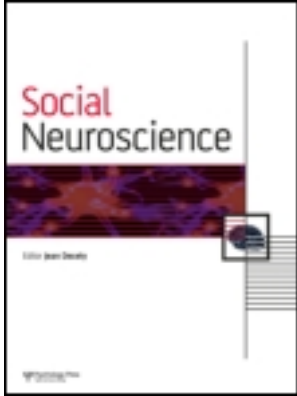


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Cortical mechanisms of pretense observation

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Pretend play emerges in children the world over around 18 months and continues into adolescence and even adulthood. Observing and engaging in pretense are thought to rely on similar neural mechanisms, but little is known about them. Here we examined neural activation patterns associated with observing pretense acts, including high-likelihood, low-likelihood, and imaginary substitute objects, as compared with activation patterns when observing parallel real acts. The association between fantasy predisposition and cortical representations of pretense was also explored. Supporting prior research that used more limited types of pretense, observed pretense acts, when contrasted with real acts, elicited activity in regions associated with mentalizing. A novel contribution here is that substitute object pretense (high- and low-likelihood) elicited significantly more activity than imaginary (pantomime) acts not only in theory of mind regions but also in the superior parietal lobule, a region thought to aid in the prediction and error-monitoring of motor actions. Finally, when high-likelihood pretense acts were contrasted with real acts, participants with elevated fantasy predispositions evidenced significantly different activation patterns than their more reality-prone peers. Future research will explore the intersection of fantasy predisposition and experience with the neural representation of pretense.

Keywords: Pretend play; Biological motion; Theory of mind; Fantasy orientation.

Pretend play is the “voluntary transformation of the here and now, the you and me, and the this or that, along with any potential action that these components of a situation might have” (Garvey, 1990, p. 82). Children the world over begin to pretend between 18 and 24 months old (Eibl-Eibesfeldt, 1989; Tamis-LeMonda & Bornstein, 1994), with the capacity to recognize others’ pretend acts emerging at 2–3 years of age (Harris & Kavanaugh, 1993; Ma & Lillard, 2006; Nishida & Lillard, 2007; Tomasello, Striano, & Rochat, 1999).

Pretense requires that observers go beyond visible information to interpret what a pretender is doing. In this vein, Bateson (1972) noted that the playful nip is not a bite, thereby implying one must not only represent a “real” bite but also discriminate a real bite from one done in the course of play (i.e., a “nip”).

If this discriminatory process is unsuccessful, the consequences could be grave: Harmless play could be met with serious injury. Although it concerned animal behavior, Bateson’s observation holds for interpreting human pretense as well: If one pretends a banana is a telephone and the observer does not ascertain the pretend nature of the action, the observer may come away believing bananas *are* telephones, a mistake that Leslie terms “representational abuse” (Leslie, 1987, p. 415). In the current study, we ask what brain systems undergird the discriminatory process that prevents representational abuse.

To inform this question, we begin by presenting a conceptual structure for discriminating pretend acts from their real counterparts: Theory of Mind (ToM). Next, we discuss varying forms of pretense and the importance of considering them simultaneously via a

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balanced empirical design. Finally, we present evidence supporting an individual differences approach to studying the cortical mechanisms of pretense.

Individuals who understand that others have different beliefs, intentions, and desires are said to have a ToM, a conceptual structure well investigated from developmental (Astington, Harris, & Olson, 1988; Wellman, 1990; Wellman, Cross, & Watson, 2001) and neurological perspectives (Carrington & Bailey, 2009; Frith & Frith, 1999; Gallagher & Frith, 2003; Saxe & Kanwisher, 2003). To illuminate how pretense and ToM might be related, consider the behavior of two children who both hop up and down like a kangaroo, yet with only one of them intending to represent a kangaroo. Examining similar situations, Lillard (1993, 1998, 2001) stipulated that concordant behavior alone is not sufficient for an action to be pretense; rather, an added intentional component is required. Children as young as 3 years old at least implicitly appreciate pretender intention: They faithfully imitate pretense acts, but do not copy mistaken ones (Rakoczy, Tomasello, & Striano, 2004; also see Joseph, 1998). Leslie (1987, 1994, 2000) even suggested pretense and ToM rely on the same cognitive architecture: a single neural mechanism that represents mental representations. Supporting this possibility, ToM and pretense are correlated in the preschool years (Astington & Jenkins, 1995; Lalonde & Chandler, 1995; Taylor & Carlson, 1997; Taylor, Carlson, Maring, Gerow, & Charley, 2004). Longitudinal studies have also shown relationships between ToM and pretend play (Jenkins & Astington, 2000; Youngblade & Dunn, 1995), again suggesting pretense interpretation could rely on the same cognitive structures as ToM.

Neuroimaging is a more direct way to address whether pretending and ToM are supported by the same cortical structures. Four research groups have attempted to examine this in neurotypical adults (German, Niehaus, Roarty, Giesbrecht, & Miller, 2004; Meinhardt, Kühn-Popp, Sommer, & Sodian, 2012; Schubotz & von Cramon, 2009; Whitehead, Marchant, Craik, & Frith, 2009). The first three of these (published in 2004 and 2009) focused on pretend acts involving substitute and/or imaginary objects.

