Evidence for conceptual combination in the left anterior temporal lobe

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ABSTRACT

Conceptual combination allows for the construction of an infinite number of complex ideas from a finite base. The anterior temporal lobes appear to be important for the process of conceptual combination. In a previous study (Baron et al., 2010) we showed that the neural representation of complex concepts (e.g., *young man*) in the left anterior temporal lobe is additive. Specifically, in that region, the representation of a complex concept can be predicted by the superimposition of the voxel-wise neural representations of its constituent concepts (e.g., *young + man*). However, this finding could be the result of phonological similarity or the simple co-activation of constituent concepts. Here we use concepts that are only related semantically: *boy*, *girl*, *woman*, *man*, *female*, *male*, *child*, and *adult*. The neural representation for each concept was evoked through a visual categorization task. Subsequent brain maps were then analyzed using a searchlight analysis meant to show areas of the cortex where multiplicative (as well as additive) conceptual combination occurred (e.g., areas in which activations for *boy* correlated with the product of the activations for *male* and *child*). Across all participants, the left anterior temporal lobe showed such an effect.

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Conceptual combination is the construction of complex concepts from simple constituents (e.g., *red car* from *red* and *car*). This process allows the creation of an infinite number of novel ideas from a limited stock of simple ones (Fodor, 2008). The cognitive processes underlying conceptual combination have given rise to much discussion in psychology (Murphy, 2004); in contrast, the neural basis of conceptual combination has received less attention.

Cortical regions responsible for conceptual combination may be involved in conceptual and semantic representation generally. Candidate regions include the left lateral frontal cortex and anterior temporal lobes (ATL). Left lateral frontal cortex—most commonly regions on or around the inferior frontal gyrus (IFG)—is consistently activated in tasks requiring the retrieval of semantic knowledge (Thompson-Schill et al., 1998; Wagner et al., 2001). Patients suffering from semantic dementia, a neurodegenerative disorder of the bilateral temporal poles, have marked deficiencies in expressing knowledge about familiar objects, vocabulary loss, inability to generate exemplars from semantic categories, recognition deficits for subordinate-level categories, and marked deficiencies in reading fluency (Hodges et al., 1992; Snowden et al., 1996). These semantic deficits are positively correlated with the severity of cortical damage (Noppeney et al., 2007). Both regions also show a preference for stimuli that require semantic composition. Thus, the left IFG responds more to complete sentences than to words, and more to ambiguous than to unambiguous sentences (Snijders et al., 2009). Left ATL shows a similar response pattern, with increased

activation to sentences compared to unintelligible speech (Spitsyna et al., 2006), and to stimuli of increasing semantic complexity (Humphries et al., 2006). These findings have led researchers to suggest that the left lateral prefrontal cortex and ATL are the locus of semantic unification (a process wherein multilexemic samples of language are bound into complex and coherent ideas; Hagoort et al., 2009) and of conceptual combination (Hickok and Poeppel, 2007; Baron et al., 2010).

In our previous study (Baron et al., 2010) we found that in the left ATL, the voxel-wise neural representation of complex concepts (e.g., *young man*) can be accurately recreated by superimposing (adding) the neural representations of their constituent concepts (e.g., *young + man*). This additive conceptual combination suggests a simple mechanism that would allow the brain to represent complex concepts in a non-redundant fashion (i.e., complex concepts are not represented separately from their constituents). Although we controlled for phonological looping by unitizing complex concepts through a behavioral task that preceded brain imaging, the possibility remains that our results were caused by sub-vocal repetition (for example, repeating *young* and *man* while conceptualizing *young man*). In the present study, this potential phonetic confound is eliminated.

Here we examine conceptual combination with phonologically distinct concepts, namely: *girl*, *boy*, *man*, *woman*, *child*, *adult*, *female*, and *male*. These concepts were presented to participants for classification during functional magnetic resonance imaging (fMRI), and whole brain neural representations for each concept were acquired. As in our previous study, neural representations were gathered while participants viewed identical stimuli (e.g., stimuli seen while categorizing *male* were the same as when categorizing *child*). Thus any differences in representation were strictly due to conceptualization.

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We hypothesized that in conceptual areas, the sum of voxel-wise activations elicited by a given concept (e.g., *girl*) would be better correlated with the sum of the activations elicited by its semantic constituents (*child + female*) than with spurious combinations (e.g., *adult + male*). This prediction derives from our earlier work with explicit combinations (e.g., *young man* versus *young + man*).

