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Neural basis for generalized quantifier comprehension

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Abstract

Generalized quantifiers like "all cars" are semantically well understood, yet we know little about their neural representation. Our model of quantifier processing includes a numerosity device, operations that combine number elements and working memory. Semantic theory posits two types of quantifiers: first-order quantifiers identify a number state (e.g. "at least 3") and higher-order quantifiers additionally require maintaining a number state actively in working memory for comparison with another state (e.g. "less than half"). We used BOLD fMRI to test the hypothesis that all quantifiers recruit inferior parietal cortex associated with numerosity, while only higher-order quantifiers recruit prefrontal cortex associated with executive resources like working memory. Our findings showed that first-order and higher-order quantifiers both recruit right inferior parietal cortex, suggesting that a numerosity component contributes to quantifier comprehension. Moreover, only probes of higher-order quantifiers recruited right dorsolateral prefrontal cortex, suggesting involvement of executive resources like working memory. We also observed activation of thalamus and anterior cingulate that may be associated with selective attention. Our findings are consistent with a large-scale neural network centered in frontal and parietal cortex that supports comprehension of generalized quantifiers.

Keywords: Quantifiers; Semantic; Neural basis

1. Introduction

Categories like "animals" and "implements" are often used in an effort to understand the neural basis for semantic memory. However, these categories are very complex. There are differences in familiarity and experience with these categories across individuals, for example, and much of this material may be education-dependent. Conversely, the semantics of generalized quantifiers like "at least 3 beers" or "less than half of the nuts" are well understood. While we have a strong understanding of the semantic underpinnings of generalized quantifiers, we know little about their neural representation. In this study, we investigated the neural basis for generalized quantifier comprehension using fMRI.

A generalized quantifier can be defined as a noun phrase that is a function from sets to truth-values. They are ubiquitous in our language, highly familiar, do not depend on perceptual familiarity and exist independent of education level. In the sentence "Some students drink beer," for example, a TRUE value is returned if there is an intersection of students and beer drinkers. Generalized quantifiers can be grouped into classes, depending on their ability to make distinctions between models of the mathematical structure constructed from sets of objects. On one hand, there are first-order quantifiers, as exemplified in (1):

(1) a. every pencil;
b. some students;
c. at least three doctors.

These expressions include quantifiers and noun phrases formed from "logical" determiners like "some," "every," or "no," as well as from numeric quantifiers like "at least *n*," "at most *n*," "exactly *n*" or "between *n* and *m*," where *n* and *m* are

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integers. First-order quantifiers thus involve determining the numeric content of a set. In the case of numeric quantities like "at least 3 doctors," for example, the states of "one doctor," "two doctors," and "three doctors" must be identified first to determine whether the statement "at least three doctors" is true. In the case of a logical determiner like "every," the truth of a quantified statement can be established similarly after all of the objects specified by the noun phrase are queried.

The work of linguists and logicians such as Barwise and Cooper (1981), Keenan and Stavi (1986) and van Benthem (1986) indicates that first-order quantifiers and number knowledge are systematically related, even in the case of "logical" quantifiers like "some *x*" or "all *y*", which do not involve explicit mention of a number. For example "some" can be reinterpreted as "at least one" or "no" can be reinterpreted as "at most zero" or "less than one". Logical quantifiers thus can be interpreted like numeric quantifiers. From this perspective, the core conceptual question is whether quantifier comprehension depends at least in part on number knowledge. We tested this possibility by examining the pattern of neuroanatomic recruitment when subjects are judging the truth-value of statements containing generalized quantifiers.

The second class of quantifiers are higher-order, as exemplified in (2):

(2) a. most lawyers;
 b. more than half of the lawyers;
 c. an even number of students.

The quantifiers in (2)a and (2)b involve tracking and comparing the relative sizes of sets. In a sentence like "More than half of the lawyers are ambulance chasers," for example, one must identify and hold in working memory (WM) the number of lawyers who are ambulance chasers and then compare this with the number equivalent to half of all lawyers to evaluate the truth value of this statement. The quantifier in (2)c involves a parity test of the cardinality of the set that is made while these elements are retained in WM. Like the quantifiers in (1), all of the quantifiers in (2) require determining the numerical content of a set, but additionally depend in part on comparative judgments involving executive resources such as working memory in a way that the quantifiers in (1) do not.