Reading a pretense action requires understanding what the pretender intends, and the objects used in the pretense can scaffold this understanding. Pretense can be object-free: pantomiming an action using an imaginary object. Alternatively, it can involve substitute objects ranging from exactly like, to not at all like the intended referent in form and/or function. Thus, there are numerous forms of pretense one might address, with examination of any one form providing only partial information about the activity as a whole.

Moreover, different forms of pretense present unique demands on observers. Many studies have shown that the more similar a pretense substitute object is in form and function to the intended referent, the more easily one can pretend with it and understand its pretend use in others (Elder & Pederson, 1978; Fein, 1975; Hopkins, Smith, & Lillard, 2013; Jackowitz & Watson, 1980; Pederson, Rook-Green, & Elder, 1981; Watson & Jackowitz, 1984). Objects similar in form and/or function to a referent are thus high-likelihood pretense substitute objects.

Existing neuroimaging studies of pretense differed in how they used objects in enacting pretense. German et al. employed two types of clips: (1) actors performing real actions with real objects (pouring tea into a cup) and (2) actors performing pretend actions with the real object present or absent. Half of the clips ended before the actions were complete, and participants' judged if each clip was complete. Whitehead et al. used clips of real actions with typical objects (e.g., write with a pen), real actions with unusual objects (e.g., scratch back with a pen), and pretend actions with substitute objects (e.g., smoke a "cigarette" with a pen). Importantly, during pretend actions the actor displayed a "play face" and exaggerated body language (C. Whitehead, personal communication, 23 April 2013). After each trial, participants were asked to either state how objects were used in the preceding clips or required to say "use" (p. 371). Finally, Schubotz and Von Cramon showed participants clips of only a pair of hands carrying out real or pretend actions with stimuli that varied with respect to whether a switch occurred. Three forms of switch trials were used: (1) *object switch* trials involved the same category of objects across two trials, but modified their form (e.g., a pen was used to write, then a different pen was used to write); (2) *manipulation switch* trials involved the identical object used in two different manners (e.g., a pen was used to write, then a cap was placed on the same pen); and (3) *goal switch* trials involved two unique objects and two unique goals (e.g., a pen was used to write, then a knife was used to cut). Action descriptions were provided (e.g., "closing pen"), and participants decided whether this description was consistent or inconsistent with the clip just viewed.

In two of these studies, viewing pretense acts was associated with activity in regions commonly associated with ToM, such as the medial prefrontal cortex (mPFC), superior temporal sulcus (STS), and lateral prefrontal regions (BA 44, 47; German et al., 2004; Whitehead et al., 2009). In contrast, Schubotz and Von Cramon (2009) documented heightened activation principally within regions associated with the

mirror neuron system (Rizzolatti & Craighero, 2004). These discrepant results, as Schubotz and von Cramon acknowledged (p. 651), likely arose from the considerable differences in experimental design between the respective studies.

However, even the first two studies failed to control the objects used across tasks, and their results could therefore at least partially be a function of object substitution types. Recall that German et al. (2004) used mimed actions with the standard objects present or absent. Whitehead et al. (2009) incorporated only substitute object pretense, but with widely varying stimuli: Some objects differed from their referents in form and function (e.g., pen as an airplane), others in function alone (e.g., banana as a telephone), and still others subtly differed in form alone (e.g., penknife as a sword). Stimuli were also unbalanced; that is, each object did not appear in each stimulus category (i.e., a pen was used as if it were a cigarette, but neither an actual cigarette nor an actual pen appeared elsewhere). Finally, Schubotz and von Cramon (2009) also included substitute object pretense and varied whether substitute objects differed with respect to the referent in form alone or both form and function, but neither incorporated pantomime acts nor showed the activity in a representative manner. To our knowledge, no prior study has included all forms of pretense while maintaining a balanced empirical design with each object appearing once in each stimulus category.

Meinhardt et al. (2012) conducted the fourth neuroimaging study of pretense. These researchers used event-related potentials, and rather than focusing on substitute objects, they asked subjects to reason about causes of behavior; results suggested that false belief is neurally distinct from pretense both in the timing and location of response. Clearly more research is needed to better understand the neural underpinnings of pretense.

An additional issue that has not yet been examined is how the neural representation of pretense might differ according to individual differences in imaginative predisposition. Although Piaget (1962) and Vygotsky (1978) asserted that pretending ceases around school age (but see Turner, 1982), recent work by Smith and Lillard (2012) demonstrated that child-like pretense continues on average well into middle childhood, and that some people even continue to pretend into adulthood. At issue is whether such individual differences might be associated with differences in the neural signatures of pretense observation. Expertise is generally associated with neural efficiency. Thus, individual differences in frequency of fantasy behaviors in adulthood might interact with strength of neural activation while observing pretense acts.

In sum, although neural correlates of observing pretense have previously been investigated, protocols have been limited in scope, focusing on select forms of pretense rather than all varieties of the activity simultaneously. Moreover, an attempt to capture interindividual variation in fantasy orientation and explore how it affects representation of pretense acts at a neural level has not been made. The present study addresses both of these issues using a balanced stimuli set. Specifically, we ask: (1) Do pretense acts, when compared to their real counterparts, evoke significantly heightened responses in brain regions associated with ToM? (2) Do different forms of pretense evoke unique neural responses? (3) Do individual differences in fantasy proneness influence the neural representation of observed pretend acts?