But as already observed in our previous report (Baron et al., 2010), an additive relation between the activations for a concept and its constituents may not represent semantic combination so much as the co-activation of relevant concepts. For example, the activation of *girl* might also evoke the neural representations of both *child* and *female*. Their superimposition might then correlate with the sum of the representations for *child* and *female* considered separately, giving the impression of semantic integration. Yet the joint activation of *child* and *female* might be merely preparatory to their composition into *child*, which could be carried out subsequently via an operation distinct from the simple addition of activations. Indeed, addition is unlikely to govern the integration of conjunctive constituents as in *girl = child + female* inasmuch as deficiency in one constituent cannot be compensated by the presence of the other (i.e., *child* and *female* interact to create the meaning of *girl*). A multiplicative rule (*girl = child × female*) conforms better to the common usage of these concepts. The predictive superiority of multiplication compared to simple addition would be evidence for genuine composition rather than co-activation. It will be seen, however, that both simple addition and multiplication work well as functions that predict activations for concepts like *girl*, especially in the left anterior temporal lobe.

Method

Participants

Fifteen Princeton University graduate and undergraduate students (all female; 18–28 years old) participated in the fMRI study. Three participants' data were not included in subsequent analyses (one forgot the task, another fell asleep, and the third made excessive movements). All participants gave their written consent and were debriefed as required for studies approved by Princeton University's Institutional Review Board.

Stimuli

In the experiment we examined eight concepts: *female, male, adult, child, woman, man, girl,* and *boy*. To instantiate them, faces were gathered from images posted on flickr.com (each designated as "noncommercial" or unclassified). One hundred and twelve images were collected, 28 for each of *woman, man, boy,* and *girl*. Observe that the concept *adult* was satisfied by both *woman* and *man* stimuli; *child* by both *boy* and *girl* stimuli; *male* by both *boy* and *man* stimuli; and *female* by both *girl* and *woman* stimuli. The face stimuli for each concept consisted of approximately the same number of happy versus neutral expressions—no faces expressed negative emotions. *Man* and *woman* (i.e., *adult*) faces were restricted to images of adults who were approximately 25–45 years of age. *Boy* and *girl* (i.e., *child*) faces were restricted to images of children who were approximately 4–11 years of age. All images were converted to grayscale and rescaled to approximately the same size. Masking removed most aspects of the source image background. No participant recognized the identity of any of the face stimuli when queried at the conclusion of the experiment.

Seventy-two of the stimuli (18 for each of *man, woman, boy* and *girl*) were used to create six sequences of 12 (no faces repeated). These sequences will henceforth be referred to as "target" sequences and the faces that make them up "target" faces. Within every target sequence the concepts *man, woman, boy* and *girl* were instantiated three times; thus, each of the concepts *adult, child, female,* and *male*

were instantiated six times. Of the remaining 40 face stimuli, 16 were used as "hash mark faces." Superimposed on each of these hash mark faces was a single, randomly placed black hash mark (#). Twelve faces (four each of *man, woman, girl,* and *boy* stimuli) were also randomly selected from the target sequences to become hash mark faces (these 12 faces remained in their respective target sequences). The remaining 24 face stimuli were used as "filler" faces.

fMRI task

Prior to the fMRI experiment, participants were shown all of the faces used in the experiment. They were also shown randomly selected examples of hash mark faces. Participants were not allowed to begin the experiment until they were comfortable classifying each face stimulus as either a member or nonmember of our eight concepts. When asked if any face was an ambiguous or poor member of their specific concept, all participants stated that concept membership was always clear.

The fMRI task consisted of four different trial types. All trials consisted of a randomized sequence of faces—each presented for 850 ms followed by a 400 ms fixation cross. At trial onset participants were presented with a written display (for 5000 ms) of one of the eight concepts or the words "hash mark." If the trial was preceded by a concept label (e.g., "*boy*"), the participant had to decide the membership of each face in the given concept category. If prompted with "hash mark," participants were required to determine for each face whether it contained a hash mark; in these "hash mark" trials the presence or absence of a hash mark on a given face was randomly determined. Question marks would occasionally appear for 3000 ms within a sequence of faces. Upon encountering a question mark while classifying faces, participants would press one button with their index finger (confirming concept membership or presence of a hash mark) or another button with their middle finger (rejecting concept membership or indicating the absence of a hash mark) in reference to the last face they had seen.

