilizing long-term spatial memory representations during the task. Our results further suggest that access to this system is obtained in systemizers immediately when they perceive the cue that triggers the system for mental simulation. Via its close links to the cuneus, as part of the system involved in mental imagery, the parahippocampal area may further contribute to the efficient utilization of mental imagery.

5.3. Contributions to E-S theory and future directions

Our findings showed that a higher systemizing "brain type" was associated with better performance in the intuitive physics task in a healthy adult population. The results are in line with the basic tenets of E-S theory (Baron-Cohen et al., 2005; Baron-Cohen, 2009) and earlier empirical studies (Carroll and Chiew, 2006; Cook and Saucier, 2010; Lindeman and Svedholm-Häkkinen, 2016; Ling et al., 2009; Morsanyi et al., 2012).

The E-S theory suggests that systemizing and empathizing are to some extent inherited and develop already during the prenatal period (e.g., Baron-Cohen, 2002, 2009). Among adults, however, systemizing and empathizing are assessed with EQ and SQ self-reports that reflect subjective interests and only self-evaluated abilities. Therefore, an important question is to what extent the differences found in abilities between empathizers and systemizers are only related to different interests that have gradually driven systemizers, for example, to acquire better abilities in intuitive physics by learning. In other words, are there also other factors, on top of interests and experience, that leads to different abilities between empathizers and systemizers? Our results cannot comprehensively answer this question. However, because our results suggest the possibility that systemizers may engage in the intuitive physics task faster, with less cognitive effort, and begin and use the mental simulation with less information than empathizers, one explanation that require further examination is that systemizers have a tendency to relate to the physical world with the internalizing system of mental imagery and simulation. On this account, it is the use of this system that enhances the systemizers' performance in intuitive physics task, which is not only related to higher task performance gained through greater amount of experience. However, if use of the internalizing system is a factor that is distinct to systemizers' even above the superior performance on intuitive physics tasks, systemizers are likely able to use this system even on tasks of which they have no experience. To increase our understanding of these processes, future studies should control for cognitive effort and could examine how the performance strategies utilized by systemizers differ from those utilized by empathizers in novel tasks where experience can be controlled. This could be the key to understanding the fundamental difference between how people with a strong systemizing profile and those with an empathizing profile view the world: tasks and situations which, for some of us, look difficult, evoke an effortless simulation in others.

Uncited reference

(Constantinidis and Klingberg, 2016).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuropsychologia.2017.11.030.

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