METHOD

Participants

Participants were 19 adults (11 female, 8 male, $M_{\text{age}} = 22.05$, age range: 18–29) recruited from the community who were compensated for their participation. An additional two participants were recruited, but their data were excluded due to excessive head movement. All participants provided written informed consent in accordance with the guidelines set by the Institutional Review Board for Health Sciences Research at the University of Virginia.

Materials and design

A series of video clips of a male actor performing 18 actions were recorded with a Sony DCR-HC26 camera and digitally converted and edited in iMovie (Apple Computer, Cupertino, CA). For each of the 18 actions, four clips were filmed: *Imaginary (I)*, *Pretend with a Low-Likelihood Substitute Object (PLS)*, *Pretend with a High-Likelihood Substitute Object (PHS)*, and *Real (R)*; see Figure 1). Likelihood was operationalized as structural similarity to the intended referent (e.g., a comb has “teeth” like a saw, thus is a more likely substitute than a spoon). In *R* clips, the actor used the target object (e.g., saw) to carry out the intended action (e.g., cutting a 2'' × 4''). *PHS* clips included an object similar in form (e.g., comb) to the intended target object (e.g., saw) and showed the actor pretending to carry out the intended action (e.g., cutting a 2'' × 4''). *PLS* clips included an object dissimilar in form (e.g., spoon) to the intended

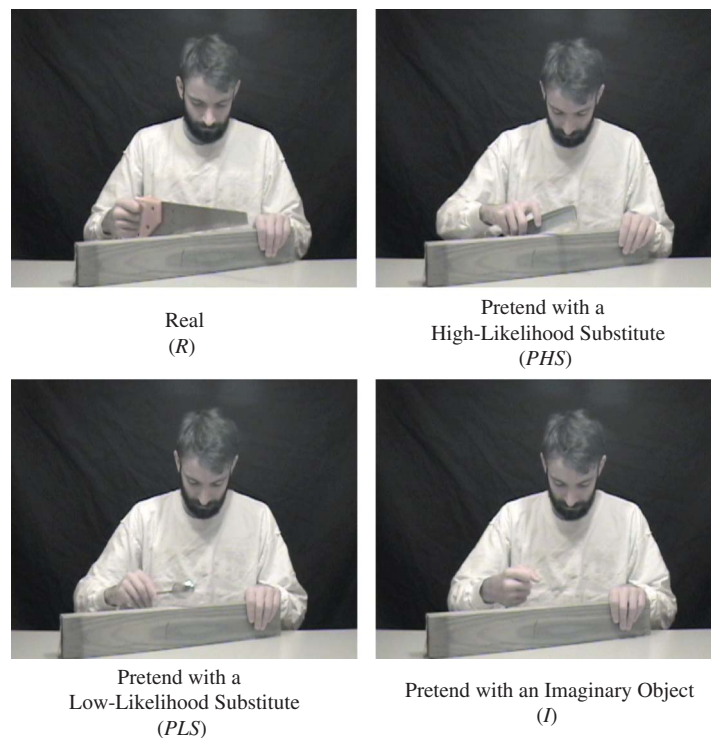


Figure 1. Four types of clips used throughout the study.

target object (e.g., saw) and showed the actor pretending to carry out the intended action (e.g., cutting a 2'' × 4''). For *I* clips, the target object (e.g., saw) was not present and the actor mimed the intended action (e.g., cutting a 2'' × 4'') without the aid of any object. Throughout all clips, the actor avoided overt signs of pretense (e.g., affective displays and exaggerated movements) and did not establish eye contact with the viewer.

Each clip was approximately 11 s long and began with the actor seated at a table in a resting state with his arms at his sides. During the first 2 s, the actor raised his arms to table level and reached out to pick up either an object (*R*, *PHS*, *PLS*) or to mime picking up an imaginary (*I*) object from the tabletop. For the next 7 s, the actor interacted with the object. During the final 2 s, the actor placed the object back on the table and returned to a resting state with his arms at his sides. Interstimulus intervals (ISIs) of 8, 10, and 12 s were placed between all clips, with the constraint that each of the three durations appeared equally. The lengths of these ISIs are in accord with other fMRI studies investigating biological motion (Morris, Pelphrey, & McCarthy, 2006; Pelphrey et al., 2003; Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009).

The clips and ISIs were arranged in four pseudorandom orders: (1) *R*, *PHS*, *I*, *PLS*; (2) *PHS*, *I*, *PLS*, *R*; (3) *I*, *PLS*, *R*, *PHS*; and (4) *PLS*, *R*, *PHS*, *I*. Participants

were randomly assigned to one of the orders, with 4–5 participants receiving each order. The actions and ISIs remained consistent between orders. For example, all orders began with the actor reading; in Order 1 he read an actual book (*R*), in Order 2 he pretended to read using a napkin (*PHS*), in Order 3 he pretended to read without any object (*I*), and in Order 4 he pretended to read using a saw (*PLS*). Thus, although intra-action order was predicated on order assignment, inter-action order remained randomized, preventing participants from predicting whether the next action was of the real or pretend variety. Orders consisted of six runs with each run including 12 clips, yielding a total of 72 clips (i.e., 18 actions in four forms each).