Target trials were composed of a target sequence (12 faces), and lasted a total of 15 seconds. During these trials a question mark never appeared.

Catch trials consisted of a random sequence of one to 11 faces, followed by a question mark, and then a fixation cross. The fixation cross was presented for varying amounts of time, and was used to bring the total trial length to 15 s. These catch trials were composed of filler and up to four randomly selected target faces. We used catch trials to ensure participants' attention during target trials; participants had no way of distinguishing a catch trial from a target trial prior to the presentation of a question mark.

Hash mark trials consisted of a sequence of 12 faces taken from the filler and hash mark faces. During these trials a question mark never appeared. Like the target trials, hash mark trials lasted a total of 15 s.

Finally, *hash mark catch trials* were composed of one to eleven faces taken from the filler and hash mark faces, followed by a question mark, and then a fixation cross. As with the catch trials, the fixation cross brought the total trial length to 15 s. Hash mark and hash mark catch trials were used to separate verification of one concept (e.g., *man*) from the next concept (e.g., *woman*). In this way, the hash mark trials "cleared" the neural representation of concepts that preceded them. We also note that by including target faces in each of the trial types we prevented participants from distinguishing trials on the basis of faces shown.

fMRI procedure

Each participant completed an anatomical image scan followed by eight data acquisition runs. Each acquisition run consisted of six target, two catch, five hash mark, and two hash mark catch trials. Participants verified concept membership for each of the eight

concepts once per run (during the six target and two catch trials). These verification trials were interleaved with seven hash mark and hash mark catch trials. The order of the concepts verified in each run was pseudo-randomized such that each concept preceded or followed every other concept across the entirety of the experiment. Catch and hash mark trials occurred randomly within acquisition runs. Across all eight runs, each concept was verified within a target trial six times (and in a catch trial twice).

An important characteristic of our design is that the same six target sequences were used for concept verification for each of the eight concepts. This means that during target trials, different concepts were represented in the mind while viewing the same set of faces. Therefore any differences in neural activation between concepts must be the result of mental representation rather than the stimuli themselves. For any given target sequence, faces were presented in random order. This was done to prevent participants from recognizing when a target sequence was occurring. (Since no response was elicited during such sequences participants could have simply ignored them and attended only to catch trials.) In fact, no participant indicated knowledge of stimulus differences between target and catch trials when asked at the conclusion of the experiment.

Image acquisition

A high-resolution anatomical image (T1-MPRAGE, TR = 2500 ms, TE = 4.3 ms, FA = 8º, matrix size = 256 × 256) was acquired for functional data registration and cross-participant spatial normalization. We used blood oxygen level-dependent (BOLD) response as a measure of neural activation. Using a Siemens 3.0 T Allegra Scanner (Siemens, Erlangen, Germany) with a standard "bird-cage" head coil, we acquired echo planar images (EPI; TR = 2000 ms, TE = 30 ms, FA = 80º, matrix size 64 × 64). Via 33 interleaved 3 mm axial slices (1 mm inter-slice gap) whole brain coverage was achieved.

Image analysis

All fMRI data were processed using Analysis of Functional Neuro-Images software (AFNI; Cox, 1996). Each participant's motion was corrected using a six-parameter 3D motion correction algorithm following slice scan-time correction. All data were then spatially smoothed using a 6 mm full width at half maximum Gaussian kernel. Data were then low-pass filtered with a frequency cut-off of 0.1 Hz. Signal was then normalized to percent difference from the mean. Each participant's EPI data were then masked so that only brain regions contributing signal were kept.

Next, multiple regression was used to generate parameter estimates for each participant. Nine regressors of interest—hash marks and the eight concepts—were convolved with a canonical hemodynamic response function and entered into a general linear model. These regressors were specific to the 15 s target and hash mark trials. As mentioned above, during these trials participants were presented with every type of face; here we are modeling the entire span of each trial rather than responses to just the type of face being searched for. There were six target trials per concept and 40 hash mark trials across the entire experiment. All catch trials, motion estimates, and estimates of time-dependent linear and quadratic trends caused by scanner drift were included as regressors of no interest. The resultant parameter maps (in percent signal change) for each concept along with hash marks were projected into Talairach space (Talairach and Tournoux, 1988). These average voxel-wise neural representations were used in subsequent analyses.