Formally, then, higher-order quantifiers can make fine-grained distinctions between mathematical models that first-order quantifiers cannot, independently of a psychological model. This difference in expressive power correlates with a difference in the computational resources required to simulate them. In particular, van Benthem (1986) has shown that a very proper subset of the first-order quantifiers can be simulated by a simple computing device—a finite state automaton—which does not require a resource like WM. In terms of a psychological model, since higher-order quantifiers presuppose that the cardinalities of sets are maintained in an active mental state during comprehension, they require WM in order to accumulate and transiently retain the cardinalities involved in the comparison. As a result, higher-order quantifiers can only be simulated by a more complex computing device—a push-down automaton—which is equipped with a simple WM device. We hypothesize from this perspective that comprehension of higher-order quantifiers depends on a numerosity component that identifies number properties, as with first-order quantifiers, and additionally requires a WM component that maintains these properties in an active mental state during processing, and a mechanism that manipulates these numbers while they are retained in WM. We, thus hypothesize that the qualitative differences between the first-order and higher-order classes of quantifiers, formally reflected in a difference in the computational machinery needed to simulate them, will also be reflected in brain anatomy. In particular, we hypothesized that processing higher-order quantifiers will call into play brain regions supporting WM and executive resources in a way that is qualitatively different from first-order quantifiers. By comparison, first-order quantifiers are likely to depend more exclusively on brain regions important for number knowledge.

Several studies of brain-damaged patients have emphasized that number knowledge constitutes a distinct domain of knowledge that is separate from, but equivalent to, domains of knowledge such as "animals" and "tools". For example, patients with corticobasal degeneration (CBD) appear to have relatively preserved semantic memory for objects and natural kinds, yet are quite impaired in their knowledge of numbers (Halpern, McMillan, Moore, Dennis, & Grossman, 2003; Halpern, Clark et al., 2004; Halpern, Glosser et al., 2004). The cortical component of the neurodegenerative disease in these patients appears to be centered in the parietal lobe, based on clinical features such as cortical sensory loss and apraxia (Pillon et al., 1995; Riley et al., 1990) and neuroimaging studies (Brooks, 2000; Grossman et al., 2004; Halpern, Glosser et al., 2004). These CBD patients and other cases of acalculia associated with parietal lobe disease have demonstrated profound difficulty determining the numerosity of small sets of stimuli, for example, or performing simple addition problems (Cipolotti, Butterworth, & Denes, 1991; Dehaene, 1997; Dehaene & Cohen, 1997; Delazer & Benke, 1997; Halpern, McMillan, Moore, Dennis, & Grossman, 2003; Halpern, Clark et al., 2004; Rossor, Warrington, & Cipolotti, 1995; Takayama, Sugishita, Akiguchi, & Kimura, 1994; Thioux et al., 1998; van Harskamp & Cipolotti, 2001; Warrington, 1982). Additional evidence concerning the inferior parietal locus of number knowledge comes from functional neuroimaging studies examining number knowledge in healthy subjects (Burbaud et al., 1995; Cohen, Dehaene, Chochon, Lehericy, & Naccache, 2000; Kazui, Kitagaki, & Mori, 2000; Le Clec'H et al., 2000; Pinel, Dehaene, Riviere, & LeBihan, 2001; Reuckert et al., 1996; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002; Stanescu-Cosson et al., 2000). For example, neuroimaging studies on magnitude comparison and subtraction support right hemisphere activation of inferior parietal cortex (Chochon, Cohen, van de Moortele, & Dehaene, 1999;

Cohen et al., 2000; Le Clec'H et al., 2000), while multiplication is associated with left inferior parietal cortex activation (Cohen et al., 2000).