Behavioral procedures

Participants were informed they would be taking part in a study designed to examine how different regions of their brain interacted when they observed an actor perform various actions. Before entering the scanner environment, they completed a computerized version of the Creative Experiences Questionnaire (CEQ; Merckelbach, Horselenberg, & Murriss, 2001). This psychometrically normed 25-item scale assesses fantasy proneness via binary questions pertaining to pretense (e.g., “As a child, I had my own make

believe friend or animal”), visualization (e.g., “When I imagine I have eaten rotten food, I really get nauseous”), and fictional medium absorption (e.g., “When I perceive violence on television, I get so into it that I get really upset”). After completing the CEQ, participants entered the scanning environment and were instructed to watch each clip carefully and completely.

Data acquisition

Scanning was performed on a Siemens 3 Tesla MAGNETOM Trio with a 12-channel head coil. A high-resolution T1 weighted anatomical image was collected using MPRAGE pulse sequence for each participant and used for co-registration with functional data. Whole-brain functional images were acquired using a T2* weighted echo planar sequence (repetition time = 2000 ms; echo time = 40 ms; voxel size, $3.0 \times 3.0 \times 4.2$ mm; 28 axial slices).

Data analysis

fMRI data processing was carried out using FEAT (FMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB’s Software Library, www.fmrib.ox.ac.uk/fsl). Motion was detected by center of mass measurements implemented using automated scripts developed for quality assurance purposes and packaged with the BXH/XCEDE suite of tools, available through the Bioinformatics Research Network (BIRN). Participants who had greater than a 3-mm deviation in the center of mass in the x -, y -, or z -dimensions were excluded from further analysis. The following prestatistics processing was applied: motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002); nonbrain removal using BET (Smith, 2002); spatial smoothing using a Gaussian kernel of FWHM 5 mm; grand-mean intensity normalization of the entire 4D data set by a single multiplicative factor; highpass temporal filtering (Gaussian-weighted least-squares straight-line fitting, with $\sigma = 50.0$ s). Registration to the Montreal Neurologic Institute (MNI) Template standard space image was carried out using FLIRT (Jenkinson & Smith, 2002; Jenkinson et al., 2001).

The beginning of each 11-s clip marked event onset times, which were used to model signal responses containing a regressor for each response type and convolved with a GAMA function to model the hemodynamic response. First-level analysis of functional data was conducted on each run for each subject

using FEAT with time-series statistical analysis executed using FILM with local autocorrelation correction (Woolrich et al., 2001). Second-level FEAT analysis was used to combine runs within-participants using a fixed-effects model, while third-level, across-participants analyses used FLAME (stages 1 and 2) random-effects analysis. All statistical inferences, including data visualization, used whole-brain corrected cluster-significance thresholds of $p < .05$ ($z > 2.3$).

For all individual differences analyses, two regressors were included: (1) group mean that identified brain regions for which there were main effects and (2) CEQ score (de-meaned) for each participant, used to determine regions in which targeted contrasts (e.g., $PHS > R$) were significantly associated with CEQ score. To investigate the effects of fantasy proneness, significant clusters associated with the CEQ regressor were registered to each participant’s native space and average $PHS > R$ values for each individual were extracted from these ROIs.

RESULTS

We first explore brain activity related to the observation of pretense acts (Table 1). Next, we examine the activity associated with observing specific pretense acts (Table 2). Finally, we review our findings related to individual differences when observing pretense acts (Table 3). For an overall summary of our results, please see Table 4.

Observing pretense acts

We first investigated the impact of viewing each form of pretense by contrasting each form with the

TABLE 1
Brain activation results associated with pretense observation

	Hem	BA	x	y	z	Z-value
<i>Imaginary > Real</i>						
MFG	L	9	-52	18	28	3.45
IFG (pars opercularis)	L	9	-46	14	28	2.76
<i>Low-likelihood substitute > Real</i>						
IFG (pars opercularis)	L	—	-44	22	20	3.49
IFG (pars triangularis)	L	—	-42	28	16	2.48
<i>High-likelihood substitute > Real</i>						
FG	L	37	-48	-58	-18	3.52
LOC	L	—	-50	-62	-8	3.31

Notes: MNI coordinates are reported; Hem, hemisphere; BA, Brodman Area; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; FG, fusiform gyrus; LOC, lateral occipital cortex.

TABLE 2
Brain activation results for substitute object > imaginary pretense

	Hem	BA	x	y	z	Z-value
<i>Low-likelihood substitute > Imaginary</i>						
SPL	L	7	-22	-52	64	3.05
	R	7	30	-52	64	3.25
IPL	L	—	-44	-30	30	3.28
	R	7	-2	-52	64	2.50
Precuneous	L	7	6	-54	62	2.65
	R	7	6	-54	62	2.65
FG	L	37	-28	-48	-16	3.59
	R	37	40	-52	-14	2.68
LOC	L	18	-32	-88	4	4.8
	R	—	-28	-62	-18	4.79
Cerebellum	L	—	30	-48	-22	4.65
	R	—	30	-48	-22	4.65
<i>High-Likelihood Substitute > Imaginary</i>						
SPL	L	7	-28	-56	58	3.85
	R	7	28	-46	68	4.15
IPL/SMG	L	—	-46	-34	34	3.76
	R	7	8	-56	66	2.68
Precuneous	L	—	-40	-66	-12	4.03
	R	—	42	-70	-12	4.19
LOC	L	18	-34	-88	-4	4.36
	R	—	42	-66	-10	4.23
Cerebellum	L	—	-32	-50	-26	3.53
	R	—	28	-42	-26	3.79