Searchlight analysis

We carried out a searchlight (SL; Kreigeskorte et al., 2006) analysis on each participant's data using the AFNI Matlab library and Matlab (R2009b; Mathworks Inc, 2009). Specifically, every voxel in the brain was analyzed as the center of a 2-voxel radius sphere (the maximum number of voxels included in such a sphere was 33—fewer when the center voxel was near an edge of the brain). In each sphere, the voxel-wise neural representation of each concept was linearly scaled to run from zero to one. Then, valid conceptual combinations (CCs) for each of our four concepts were created. These valid CCs were as follows: *boy = child + male*; *girl = child + female*; *man = adult + male*; *woman = adult + female*. For each valid CC, the neural representations for the constituent concepts (e.g., *boy* and *girl*, for *child*) were added together. Within the sphere, spurious CCs were also created (three for each concept). These spurious CCs were as follows. For *boy*: *child + female*, *adult + male*, and *adult + female*; for *girl*: *child + male*, *adult + female*, and *adult + male*; for *man*: *adult + female*, *child + male*, and *child + female*; for *woman*: *adult + male*, *child + female*, and *child + male*. Williams test of dependent correlation (Steiger, 1980) was used to determine whether a given concept was significantly better correlated with its valid CC (e.g., *child + male* for *boy*) than with one of its spurious CCs (e.g., *child + female* for *boy*). Each concept's valid CC could be significantly better than three spurious CCs. Hence, up to 12 times (four concepts × three spurious CCs) a given concept could be significantly better correlated to its valid CC than to its spurious CCs. Consequently, our measure of performance—that is, the value attributed to the center voxel of each sphere—was a number between zero and 12. We assigned the score of zero to any SL sphere with less than ten voxels, and also to any sphere with ten voxels of the same value. For each participant, the SL analysis resulted in a brain map showing SL performance across the entire cortex. The preceding analysis was also completed with multiplication (e.g., *male × child = boy*) as a combinatorial function, in place of addition.

Group analysis

For both addition and multiplication (treated separately), we identified brain regions that showed conceptual combination across participants. In both cases, this was achieved by averaging the SL analysis brain maps for all participants. This average brain map was then masked to exclude voxels that were absent from the cortex of any participant's data. The group level threshold for significance was determined through a label-shuffle test. For each shuffle iteration, one randomly permuted order of labels for the eight concepts was generated, the same SL analysis described above was completed for each participant, and the results were averaged to create a group level brain map.

For each combinatorial function (+ and ×), a total of 800 label permutations were completed. For both addition and multiplication, this analysis revealed that the likelihood of finding a group level voxel with a mean SL analysis value greater than four corresponded to a voxel-wise α-level of $p < 0.0005$. We therefore thresholded the group average brain map for both functions at four. We note that our shuffle test acts as a familywise correction for multiple comparisons because it reveals the probability of attaining a given mean voxel value across the entire brain-space. Functional regions of interest (fROI) were defined as clusters containing more than twenty contiguous voxels.

Table 1a
Regions that process concepts multiplicatively across participants.

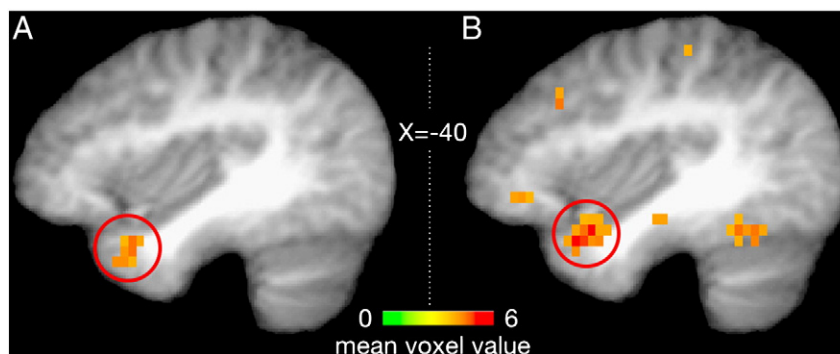| Region	Peak voxel (x, y, z)	Cluster volume (mm³)	Mean performance
L. anterior temporal lobe (BA38)	−40.5, 10.5, −24	1476	7.50
Bilateral posterior cingulate (BA23/30)	1.5, −31.5, 8	963	5.83

Fig. 1. Regions of the left anterior temporal lobe showing significant multiplicative (A) and additive (B) conceptual combination ($M = 4.75$; $p < 0.0005$ and $M = 5.33$; $p < 0.0005$, respectively). These statistical maps show average results of the SL analyses performed on all 12 subjects.