Evidence for the category-specific nature of number knowledge comes from patients with semantic dementia who appear to have profound difficulty understanding object concepts like natural kinds although their number knowledge appears to be relatively preserved (Cappelletti, Butterworth, & Kopelman, 2001; Halpern, Glosser et al., 2004). While number knowledge is related to parietal cortex, object knowledge in semantic dementia appears to be associated with ventral temporal lobe disease (Cappelletti et al., 2001; Halpern, Glosser et al., 2004).

Portions of frontal cortex appear to support WM, and thus may contribute to the comprehension of higher-order quantifiers. Functional neuroimaging work in healthy adults underlines the key role of dorsal portions of inferior frontal cortex (dIFC) and adjacent premotor cortex in WM (Grady et al., 1998; Paulesu, Frith, & Frackowiak, 1993; Smith & Jonides, 1999). When an *n*-back task is used to examine WM, additional recruitment of dorsolateral prefrontal cortex may support WM by maintaining information in WM for a longer period of time (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Braver et al., 1997) or by requiring strategic manipulation or switching to support greater WM demands (Smith et al., 2001; Sylvester et al., 2003).

Based on these observations, we predicted activation of parietal cortex for first-order quantifiers since their comprehension depends largely on number knowledge. We also expected parietal activation for higher-order quantifiers since comprehension of this class of quantifiers is also thought to depend in part on number knowledge. By comparison, we expected additional activation of dIFC and dlPFC during comprehension of higher-order quantifiers. These quantifiers require executive resources such as working memory since a quantity is maintained in an active mental state during processing and involves the manipulation of the quantities maintained in WM.

2. Methods

2.1. Subjects

We studied 12 healthy right-handed native English-speaking adults (8 males, 4 females; mean (±S.D.) age = 24.4 (±2.9) years, mean (±S.D.) education = 16.4 (±2.3) years). All subjects were volunteers participating in accordance with an informed consent procedure approved by the University of Pennsylvania Institutional Review Board.

2.2. Materials

Subjects were presented with 120 grammatically simple propositions containing a quantifier that probed a color feature of a familiar object in a visual stimulus array (e.g. "at least 3 of the balls are blue"). Six different quantifiers were each presented in 20 trials: half were first-order quantifiers (at least 3, all, some) and half were higher-order quantifier (less than half, odd, even). Looking at subsets of these quantifiers allowed us to explore other features potentially contributing to quantifier comprehension, such as the presence of an explicit number, and the need for precise quantification rather than approximation.

Each quantifier problem involved two consecutive 10 s events. In the first event, only the proposition was presented; in the second event the same proposition in addition to a stimulus array containing eight randomly distributed familiar objects (women, balls, flowers, cars, dinosaurs) was presented for 2500 ms followed by a blank screen for 7500 ms. Subjects were asked to decide if the proposition accurately described the stimulus array. They responded by pressing the right button of a fiber optic response pad if true; the left button was pressed if false. Half of each type of item was true and half false. Also, half of the stimulus arrays contained a quantity of target items near the criterion for validating or falsifying the proposition, therefore requiring a precise judgment (e.g. four targets in "at least 3") and half were distant from the criterion, therefore allowing an approximate judgment (e.g. eight targets in "at least 3). Debriefing following the experiment revealed that none of the participants were aware that the stimulus array consisted of eight objects. We monitored behavioral accuracy.

All stimuli were counterbalanced and randomly distributed throughout the experiment, divided into four equal runs. The stimuli were presented to the subject using an LCD projector (Epson 5000) back-projected on to a screen placed at the bore of the magnet. The subject viewed the screen using a mirror system in the standard GE head coil. A Macintosh G3 was used to run PsyScope 1.2.5 presentation software (Cohen, MacWhinney, Flatt, & Provost, 1993) in order to present the stimuli and record behavioral accuracy.

2.3. Imaging acquisition and analysis

Images were acquired using a 1.5 T GE Horizon Echospeed scanner (GE Medical Systems, Milwaukee WI). The protocol began with a 10–15 min acquisition of 5 mm thick adjacent slices for determining regional anatomy, including sagittal localizer images (TR = 500 ms, TE = 10 ms, 192 × 256 matrix), T2-weighted axial images (FSE, TR = 2000ms, TE_{eff} = 85 ms), and T1-weighted axial images of slices used for fMRI anatomic localization (TR = 600 ms, TE = 14ms, 192 × 256 matrix).

