Spatiotemporal Maps of the Brain Placing Regular and Irregular Verbs into the Past

Rupali P. Dhond * †, Ksenija Marinkovic †, Anders M. Dale †, Thomas Witzel †, Eric Halgren * †

* Dept. of Radiology, University of Utah, Salt Lake City, Utah 84105
† Nuclear Magnetic Resonance Center, Massachusetts General Hospital

Charlestown, MA 02129

Address correspondence to:

Eric Halgren
Massachusetts General Hospital Nuclear Magnetic Resonance Center
Room 2301, Building 149, 13th Street
Charlestown, MA 02129
Phone: (617) 726-5464; Fax: (617) 726-7422
halgren@nmr.mgh.harvard.edu
ABSTRACT:

Does the brain inflect verbs by applying rules, by associative retrieval of the inflected form, or both? Placing either regular or irregular verbs into the past tense sequentially activates bilateral visual, left inferotemporal, Wernicke’s, Broca’s and right prefrontal areas. At ~340ms, irregular verbs evoke greater activity in left occipitotemporal cortex, consistent with associative activation of past-tense forms. This may result in decreased grammatical processing, and thus less Broca’s activation at ~470ms. Increased right prefrontal activity at ~570ms may represent directed/effortful retrieval of irregular past-tense forms. Thus, the brain inflects verbs by dynamically activating different functional divisions of an integrated language system.
Most English verbs follow the simple rule of adding ‘-ed’ when they are placed into the past tense. Irregular verbs that do not follow this rule tend to fall into categories (e.g., ‘ring-rang,’ sing-sang’), leading to models where all verbs are placed into the past tense by following a limited number of rules (1). This view was challenged by connectionist models which did not require explicit rules for past-tense production, but directly associate phonological input and output units (2). A third approach notes that inflection of regular and irregular verbs is differentially affected by developmental factors and brain lesions (3-6). This leads to a dual-mechanism theory, where regular verbs are inflected using rules, and irregular via associative retrieval of the corresponding past-tense form (7). These data have also led to modification of the connectionist models to include semantic and other ‘hidden’ modules (8).

Since the rule-based and associative mechanisms are posited to involve different brain structures, the uniformity of the brain substrate for inflection of irregular versus regular verbs has become a crucial point of evidence in this debate. Normal brain activation during grammatical transformations has been imaged using Positron Emission Tomography (PET) and functional Magnetic Resonance Imaging (fMRI) (9). In one study (10), the left dorsolateral prefrontal cortex was activated during regular verb inflection while the left middle temporal gyrus was more active for irregular verbs. However, this and similar studies have been critiqued on methodological and theoretical grounds (11, 12).

Although PET/fMRI have good spatial localization, their temporal accuracy is poor (>1sec) in comparison with magnetoencephalography (MEG) and electroencephalography (EEG), which provide millisecond temporal resolution, and adequate spatial resolution (13). Several studies have found that reading incorrect irregular verbs or nouns evokes a left anterior negativity (LAN), whereas incorrect regular words do not (14-16). Additionally, priming
studies showed that regular past-tense forms serve as more powerful primes for their corresponding stems than do irregulars, thus lending further support for dual mechanism models (17).

These EEG effects were evoked either by the perception of grammatical mistakes, or by implicit cross-tense priming, and thus are difficult to compare to the PET/fMRI activations which were evoked by the generation of correct grammatical forms. Furthermore, the cortical origins of the EEG effects are unclear. Thus, despite important findings, the location as well as dynamics of cerebral processing underlying verb inflection remain to be established.

We made high-density measurements of the magnetic field simultaneously over the entire scalp while subjects were shown irregular and regular verbs in random order, and silently generated their past tense forms (18). The cortical surface was reconstructed, and the significance of activation was estimated from the MEG for each cortical location every 5ms (19). Cortical activation patterns were averaged across individuals and mapped onto an average cortical surface created by aligning individual sulcal-gyral patterns (20).