Results

Regions showing multiplicative conceptual combination across all participants

In the group analysis, two fROIs emerged from the use of multiplication as a combinatorial operation (Table 1a and Fig. 1A). There was a 1476 mm³ region of left anterior temporal lobe (lATL: BA38), and a 963 mm³ region of bilateral posterior cingulate cortex/ lingual gyrus (PCC: BA23/30; Fig. 2A). Across participants, the average number of times (out of 12) that a valid CC was better correlated with a concept than with any of its spurious CCs was 7.5 ($SD = 2.24$) for lATL and 5.83 ($SD = 1.75$) for PCC.

Regions showing additive conceptual combination across all participants

Twenty-two regions showed significant additive conceptual combination in the group analysis (see Table 1b). The second and ninth largest of these fROIs (2520 mm³ and 1692 mm³, respectively) overlapped the multiplicative lATL and PCC fROIs. In fact, 29% of the combined fROIs for addition and multiplication in lATL was common to both. For PCC, this overlap was 32%. In the additive lATL (see Fig. 1B) and PCC fROIs (see Fig. 2B), the average number of times (out of 12) that a valid CC was better correlated with a concept than with any of its spurious CCs was 6.17 ($SD = 1.99$) and 6.25 ($SD = 2.30$), respectively.

Comparing multiplicative and additive performance

Paired t-tests were used to compare the performance of regions that emerged from both the multiplicative and the additive group-level analyses; once again performance is quantified as the average number of times (out of 12) that a valid CC was better correlated with a concept than with any of its spurious CCs. Within the anterior temporal lobe, multiplicative-lATL ($M = 7.5$; $SD = 2.24$) performed significantly better than additive-lATL ($M = 6.17$; $SD = 1.99$; $t(11) = 3.22$, $p = 0.008$). There was no significant difference in performance between multiplicative-PCC ($M = 5.83$; $SD = 1.75$) and additive-PCC ($M = 6.25$; $SD = 2.30$; $t(11) = 0.92$, $p = 0.38$).

fROI performance was also assessed by calculating the median correlation across participants for each CC (both valid and spurious). For the multiplicative-lATL, three of the four concepts were better correlated with their valid CC than they were with any of their three spurious CCs (see Table 2a). Additionally, collapsing over the four concepts, the mean of the valid CC correlations was greater than the means of each of the three spurious CCs (see Table 2a). This was not the case for the additive-lATL fROI, where only two of the four concepts were better correlated with their valid CC than with their spurious CCs (see Table 2b). Further, the mean of the valid CC correlations was only greater than two of the spurious CC means. PCC did not perform as well. For the multiplicative and additive PCC fROIs, respectively, only two and one of the four concepts were better correlated with their valid CC than with any of their spurious CCs. Nonetheless, for both fROIs the mean correlation of the valid CCs was greater than the means of any of the spurious CCs; see Table S1.

Discussion

In our previous study (Baron et al., 2010), we observed additive conceptual combination in left lateral ATL. However, the complex concepts used in that study (e.g., *young man*) were phonologically related to their constituents (*young* and *man*). In the present experiment, we addressed this potential confound by using concepts that were related on a purely semantic level (e.g., *boy* versus *male* and *child*). We also compared the performance of additive combination to a more semantically appropriate multiplicative rule.

The significant additive conceptual combination here observed within the left anterior temporal lobe replicates the results of our
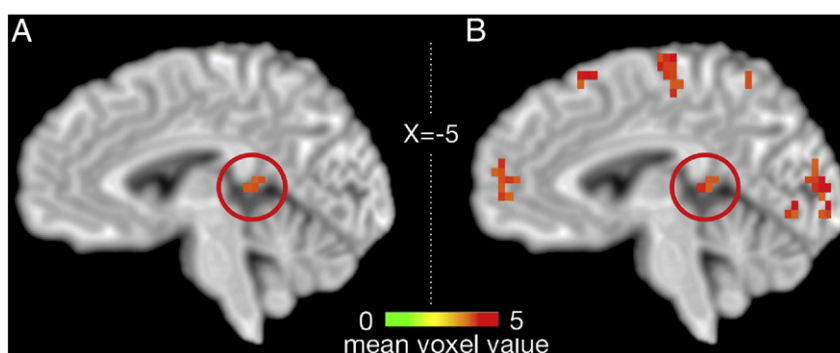

Fig. 2. Regions of posterior cingulate cortex showing significant multiplicative (A) and additive (B) conceptual combination ($M = 4.22$; $p < 0.0005$ and $M = 4.24$; $p < 0.0005$, respectively). These statistical maps show average results of the SL analyses performed on all 12 subjects.