Notes: MNI coordinates are reported; Hem, hemisphere; BA, Brodman Area; SPL, superior parietal lobule; IPL, inferior parietal lobule; FG, fusiform gyrus; LOC, lateral occipital cortex; SMG, supramarginal gyrus.

observation of real actions. An $I > R$ analysis yielded significant clusters with maxima in the left middle frontal gyrus (MFG; BA 9). The pars opercularis region of the left inferior frontal gyrus (IFG; BA 9; $x = -46$, $y = 14$, $z = 28$, $Z = 2.76$) also evidenced

TABLE 3
Brain activation results for high-likelihood substitute > real, regressing CEQ score

	Hem	BA	x	y	z	Z-value
<i>High-likelihood > Real</i>						
MFG	R	8/46	48	18	40	3.25
IFG (pars opercularis)	R	—	54	18	28	3.29
SPL	R	7	42	-48	58	3.20
SMG	R	40	46	-38	38	3.14

Notes: MNI coordinates are reported; Hem, hemisphere; BA, Brodman Area; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; SPL, superior parietal lobule; SMG, supramarginal gyrus.

significantly more activation when participants viewed I pretense than R clips. Similarly, a $PLS > R$ contrast revealed a significant cluster with maxima in the pars opercularis region of the left IFG. The pars triangularis region of the left IFG was also more active ($x = -42$, $y = 28$, $z = 16$, $Z = 2.48$) in the $PLS > R$ contrast. Finally, we carried out a $PHS > R$ analysis that yielded significant clusters with maxima in the left fusiform gyrus (BA 37) and left lateral occipital cortex (LOC). Table 1 shows a complete list of regions that demonstrated significantly more activation when participants observed pretense than real actions.

Differentiating forms of pretense

Beyond distinguishing activation when participants viewed real actions, we also examined the differences in brain activity between specific forms of pretense. We contrasted the forms of pretense where objects

TABLE 4
Summary of results

Region	Contrast					
	$PHS > R^*$	$PHS > R$	$PLS > R$	$I > R$	$PHS > I$	$PLS > I$
<i>Frontal</i>						
MFG	R (BA 8/46)			L (BA 9)		
IFG (pars opercularis)	R		L	L (BA 9)		
IFG (pars triangularis)			L			
<i>Parietal</i>						
SPL	R (BA 7)				L/R (BA 7)	L/R (BA 7)
IPL	R (SMG BA40)				L (IPL/SMG)	L
Precuneus					R (BA 7)	L/R (BA 7)
<i>Temporal</i>						
FG		L (BA 37)			L/R	L/R (BA 37)
LOC		L			L (BA 18)/R	L (BA 18)
Cerebellum					L/R	L/R

Notes: L, left; R, right; BA, Brodman Area; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; SPL, superior parietal lobule; IPL, inferior parietal lobule; SMG, supramarginal gyrus; FG, fusiform gyrus; LOC, lateral occipital cortex.
*Regressing CEQ score.

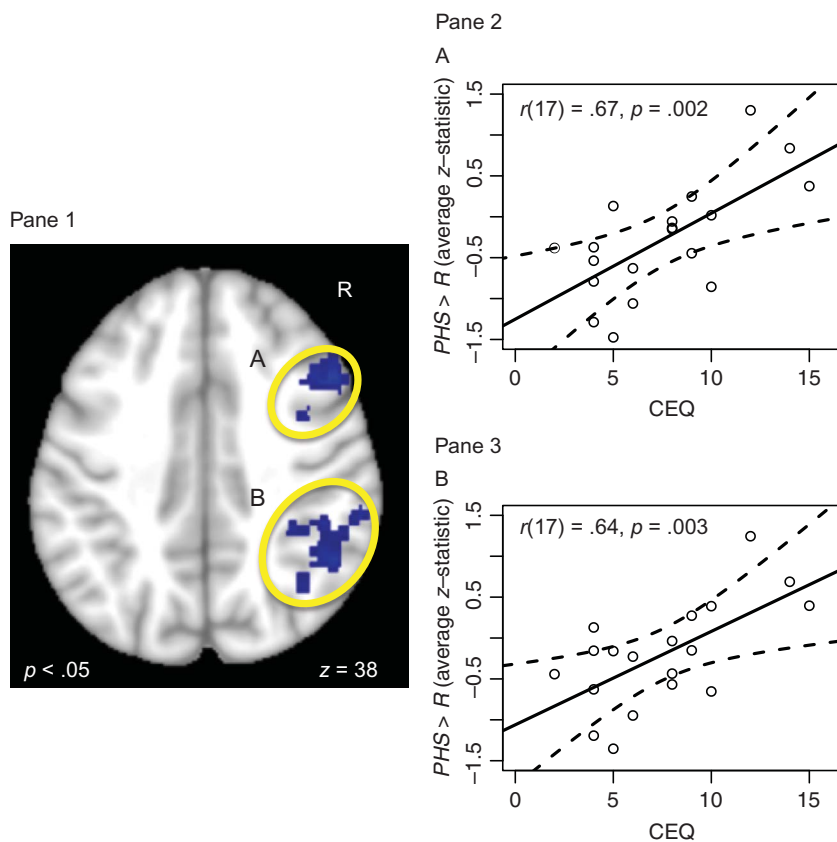


Figure 2. Regions that demonstrated a significant relationship between fantasy proneness (CEQ) and *PHS* > *R* activity. Clusters from whole-brain analysis are shown in MNI space. Average *z*-statistic values from the contrast of parameter estimates in the right IFG (A in Pane 1 and 2) and SMG (B in Pane 1 and 3) are plotted against fantasy proneness (CEQ) for each participant. Dashed lines indicate 95% confidence interval around the fit line. Analyses completed with whole-brain corrected cluster-significance thresholds of $p < .05$ ($z > 2.3$).

were present (i.e., *PHS* and *PLS*), that is, the more scaffolded forms, with those cases where they were absent (i.e., *I*). A summary of results is provided in Table 2.