Gradient echo echoplanar images were acquired for detection of alterations of blood oxygenation accompanying increased mental activity. All images were acquired with fat saturation, a rectangular FOV of 20 × 15 cm, 90° flip angle, 5 mm slice thickness, 50 ms TE and a 60 × 40 matrix, resulting in a voxel size of 3.75 mm × 3.75 mm × 5 mm. The echoplanar acquisitions consisted of 24 contiguous slices covering the entire cerebrum every 2 s. A separate acquisition lasting 1–2 min was needed for phase maps to correct for distortion in the echoplanar images (Alsop, 1995). Raw data were stored by the MRI computer on DAT tape and then processed off-line.

Initial data processing was carried out with Interactive Data Language (Research Systems, Boulder, CO) on a Sun Microsystems (Cupertino, CA) SunBlade 1000 workstation. Raw image data were reconstructed using a 2D FFT with a distortion correction to minimize artifact due to magnetic field inhomogeneties. Individual subject data were then prepared for analysis using statistical parametric mapping (SPM99), operating on a MatLab (V5.3, Natick, MA) platform, developed by the Wellcome Department of Cognitive Neurology (Frackowiak, Friston, Frith, Dolan, & Mazziota, 1997). The images in each subject's time series were registered to the initial image in the series. The images were then aligned to a standard coordinate system (Talairach & Tournoux, 1988). The data were spatially smoothed using an 8 mm Gaussian kernel to account for small variations in the location of activation and sulcal anatomy across subjects. Low-pass temporal filtering was implemented to control autocorrelation with a first-order auto-regressive method. The data were pooled and analyzed parametrically using random effects *t*-test comparisons converted to *z*-scores for each compared voxel. All contrasts used a subtraction method to look at the "proposition and response" event minus the "proposition alone" event. Our model states that quantifier comprehension requires determining the numeric content of a set. This subtraction method allowed us to focus on the verification process that is in itself quantifier comprehension while also controlling the possible linguistic confounds of the carrier sentences of the stimuli, and thus minimize this potential confound on activation for number knowledge. A direct contrast of first-order and higher-order quantifiers allowed us to examine the processes contributing to the comprehension of a higher-order quantifier relative to a first-order quantifier. The event-related analysis collapsed items across TRUE and FALSE judgments and filtered problems to include only correct judgments. We used a 20 voxel extent threshold. Our hypotheses about activations for main effects were tested with a statistical threshold of $p < 0.05$ corrected for multiple comparisons. We used a statistical threshold of $p < 0.001$ (uncorrected for multiple comparisons), unless otherwise noted, for direct subtractions comparing first-order and higher-order quantifiers.

3. Results

3.1. Behavioral data

We analyzed the behavioral data using a paired-samples *t*-test comparing first-order accuracy to higher-order accuracy. Higher-order quantifier judgments (mean = 84.5% correct, S.D. = 8.6%) were significantly more difficult than first-order judgments (mean = 92.3%, S.D. = 4.5%) ($t(11) = 3.43$; $p < 0.01$)).

3.2. Imaging data

Table 1 summarizes the loci of peak activations, and Fig. 1 illustrates the anatomic distribution of the corresponding activations, for first-order quantifiers, higher-order quantifiers and the direct contrast of these two conditions. First-order quantifiers recruited only right inferior parietal and bilat-

Table 1
Locus and extent of peak activations in brain regions for first-order and higher-order quantifiers, direct contrast of higher-order minus first-order quantifiers, direct contrasts of precise and approximate judgments and a contrast to examine the presence of an explicit number