Table 1b
Regions that process concepts additively across participants.

Region	Peak voxel (x, y, z)	Cluster volume (mm^3)	Mean performance
Bilateral primary visual cortex (BA17/18)	−1.5, −88,5, 12	2808	7.42
L. anterior temporal lobe (BA38)	−40.5, 10.5, −20	2520	6.17
R. inferior frontal gyrus (BA44/45)	52.5, 7.5, 4	2520	6.25
R. middle frontal gyrus (BA6)	46.5, 7.5, 44	1980	6.75
L. postcentral gyrus/precuneus (BA7)	−25.5, −49.5, 64	1908	6.83
R. precentral gyrus (BA4/6)	40.5, −13.5, 40	1800	7.33
R. postcentral gyrus (BA3/43)	55.5, −10.5, 24	1764	7.33
L. parahippocampal gyrus (BA28)	−19.5, −13.5, −20	1692	6.08
Bilateral posterior cingulate gyrus (BA23/30)	1.5, −31.5, 8	1692	6.25
R. cingulate gyrus (BA31)	4.5, −19.5, 44	1548	7.92
R. cingulate gyrus (BA32)	7.5, 13.5, 36	1512	6.67
R. inferior parietal lobule (BA40)	43.5, −55.5, 48	1512	6.25
R. superior frontal gyrus (BA10)	22.5, 46.5, 24	1188	7
R. superior parietal lobule (BA7)	10.5, −64.5, 56	1152	5.83
L. medial superior frontal gyrus (BA10)	−7.5, 52.5, 12	1080	6.33
R. medial superior frontal gyrus (BA8)	13.5, 31.5, 40	1044	6.17
R. fusiform gyrus (BA37)	46.5, −49.5, −12	1008	6.08
L. superior frontal gyrus (BA6)	−4.5, 16.5, 60	1008	6.92
L. fusiform gyrus (BA37)	−34.5, −49.5, 16	900	6.67
R. precentral gyrus (BA6)	37.5, −10.5, 56	828	7
R. middle temporal gyrus (BA21)	61.5, −4.5, −12	756	6.5
R. anterior insula (BA12)	34.5, 19.5, 16	756	7.25

Note. Peak voxel coordinates are referenced using Talairach coordinate system. The *mean performance* of a fROI is the average number of times that an appropriate CC performs better than spurious CCs across participants.

previous study while obviating concerns about phonological confounds. But as noted earlier, the success of additive combination may not reflect semantic composition at the neural level; it may rather result from the co-activation of semantically related concepts whose superimposition on the cortex yields additivity. Multiplicative combination, in contrast, is incompatible with the co-activation hypothesis inasmuch it rests on the interaction of conceptual constituents (rather than on simple overlay). Multiplication also makes semantic sense of concepts like *girl*, whose meaning implies the joint satisfaction of *female* and *child*.

It is thus of interest that in the present experiment, regions of the left anterior temporal lobe and the posterior cingulate cortex showed evidence of multiplicative conceptual combination. In these regions, the pattern of brain activity for a given concept was predicted by the product of activations for its constituents taken singly. The appearance of the posterior cingulate cortex was unanticipated, but it has been reported in other studies of semantic processing (Demonet et al., 1992, 1994; Pinel et al., 2001; Price et al., 1994). In fact, a recent meta-analysis found the posterior cingulate cortex to be one of the seven most reliably activated brain regions across 120 studies of semantic processing (Binder et al., 2009). Binder et al. (2009) suggest that this region mediates between semantic retrieval and episodic encoding (communicating representations from frontal regions to the hippocampal complex). In the present context, the multiplicative behavior of PCC might be driven by connections to lATL, or it may participate directly in conceptual combination (e.g., Graves et al., 2010). Further work is obviously needed.