A *PLS* > *I* analysis revealed significant clusters in the left FG, left LOC, and bilateral portions of the cerebellum. In addition, the left inferior parietal lobule (IPL) ($x = -44$, $y = -30$, $z = 30$, $Z = 3.28$), right fusiform gyrus (FG) ($x = 40$, $y = -52$, $z = -14$, $Z = 2.68$) and bilateral portions of the precuneus (left: $x = -2$, $y = -52$, $z = 64$, $Z = 2.5$; right: $x = 6$, $y = -54$, $z = 62$, $Z = 2.65$) and superior parietal lobule (SPL) (left: $x = -22$, $y = -52$, $z = 64$, $Z = 3.05$; right: $x = 30$, $y = -52$, $z = 64$, $Z = 3.25$) were significantly more active during *PLS* than *I* clips. A *PHS* > *I* analysis yielded significant clusters with maxima in the left IPL/supramarginal gyrus (IPL/SMG) and bilateral portions of the SPL (BA 7), FG, and LOC. The right precuneus (BA 7; $x = 8$, $y = -56$, $z = 66$, $Z = 2.68$) and bilateral portions of the cerebellum (left: $x = -32$, $y = -50$, $z = -26$, $Z = 3.53$; right: $x = 28$, $y = -42$, $z = -26$, $Z = 3.79$) also evidenced

significantly more activity when participants viewed *PHS* than *I* pretense. Finally, neither *I* > *PLS* nor *I* > *PHS* analyses yielded any significant clusters or activity.

Individual differences when observing pretense

To explore if individual differences in fantasy proneness affected how participants neurally represented observed pretense, we entered participants' centered CEQ scores as a regressor in the *PHS* > *R* analysis. The result revealed right-lateralized significant clusters with maxima in the SMG (BA40), MFG (BA 8/46), SPL, and IFG, pars opercularis (see Table 3 and Figure 2).

DISCUSSION

Pretense is a universal and early-appearing skill (Eibl-Eibesfeldt, 1989; Tamis-Lemonda & Bornstein, 1994)

that continues for some into adulthood (Smith & Lillard, 2012). Building on prior research (German et al., 2004; Schubotz & von Cramon, 2009¹; Whitehead et al., 2009), we examined neural correlates associated with observing three unique forms of pretense carried out with a balanced set of substitute objects. We also examined the association between those neural representations and individual differences in fantasy proneness. Next, we discuss the results with reference to the three guiding questions of our study: (1) Do pretense acts, when compared to their real counterparts, evoke significantly heightened responses in brain regions associated with ToM? (2) Do different forms of pretense evoke unique neural responses? (3) Do individual differences in fantasy proneness influence the neural representation of observed pretend acts?

Pretense and theory of mind

Developmental psychologists posit that grasping a pretender's mental state is a component of a mature understanding of pretense (Leslie, 1987; Lillard, 1993, 1998, 2001). Past research on the neural correlates of observing select forms of pretense reinforces this claim, with both German et al. (2004) and Whitehead et al. (2009) reporting increased activation in the mPFC, IFG, and STS (regions associated with ToM; Amodio & Frith, 2006; Gallagher & Frith, 2003), when participants viewed mimed actions and substitute object pretense, respectively. However, these pioneering studies did not strictly control the stimuli presented and the possible contribution of these variations in stimuli was unclear.

In the current study, using rigorously controlled stimuli and different forms of pretense, we found activity in regions concordant with prior studies, as well as in additional regions. First, we documented IFG activity when participants viewed *I* and *PLS* forms of pretense. The IFG is considered to be a key component of the human "mirror neuron system" (Binkofski & Buccino, 2004; Buccino et al., 2001; Hari et al., 1998), responding both to the observation and imitation of gestures (Grèzes, Armony, Rowe,

& Passingham, 2003; Iacoboni et al., 1999; Nishitani & Hari, 2000); it was also activated in Schubotz and von Cramon (2009). Prior research has demonstrated that activity within this region need not necessarily be linked to action. For example, the IFG activates when participants assess mental states conveyed by photographs of eyes (Adams et al., 2010; Baron-Cohen et al., 1999), select the proper conclusion to a comic strip conveying intentionality (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Völlm et al., 2006), and evaluate how pleased an individual is to have a picture taken of them (Mitchell, Banaji, & Macrae, 2005). In both our study and these others, the element of trying to figure out actor intent could be involved.

In addition to the IFG, our targeted contrasts revealed activity within the left MFG, with observed instances of *I* pretense eliciting significantly more activity than real actions. The MFG, like the IFG, has been implicated in ToM processes (Gallagher et al., 2000; Gobbini, Koralek, Bryan, Montgomery, & Haxby, 2007; Goel, Grafman, Sadato, & Hallett, 1995) and was also active when participants viewed imaginary object pretense acts in a prior study (German et al., 2004).