Inflection of irregular and regular verbs both evoked a posterior to anterior sequence of brain activation (Fig 1), consistent with classical models of language processing (21). The earliest brain response occurs at ~100ms post-stimulus in primary visual cortex at the occipital pole. Activation spreads rapidly to anteroventral occipital cortex where by ~165ms it is strongly lateralized to the language dominant, left hemisphere, an area that may be specifically engaged in encoding letter-strings and other word-like stimuli (22). Activation moves forward to left temporal regions by~240ms. Strong activation in the superior posterolateral temporal cortex encompasses classical Wernicke’s area implicated in lexico-phonemic processing including grapheme to phoneme conversion (21, 23). Overlapping activation is also present in
ventral occipitotemporal cortex associated with lexico-iconic encoding (24) as well as anterotemporal regions associated with lexico-semantic processing (25).

Thus, at an early latency, verbs activate areas that may encode them iconically, phonemically, and semantically. The dominant focus of activation continues to move forward, and by ~340ms includes left anterotemporal cortex with significant recruitment of inferior prefrontal regions. The prefrontal activation increases over the next 100ms, peaking at ~440ms with a strong left lateralization. The cortical distribution and timing of this response, as well as its attenuation with repetition priming, are similar to those of the N400 (24, 26-29). Shortly thereafter, by ~470ms, activation becomes more bilateral and spreads posteriorly to again involve occipitotemporal regions. Fronto-temporal activation continues until the end of the epoch, with prefrontal areas showing their greatest activity at the longest latencies. These areas include classical Broca’s area and surrounding regions in the left ventroposterior prefrontal cortex (21), as well as the right dorsolateral prefrontal cortex often activated during memory retrieval (30).

After ~200ms simultaneous activation is found in a large number of areas in multiple lobes. This activation is concentrated in language areas that are highly similar to those observed in other visual-verbal tasks, such as semantic judgments on nouns (26), word-stem completion (24), or explicit recognition (27-29). These data indicate that areas involved in semantic processing are strongly activated by a visual inflection task, calling into question early theories suggesting that verb inflection proceeds by purely phonological (2) or purely grammatical (1) manipulation. Within the context of strikingly similar spatiotemporal activation patterns evoked by irregular vs regular verbs, close examination of Fig. 1 suggests that there are subtle differences. The significance of these differences was evaluated by mapping the difference in
the magnetic fields evoked by inflecting irregular versus regular verbs in each subject. An average dynamic statistical parametric map was made for this subtracted condition, and activations at times when differences occurred are shown in Fig. 2. Significant differences did not occur until >300ms, i.e., after all elements of the widespread network invoked by this task (with the exception of right dorsolateral prefrontal cortex), had been engaged. Since inadvertent low level lexical and sensory differences between conditions, as well as strategic expectations due to non-random condition order, would be expected to produce differences in early activation, the lack of such differences increase the likelihood that later differences are actually due to the verb type.

The first significant differential response between irregular and regular verb inflection is seen in the left ventral occipitotemporal cortex, centered on the fusiform gyrus. A variety of data suggest that this area is engaged in lexico-iconic or “word-form” encoding, beginning at ~180ms (22, 24, 26, 28). The irregular/regular difference appears considerably later, at ~340ms post-stimulus, when irregular verbs evoke greater activation. Note that the irregular/regular difference does not appear until widespread frontotemporal language circuits have been engaged for >100ms, and that these circuits also show a non-significant tendency to be more active at ~340ms to irregular words, suggesting that the ventral occipitotemporal activation, centered in a lexico-iconic area, actually is the nexus of a more widely distributed activation. The dual-mechanism model states that while a separate lexical representation for the past tense is necessary for irregular verbs, it is in most cases unnecessary and unlikely for regular verbs (7). Thus, this model predicts that irregular verbs would evoke a more extended activation of locations where lexical representations are stored and/or accessed. The increased left ventral occipitotemporal activation at ~340ms to irregular verbs is consistent with that prediction.
The next location where significantly different activation occurred was Broca’s area, where activity was larger to regular verbs, maximal at ~470ms. Classical studies of agrammaticism, as well as modern neuroimaging studies suggest that this area participates in rule-based past-tense generation, syntactic parsing, and grammar (23, 31, 32). This finding suggests that rule-based syntactic processing may be greater to regular verbs, and thus is also consistent with the dual-mechanism model (7). However, Broca’s activation has been found in a wide variety of tasks in addition to syntactic processing, including semantic encoding (33), verbal working memory (34), and response selection (35). In the present study, incidental semantic encoding should be equal between conditions, and the temporal areas also implicated in this process showed only nonsignificant increases in favor of irregular verbs at this latency. Working memory demands should be greater for irregular verbs, which take longer to inflect (7, 11). Similarly, irregular verbs by definition have a variety of endings which might be considered as response alternatives, whereas regular verbs have only one. Thus, it seems unlikely that increased Broca’s activation to regular verbs would be due to semantic encoding, working memory, or selection from multiple response alternatives, as these functions are expected to be more strongly engaged by irregular verbs.