Condition	Activation locus (Brodmann area)	Coordinates			*Z*-value	*p*-Value
		x	*y*	*z*		
First-order	Right inferior parietal (40)	44	−48	36	4.90	0.000
	Bilateral anterior cingulate (32)	8	16	40	4.52	0.000
Higher-order	Right inferior parietal, lateral occipital (40, 19)	44	−48	36	4.91	0.000
	Right dorsolateral prefrontal, inferior frontal (46, 45)	32	32	24	4.54	0.000
	Bilateral anterior cingulate (24)	12	0	52	5.14	0.000
	Bilateral thalamus	−28	−20	−12	4.70	0.000
Higher-order minus first-order	Left anterior cingulate (24)	−16	−4	52	3.64	0.000
	Left dorsolateral prefrontal (46)	−40	28	20	2.95	0.002*
	Right inferior frontal (47)	24	20	−8	3.38	0.000
	Right lateral occipital, inferior parietal (19, 40)	36	−88	4	3.22	0.001
Precise minus approximate	Left lateral occipital (18)	−4	−76	4	3.14	0.001
	Right inferior parietal (40)	32	−28	40	3.83	0.000
Approximate minus precise	Left anterior frontal (10)	−20	44	20	3.17	0.001
	Right superior temporal (21, 22)	48	−28	0	4.13	0.000
At least 3 minus [all and some]	Bilateral lateral occipital (17, 18)	4	−92	4	3.15	0.001
	Medial frontal, anterior cingulate (10, 32)	4	40	−8	3.09	0.001

* This activation was significant at $p < 0.002$, which did not surpass our high statistical threshold ($p < 0.001$), but was accepted because it is theoretically–motivated by our model of higher-order quantifier comprehension.

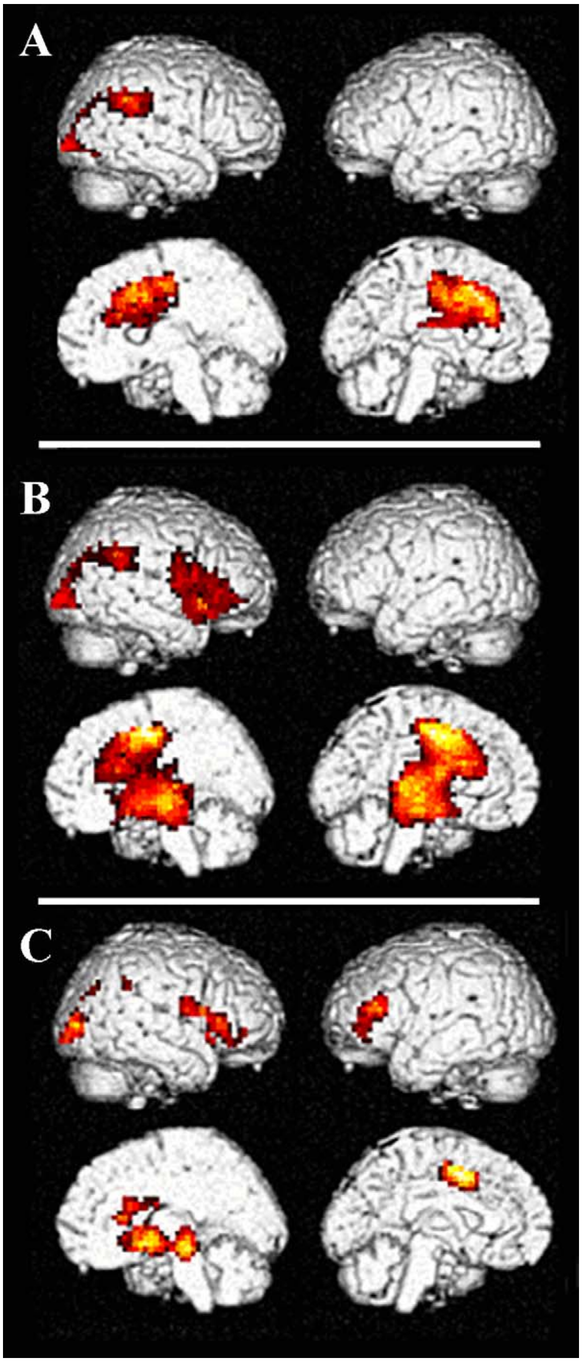

Fig. 1. Areas of activation for first-order, higher-order, and higher-order minus first-order. (A) First-order quantifiers; (B) higher-order quantifiers; (C) higher-order minus first-order quantifiers.