Finally, like both German et al. (2004) and Whitehead et al. (2009), we found significant activity within the FG when participants viewed *PHS* pretense. The FG has been implicated in a wide variety of sociocognitive tasks. Although often characterized for its role in face perception (Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997; McCarthy et al., 1997; but see Gauthier & Logothetis, 2000), a growing body of literature suggests that FG may play a broader role in social cognition. For example, films of shapes engaged in apparently purposeful social behavior elicited significantly more FG activity than did films of shapes randomly bouncing off walls (Castelli et al., 2000). Moreover, other independent research groups have used agentive shape stimuli to demonstrate that the FG activates in response to sociocognitive scenarios even where faces are not present (Gobbini et al., 2007; Schultz et al., 2003; Wheatley, Milleville, & Martin, 2007). The region has also been shown to activate when participants are asked to make semantic judgments about people, such as whether a person could be considered "assertive" (Mitchell, Heatherton, & Macrae, 2002). Because the high-likelihood objects (*PHS* stimuli) are more likely to elicit a pretense judgment than *PLS* and *I* stimuli, this could explain the greater activation of the FG in response to *PHS* (vs. *R*) stimuli. Perhaps for some subjects, watching the *PLS* and *I* clips did not evoke a semantic judgment.

¹Note that Schubotz and von Cramon (2009) documented activity principally within areas of the "mirror neuron system" (Rizzolatti & Craighero, 2004) and not the ToM network. We agree with these authors that the source of this disparity is methodological differences, with Schubotz and von Cramon's stimuli consisting of only hands interacting with objects and not an actor carry out the actions. Furthermore, our primary interest in this line of work concerns observing pretense as it naturally occurs. For this reason, we chose to compare our study with previous work that most closely matches its methodology.

Surprisingly, unlike German et al. (2004) and Whitehead et al. (2009), we did not detect activity within the mPFC or STS when participants viewed pretense acts. A study carried out by de Lange, Spronk, Willems, Toni, and Bekkering (2008) might explain this result. Participants in that study viewed images of an actor carrying out standard acts (e.g., drinking from a coffee cup) and acts characterized by either extraordinary intentions (e.g., holding a coffee cup to the ear) or means (e.g., gripping a coffee cup in a nonstandard way). On a trial-by-trial basis, participants were explicitly instructed to judge whether the actor's intentions or the means by which she accomplished the actions were ordinary. The extraordinary intention trials were similar to our object substitute pretense trials: objects were being used in a manner inconsistent with their prototypical use. In de Lange et al.'s study, significant activation within the mPFC and STS occurred *only* when participants were explicitly prompted to judge the ordinariness of the actor's intentions, whereas IFG activity occurred irrespective of participants' judgments. In our study, we never asked for explicit judgments; in both German et al. (2004) and Whitehead et al. (2009), they did by asking (respectively) if an action was completed and how an object was being used. Thus, one explanation for the current study's inconsistent results with German et al. (2004) and Whitehead et al. (2009) could be the methodological difference of asking for explicit judgments concerning actor intent.

Another candidate explanation for our discordant results relates to Whitehead et al.'s pretense stimuli, marked by affective displays and exaggerated movements. We chose to avoid such overt signals as they could have created neural artifacts solely linked to the actor's affective responses, rather than to the pretense acts themselves. To more carefully test this possibility, researchers could pit clips of pretend acts with affective overtones and exaggerated movements against clips devoid of such elements.

In sum, we hypothesized that observing pretense acts would elicit brain activity in regions previously associated with ToM and the results partially supported our hypothesis. Neural activity occurred in similar ToM regions as prior pretense studies where the pretender was in full view while pretending (German et al., 2004; Whitehead et al., 2009), as well as in ToM regions identified in studies beyond the domain of pretense. However, we did not detect activity within two principal areas that German et al. and Whitehead et al. did (e.g., mPFC and STS) likely due to paradigmatic differences in either what participants were asked to do following the viewing of pretense acts or the nature of the pretense acts. Coupled with previous research,

this study lends further credence to developmental perspectives emphasizing links between ToM and pretend play.

Unique pretense forms evoke unique neural responses

A novel aspect of the current study's design was the inclusion of three unique forms of pretend play, rather than just pantomime (German et al., 2004) or substitute object pretense (Schubotz & von Cramon, 2009; Whitehead et al., 2009). This design permitted us to investigate neural differences between pretense forms. Recall that prior research demonstrates that children first produce (Elder & Pederson, 1978; Fein, 1975; Hopkins, Smith, & Lillard, 2013; Jackowitz & Watson, 1980; Pederson, Rook-Green, & Elder, 1981; Watson & Jackowitz, 1984) and then understand (Bigham & Bouchier-Sutton, 2007) substitute object pretense when the substitute is similar in form and function to the intended referent. Only later do they understand substitute object pretense where the substitute differs in form and function from the referent, and even then their understanding is tenuous (Bigham & Bouchier-Sutton, 2007). Yet, forms of substitute object pretense intuitively seem "easier" to understand than imaginary pretense. Indeed, Vygotsky (1967) stated that in pretense "an object [e.g., a stick] . . . becomes a pivot for severing the meaning of horse from a real horse" (p. 15). Through substitute object pretense children mentally represent objects that are not there, gaining the ability to use alternative objects to symbolize absent ones. The paramount case of this process is imaginary object pretense (or pantomime) where one intends to symbolize something without the aid of anything. Thus, we contrasted *PHS* and *PLS* forms, respectively, against *I* pretense.