The third location where irregular and regular verb inflection differs in activation is the right dorsolateral prefrontal cortex at ~570ms to irregular verbs. Several neuroimaging studies have found activation in this area during intentional retrieval of words from memory (36). Again, this activation is consistent with predictions of the dual-mechanism model, as underlying the intentional recollection of the irregular past-tense verb forms (whereas the earlier inferotemporal activation may reflect automatic spread of activation to multiple lexical representations).
Since irregular verbs evoked more activity in some areas, and regular in others, these differences are unlikely to result from nonspecific factors such as differences in difficulty, and thus provide good evidence for differential localization of processing across conditions, i.e., for dual-mechanism models. However, it has been argued that such dissociations can also be obtained within single-process connectionist models by positing separate (but interacting) network modules for verb inflection and semantic associations, i.e., a single mechanism operating across two or more modules (8).

While the overall similarity in activation might tend to support unitary mechanism models, dual-mechanism models may include parallel activation in multiple processing areas that modulate each other as intermediate results are obtained. In such models, verbs do not arrive with a tag specifying that they are regular or irregular, automatically directing them to areas specialized for rule-application or lexical-retrieval; rather they are processed by both mechanisms until lexical-retrieval either finds a past tense form, or it definitively fails. Furthermore, associative activation of the irregular past tense form is hypothesized to inhibit rule-based inflection (7). The differential spatiotemporal dynamics when inflecting regular versus irregular verbs is consistent with this proposal; increased inferotemporal activation to irregular verbs at ~340ms may inhibit the Broca’s area response to the same stimuli at ~470ms.

In summary, these data demonstrate a progression of brain activation during inflection of visually-presented verbs, from areas associated with basic visual processing to those associated with wordform, then phonological, and finally semantic and syntactic processing. Within the context of largely identical activation to irregular and regular verbs, significant differences between these stimuli suggest a dynamic process where specialized language areas interact over an extended period. It may be useful to more precisely delineate the neurophysiological
mechanisms in models where the similarities and the differences between the neural activity evoked by irregular and regular verbs are equally important.
FIGURE LEGENDS:

Figure 1: Similar spatiotemporal patterns of brain activation during the inflection of irregular and regular verbs. Activation begins in occipital and progresses through temporal and then prefrontal cortices, engaging successively areas involved in perceptive, lexical, semantic, grammatical, and strategic processing. Snapshots of activity at 5 latencies from 165 to 570ms after word onset are shown for lateral and ventral views of the left and right hemispheres. Shortly after the onset of cortical activity in bilateral primary visual areas at ~100ms (not shown), activity spreads to specialized form processing areas in the anteroventral occipital cortex (avO). This activity peaks at ~165ms, and is strongly lateralized to the left (language dominant) hemisphere. By ~240ms, activation has advanced further anteriorly to encompass Wernicke’s area (Wa) and surrounding cortex in the left superior temporal lobe associated with lexico-phonemic representations, as well as ventral occipitotemporal (vOT) areas associated with lexico-iconic processing. By ~340ms, activation is predominantly in the anterior temporal lobe (aT) including areas thought to contain multimodal semantic representations. Activation then shifts by ~470ms to become more bilateral and frontal (including Broca’s area, Ba), with a reactivation of the occipitotemporal areas. At ~570ms activity is especially prominent in right dorsolateral prefrontal cortex (dlpF). Activity (threshold p<10^-8) is estimated from MEG for each patch of cortex, and averaged across 12 individuals. Cortical surfaces are inflated, with sulcal cortex in a darker shade of gray.