eral anterior cingulate regions (Fig. 1, Panel A). Higher-order quantifiers also recruited these regions. In addition, only higher-order quantifiers recruited right dorsolateral prefrontal, bilateral inferior frontal and right lateral occipital cortices as well as thalamus (Fig. 1, Panel B). Higher-order minus first-order quantifiers (Fig. 1, Panel C) revealed activation in large areas of dorsolateral prefrontal and inferior frontal cortices bilaterally. We also saw small areas of right inferior parietal, right lateral occipital and left anterior cingulate activation. These findings emphasize the role of inferior parietal cortex during comprehension of first-order quantifiers, and the additional activation of prefrontal regions during judgments involving higher-order quantifiers.

We performed other contrasts to help improve our understanding of quantifiers. One model of number knowledge (Dehaene, 1997) proposes that a verbally mediated representation is needed for precise judgments involving numbers (e.g. discriminating between “6” and “7”) while far apart numbers can be approximated (e.g. discriminating between “4” and “7”). To explore the role of number knowledge in quantifier comprehension further, we assessed performance on the subset of trials in which the quantity of target items either allowed an approximate judgment or forced a precise judgment. Table 1 summarizes the loci of peak activations for these contrasts. A precise judgment was required when the number of target items was as close as possible to the criterion for validating or falsifying the proposition (e.g. three out of eight objects, and five out of eight objects, for the quantifier “less than half of the *x*”); and an approximate judgment was adequate when the number of criterial stimuli was far from the threshold criterion (e.g. one out of eight objects, and seven out of eight objects, in the quantifier “less than half of the *x*”). These quantifiers involve similar WM demands since they both involve higher-order quantifiers. Judgments of precise arrays minus approximate arrays revealed activation of right inferior parietal and left lateral occipital cortices. The absence of differential activation of left peri-Sylvian language regions for precise judgments suggests that this class of generalized quantifiers is not verbally mediated. We also assessed the direct subtraction of judgments for approximate arrays minus precise arrays. This revealed activation of left anterior frontal and right superior temporal cortices consistent with other studies involving approximation.

We explored the role of an explicit numeral in a quantifier by comparing quantifiers containing an explicit number (e.g. “at least 3”) and quantifiers without an explicit number (e.g. “some” and “all”). These two conditions require the same amount of working memory, since they are both first-order quantifiers. Behavioral accuracy did not differ across these conditions and Table 1 summarizes the loci of peak activations. Activation for “at least 3” minus (“all” and “some”) revealed activation of bilateral lateral occipital, medial frontal and anterior cingulate regions. We did not observe inferior parietal activation in association with an explicit number compared to a generalized quantifier that does not explicitly mention a number. This suggests that the parietal activation observed in quantifier comprehension is not necessarily related to processing an explicit Arabic numeral, but is associated instead with processing number knowledge.

4. Discussion

Generalized quantifiers are exceedingly common in language. Nevertheless, this is the first investigation of the neural basis of generalized quantifier comprehension using BOLD fMRI. We found activation of inferior parietal cortex during judgments of first-order quantifiers. This is consistent with the hypothesized role of number knowledge in first-order quantifier comprehension. Inferior parietal activation was also seen for higher-order quantifiers, suggesting that number knowledge plays a role in understanding these quantifiers as well. Furthermore, only higher-order quantifiers recruited dorsolateral and inferior prefrontal cortex. This is consistent with the hypothesized role of executive resources such as WM in higher-order quantifier comprehension. A direct contrast of these two classes of quantifiers confirmed the exclusive role of dorsolateral and inferior frontal cortex in higher-order quantifiers. Taken together, these findings support a large-scale frontal-parietal neural network for generalized quantifier comprehension and honor the linguistic theory that there are two classes of generalized quantifiers. We discuss these patterns of activation for generalized quantifiers in greater detail below.