It is well established that the anterior temporal lobes play an important role in conceptual processing (Patterson et al., 2007; Visser et al., 2009). The pathological deterioration of ATL negatively affects conceptual knowledge quite broadly (Snowden et al., 1996). The effects of pathology have been reproduced in healthy participants through temporary lesions of bilateral ATL induced by transcranial magnetic stimulation (Lambon Ralph et al., 2009). Moreover, the left ATL has been implicated in tasks requiring semantic composition and processing (Vandenberghe et al., 2002; Spitsyna et al., 2006; Humphries et al., 2006; Snijders et al., 2009). That conceptual combination was here observed within lATL is thus unsurprising, and provides further evidence for its importance in semantic processing.

Many of the regions that here showed significant additive combination have also appeared in previous studies of conceptual processing. The left hemisphere fusiform gyrus (Demonet et al., 1992; Baker et al., 2001; Binder et al., 2009), parahippocampal gyrus (Binder et al., 2009), medial superior frontal gyrus (Roskies et al., 2001), superior frontal gyrus (Devlin et al., 2002) and postcentral gyrus/precuneus (Pexman et al., 2007; Zannino et al., 2010), are all found to respond to semantic tasks. The same is true for the right hemisphere inferior frontal gyrus (Friederici et al., 2000), middle frontal gyrus (Burianova and Grady, 2007), superior frontal gyrus (Goldberg et al., 2007), middle temporal gyrus (Wible et al., 2006; Zannino et al., 2010), fusiform gyrus (Baker et al., 2001; Zannino et al., 2010), and insula (Goldberg et al., 2007). Since these regions fail to show multiplicative conceptual combination, it may be that the additivity

Table 2a
Median correlations for the multiplicative lATL fROI of valid and spurious CCs with each concept.

Concept	Valid CC	Spurious CC (partial match I)	Spurious CC (partial match II)	Spurious CC (no match)
Boy	**0.71**	0.51	0.62	0.36
Girl	**0.52**	0.41	0.45	0.23
Man	**0.57**	0.45	0.50	0.50
Woman	0.43	**0.50**	0.46	0.34
Mean	**0.56**	0.47	0.51	0.36

For each concept, the value of the highest performing CC is shown in bold.

Table 2b
Median correlations for the additive lATL fROI of valid and spurious CCs with each concept.

Concept	Valid CC	Spurious CC (partial match 1)	Spurious CC (partial match 2)	Spurious CC (no match)
Boy	**0.74**	0.56	0.62	0.50
Girl	0.53	0.53	**0.59**	0.46
Man	**0.64**	0.52	0.62	0.55
Woman	0.42	**0.54**	0.52	0.49
Mean	0.58	0.54	**0.59**	0.50

Notes. *Valid CCs* correspond to their concepts (e.g., *male × child* for *boy*). *Spurious CCs* (partial match 1) corresponds to the age constituent of the concept being present (e.g. *female × child = boy*). *Spurious CCs* (partial match 2) correspond to the gender constituent of the concept being present (e.g. *male × adult = boy*). *Spurious CCs* (no match) correspond to neither constituent of the concept appearing in the CC (e.g. *adult × female* for *boy*). For each concept, the value of the highest performing CC is shown in bold.

results from co-activation of semantically related concepts (rather than semantic integration).

Hagoort et al. (2009) suggest that the sensitivity of the left lateral frontal lobe to lexical ambiguity and multi-sentence utterances reveals its role in semantic unification. Such unification, however, may operate over more semantically complex representations than those manipulated by lATL. This might explain why no region of the left lateral frontal lobe showed significant evidence of composition in the present study.

Finally, it is well to underline the variety of combination rules underlying language and thought, of which the conjunctive relation between (for example) *girl* versus *female* and *child* is among the simplest. To illustrate with just one issue, conceptual constituents do not always interact in commutative fashion. Thus, whereas *female child* is semantically close to *child female*, the difference in meaning between *gold mountain* and *mountain gold* is more apparent. (See Graves et al., 2010 for a discussion of non-commutative semantic integration.) Understanding the basis of such complex phenomena will require insights from Linguistics as well as Neuroscience.

Conclusion

Within the left anterior temporal lobe, the voxel-wise activations associated with certain concepts can be predicted by multiplying the activations of their semantic constituents. This phenomenon might reflect a stage of conceptual combination, carried out in lATL. We note that both the present and earlier study (Baron et al., 2010) utilized social categories, and it is possible that our observations will not generalize to alternative concepts (e.g., *lion* and *dog*). However, the broad range of conceptual knowledge affected by lesions to ATL (Snowden et al., 1996) suggests that similar results might be obtained with other kinds of categories.

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2011.01.066.

Acknowledgments

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