Figure 2: Significant differences in brain activation to irregular versus regular verbs in the first 670ms after word presentation. At ~340ms irregular verbs evoke greater activity in the left ventral occipitotemporal cortex (vOT), an area where lexico-iconic representations are thought to be stored or accessed. At ~460ms, regular verbs evoke greater activity in Broca’s area (Ba),
a location classically associated with rule-based grammatical transformations. At ~570ms activation again increases to irregular verbs, this time in *right* anterior dorsolateral prefrontal cortex (dlpF), as area associated with controlled retrieval and other strategic processes (threshold $p<10^{-5}$). Red/yellow indicates greater activation to irregular verbs; blue to regular. To the right of each brain is the time-course of the activation, for irregular and regular verbs considered individually, with an arrow at the latency of the image at left, and the height of the y-axis at $p<10^{-8}$. 


18. MEG signals were recorded from 204 channels at 0.1-100 Hz using a Neuromag VectorView in 12 normal right-handed native English-speaking males (18-30 years old). Separate averages of novel and repeated verb trials were constructed for each subject after artifact rejection. Subjects were shown 80 novel (presented only once) regular verbs, 80 novel irregular verbs, 5 repeated regular verbs (repeated 16 times each) and 5 repeated irregular verbs, for a total of 320 trials. Regular/irregular and novel/repeated trials were fully crossed and randomly intermixed. Verbs were presented in the central 5% of visual angle for 250ms in the infinitive form. Stimulus onset asynchrony was 2.3 sec. Irregular and regular verbs were matched for word frequency (average 234 for irregular and 240 for regular, p> .5, (37)), and number of letters (5.4 for both verb types). Subjects silently generated the past tense form, and then lifted their left index finger if it ended in “-ED”. Subjects fixated on a central “+” sign between words. Practice consisted of past tense generation to 4 repetitions of each of the 10 repeated verbs. Repetition strongly decreased activation in the left anteroventral temporal and posteroventral prefrontal cortices, maximal at ~400ms, as has been reported elsewhere for other verbal tasks (24, 26). All data reported here are to novel words. For novel words, response latencies ranged from 760 to 1196ms across subjects (mean 928±119ms), with 96±4.1% correct. Similar response times were found for overt verbal responses in otherwise similar studies (5). Analysis was terminated at 670ms (i.e., 100ms prior to the most rapid subject’s RT) in order to avoid interpretive confounds arising from the fact that only regular verbs evoked an overt behavioral response.
19. Geometrical representations of individual cortical surfaces were reconstructed (~150,000 vertices/hemisphere) from high-resolution 3-D T1-weighted structural images (1.5T Picker Eclipse). Source modeling followed the previously described anatomically-constrained linear estimation approach (24, 26). Normalization for noise sensitivity provides statistical parametric maps of cortical activity with relatively constant point-spread of ~10-15mm (26). Dipole orientation was unconstrained. The cortical surface was decimated to approximately 3000 dipoles per hemisphere, which is roughly equivalent to 1 dipole every 10 mm along the cortical surface.


38. We thank Bruce Fischl, Steven Pinker, Nedim Sahin, Maria Mody, Arthur Liu, Jeff Lewine, Kim Paulson, Bruce Rosen. This work was funded by USPHS (NIH grants NS18741 and MH57506), and the MIND Institute (DOE grant DE-FG03-99ER62764).
Fig 1.
IRREGULAR vs REGULAR

340ms left
Irregular > Regular

470 left
Regular > Irregular

570 right
Irregular > Regular

Regular

Irregular

p < 10^-8

Fig 2.