4.1. All generalized quantifiers have in common number knowledge and activation of inferior parietal cortex

Our investigation revealed recruitment of right inferior parietal cortex when assessing both first-order quantifiers and higher-order quantifiers. This is consistent with the hypothesized role of number knowledge in the comprehension of both first-order and higher-order quantifiers. Neuroimaging studies have associated number knowledge with parietal activation (Burbaud et al., 1995; Cohen et al., 2000; Kazui et al., 2000; Le Clec'H et al., 2000; Pinel et al., 2001; Reuckert et al., 1996; Simon et al., 2002; Stanescu-Cosson et al., 2000) and patient studies have demonstrated loss of number knowledge following parietal lobe disease (Cipolotti et al., 1991; Dehaene, 1997; Dehaene & Cohen, 1997; Delazer & Benke, 1997; Halpern, Glosser et al., 2004; Rossor et al., 1995; Takayama et al., 1994; Thioux et al., 1998; Warrington, 1982).

A model of number knowledge proposed by Dehaene (1997) distinguishes between approximate and precise number knowledge. This theory suggests that the distinction between close numbers (e.g. 6 and 7) requiring precise number knowledge depends on a verbally mediated representation, and this involves recruitment of left peri-Sylvian language regions (Chochon et al., 1999; Cohen et al., 2000; Dehaene, 1997; Dehaene & Cohen, 1991; Stanescu-Cosson et al., 2000). Dehaene, Spelke, Pinel, Stanescu, and Tsivkin (1999) showed activation of inferior parietal cortex bilaterally and left orbital frontal cortex during an assessment of precise addition compared to approximate addition. These investigators argue that left orbital frontal activation mediates the verbal representation necessary for precise calculations, although orbital frontal cortex is not peri-Sylvian and is anterior to Broca's area that is traditionally implicated in language processing. We did not observe activation of left peri-Sylvian regions typically associated with language during comprehension of quantifiers, and the contrast of activations during comprehension of precise quantifiers minus approximate quantifiers also failed to demonstrate evidence for verbally-mediated precise number knowledge. Instead, we observed right inferior parietal cortex recruitment.

The finding of right parietal activation is consistent with the neuroimaging and patient literature investigating the neural basis of number knowledge. Studies such as Chochon et al. (1999) have demonstrated greater right hemisphere activation in a magnitude comparison task, but greater left hemisphere activation in a multiplication task. Le Clec'H et al. (2000) and Piazza, Mechelli, Butterworth, and Price (2002) have also demonstrated right lateralized activation of inferior parietal cortex associated with determining and manipulating the numerical quantities of a set. Moreover, our finding of right lateralized activation is consistent with a patient study demonstrating number knowledge impairment in CBD patients associated with right hemisphere parietal lobe disease (Halpern, Glosser et al., 2004).

It is unlikely that parietal and occipital activation is due to the spatial property of the object array since our design involved subtracting out the visual stimuli, with only the decision about the quantifier differing across phases of the stimuli. Moreover, quantifiers like "all *x*" and "some *x*" do not depend on the spatial properties of an array. We also note that the anterior prefrontal activation seen for the contrast of the approximate condition minus the precise condition is consistent with other fMRI studies of estimation and approximation (Bechara, Damasio, Tranel, & Anderson, 1998; Elliott, Rees, & Dolan, 1999; Sanfey, Hastie, Colvin, & Grafman, 2003).

Both first-order quantifiers and higher-order quantifiers activated the anterior cingulate region. This may be a task-related effect rather than one related to quantifier comprehension per se. Some investigators have associated anterior cingulate activation with resolving the competition between alternative responses (Botvinick et al., 2001; Braver, Barch, Gray, Molfese, & Snyder, 2001; Carter, MacDonald, Ross, & Stenger, 2001). Others have observed anterior cingulate recruitment during tasks that require selective attention (Coull, Frith, Frackowiak, & Grasby, 1996). Also, when comparing quantifiers with an explicit number to those without an explicit number, we found anterior cingulate activation. This could be due to the participants needing to attend to the specific number of objects displaying a property in an array. Evidence consistent with this attention-based account comes from the concurrent thalamic activation seen for higher-order quantifiers. The thalamus is also thought to play a role in selective attention (Frith & Friston, 1996; LaBerge, 1997; Shulman et al., 1997).