Since *PHS* and *PLS* pretense forms activated similar brain regions when contrasted with *I*, hereafter we use "substitute object pretense" in reference to both. Our targeted contrasts revealed significant activity in the precuneus, IPL, fusiform, and SPL associated with substitute object pretense. The precuneus (Fletcher et al., 1995; Gallagher et al., 2000; Mitchell, 2008; Saxe & Kanwisher, 2003) and IPL (Gobbini et al., 2007; Goel et al., 1995; Kobayashi, Glover, & Temple, 2007) have been shown to activate when participants consider the beliefs, desires, and intentions of others. Similarly, as we discussed in the preceding section, there is mounting evidence that FG activity is not just indicative of face processing, but also may be active in sociocognitive assessments where faces are absent. Therefore, observing pretense where

a substitute object (i.e., a “pivot”) was present evoked more activation in ToM regions than pretending without a substitute object. This might seem surprising; the ability to interpret object substitute pretense, especially when the substitute is similar in form, develops before the ability to interpret imaginary object pretense, thus one might expect imaginary pretense to be associated with greater activation in ToM regions. However, even though the objects in *PHS* clips resembled their intended referents in form they were, by definition, substitutes: artifacts intended to be used in a select manner, a manner that deviated from their use in our study.

One possible explanation for the results stems from functional fixedness (Adamson, 1952; Duncker, 1945; Glucksburg & Weisberg, 1966): an expectation that objects will be used in ways that conform to their intended purposes (e.g., boxes hold tacks, they do not support candles). For example, when participants viewed an actor grasp a comb in the current study, they likely believed that he would proceed to comb his hair, and in one clip he did (*R*), but in others he pretended to saw (*PHS*) and hammer (*PLS*) with the object. The presence of substitute objects during pretense could have encouraged participants to more deeply engage with the ensuing action, one that violated their predictions given the artifact. If so one would expect significantly more activation in the SPL, a region recognized for its role in predicting and detecting errors in motor actions (Corbetta & Shulman, 2002; Frith, Blakemore, & Wolpert, 2000; Liew, Han, & Aziz-Zadeh, 2011; Wolpert, Goodbody, & Husain, 1998). Also, it is important to note that the SPL has been implicated in spatial (Chaminade, Meltzoff, & Decety, 2005; Salmi, Rinne, Degerman, Salonen, & Alho, 2007) and dorsal visual system (Goodale & Milner, 1992; Milner & Goodale, 2008) processes, both of which are relevant to the current study.

Thus, our results suggest that forms of pretense are uniquely represented, with substitute object pretense eliciting significantly more activity, compared to pretense without the aid of a substitute, not only in regions associated with ToM but also in a region thought to aid in the prediction and error-monitoring of motor actions.

Individual differences in fantasy proneness

Typically developing children begin to pretend in their second year of life, but the degree to which they do so is not uniform. This heterogeneity does not cease in childhood: approximately 40% of college

undergraduates still pretend in their daily lives, whereas 60% do not (Smith & Lillard, 2012). The current study is the first to explore whether individual differences in fantasy proneness, assessed through the CEQ, affect the neural representation of pretense.

When we regressed participants' CEQ scores in our contrast analyses, fantasy proneness resulted in significantly increased activity associated with *PHS* pretense, compared to *R* actions, in regions such as the MFG (BA 8/46), IFG (pars opercularis), and SPL, all previously discussed as either affiliated with ToM or predicting motor actions. In addition, *PHS* pretense elicited activity in the SMG, a region associated with action observation (Grèzes & Decety, 2001; Rizzolatti & Craighero, 2004). These results suggest that individual differences in fantasy proneness might explain unique variance in neural responses to one form of pretense, *PHS*. However, these results are exploratory. The CEQ consists of a variety of questions pertaining to fantasy proneness, with only a select number probing participants' pretense engagement. Future research is necessary to replicate and extend this result. A more focused questionnaire, directly targeting only elements of pretense engagement, could provide a more comprehensive picture of how individual differences in pretend play trajectories impact how the activity is neurally represented.

CONCLUSION

Under very tightly controlled conditions, pretense observation elicited neural responses consistent with the observer considering the pretender's intentions. Moreover, differences emerged between substitute object pretense and pantomime, with the former associated with significantly more activity in the precuneus, IPL, SPL, and FG than the latter. Finally, our exploratory analyses indicated that proneness toward fantasy could impact the cortical mechanisms of pretense observation. Future research should examine the neural correlates of pretense from a developmental perspective. Lillard (1998, 2001) has shown that younger children do not view intentionality to be a requisite component of pretense: simply behaving as if one is doing an action is sufficient to be pretending to do said action. It is only later, usually around 6–8 years old, that children explicitly acknowledge intentionality as a requisite component of a pretense act, thus setting up a potential dichotomy in the neural substrates of observing pretense between these two groups of children. In sum, the current study suggests that the cortical mechanisms undergirding the observation of the activity include components of ToM and action

prediction, with both systems evidencing a degree of malleability contingent upon individual propensity for fantasy.

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