4.2. Working memory and prefrontal activation during higher-order quantifier comprehension

Assessment of the effect of quantifier order through a direct subtraction of higher-order quantifiers minus first-order quantifiers revealed recruitment of inferior frontal and dorsolateral prefrontal cortices. This activation is consistent with our hypothesis that executive resources such as working memory and switching contribute exclusively to the comprehension of higher-order quantifiers. Other neuroimaging studies have demonstrated recruitment of inferior frontal and dorsolateral prefrontal cortex in measures of working memory (Baker et al., 1996; Botvinick et al., 2001; Braver et al., 1997; Grady et al., 1998; Owen, 1997; Paulesu et al., 1993; Petrides, 2000; Smith & Jonides, 1999). Paralleling the role of WM resources during the comprehension of higher-order quantifiers, fMRI studies of sentence comprehension involving WM resources also incorporate dIFC regions in addition to peri-Sylvian activation of ventral portions of IFC and posterolateral temporal cortex in the left hemisphere (Cooke et al., 2002; Grossman et al., 2003). This suggests a large-scale neural network model of cognitive functioning where brain regions supporting core portions of a task are supplemented by other brain regions that support cognitive resources like WM.

It is also important to note that we observed no differences in prefrontal cortex activation when manipulating the stimulus arrays for precise and approximate judgments. According to our model the executive resources required for higher-order quantifiers, but not first-order quantifiers, are (a) holding one number property in mind while identifying another and (b) comparing properties in order to evaluate the truth-value of the proposition. A lack of differential activation across precise and approximate judgments is congruent with our model since precise does not imply more resources. In other words, regardless of the manipulation of the stimulus array, the same executive resources are required for higher-order quantifier comprehension.

In the absence of an explicit model where cardinalities can be judged, it may be argued that first-order quantifiers and higher-order quantifiers do not differ. However, even in the absence of such an explicit model, a sentence containing a higher-order quantifier communicates information about cardinalities that must hold in any acceptable model that satisfies the sentence; this information cannot by its very nature be reduced to first-order expressions. In other words, there is an inherent difference in the complexity of first-order and higher-order expressions (van Benthem, 1986). Indeed, the recruitment of prefrontal cortex only for higher-order quantifiers may be associated with the additional storage needed to maintain multiple number properties in an active mental state during comprehension, or with the switching and strategic manipulation involved in comparing the relative cardinalities of the sets in order to evaluate the truth-value of the proposition. Several neuroimaging studies have supported dorsolateral prefrontal recruitment in tasks involving switching and manipulation (Baker et al., 1996; Owen, 1997; Petrides, 2000; Smith et al., 2001), while others have shown results consistent with the increased storage account (Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999). It is beyond the scope of the present study to distinguish between the "increased storage" and the "switching" accounts—both of which are subcomponents of our higher-order quantifier model. The design of the present experiment also does not allow us to distinguish between modality-neutral and modality-specific forms of WM. Additional work thus will be needed to determine whether right inferior frontal activation is related to WM support for number knowledge, while left dorsolateral prefrontal activation is associated with manipulation and switching needed to compare critical values involved in understanding higher-order quantifiers.

It is also beyond the scope of this study to experimentally separate the meaning associated with a quantifier from the verification process used to assess word meaning. However, our finding of a different activation pattern in higher-order quantifiers relative to first-order quantifiers suggests that the activation we observed is due to differences in quantifier meaning rather than the verification process. This is further supported by our finding of right parietal activation for all quantifier comprehension, which has been demonstrated to contribute to number knowledge and to our awareness has not been demonstrated to contribute to the verification process per se in other investigations.

5. Conclusion

We have demonstrated support for anatomical differences in processing first-order and higher-order quantifiers. This difference is consistent with a model of quantifier comprehension implicating number knowledge for all quantifiers, and WM only for higher-order quantifiers. These findings honor the distinction between first-order and higher-order quantifiers posited by linguists and logicians, and provide neuroanatomic constraints on the constituents of quantifier knowledge.

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