Research report

Individual differences in encoded neural representations within cortical speech production network

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HIGHLIGHTS

- Individuals consistently attend to either primarily words or primarily pictures.
- RSA was used to identify regions where meaningful information is processed.
- Individuals who attend to words process meaningful information in language regions.
- Processing in language regions occurs even when items were presented as pictures.

ABSTRACT

When two individuals view the same item, they do not necessarily perceive an item in the same way. If an individual is presented with a stimulus to be recalled later, the information that is encoded is dependent on the features of the stimulus to which one attends. Past studies have shown that, on the group level, verbal and visual information (e.g., words and pictures) are encoded in disparate regions of the brain. However, this account conflates external and internal representational formats, and it also neglects individual differences in attention. In this study, we examined neural and behavioral patterns associated with individual differences in attention to verbal representations—both external and internal. We found that the encoded neural representation of semantic content (meaningful words and pictures) varied as a function of individual differences in verbal attention, independent of the stimulus presentation format. Individuals who demonstrated an attentional bias toward words showed similar multivariate BOLD activity patterns within an *a priori* speech production network when encoding object names as when encoding pictures of objects. This result indicates that these individuals encode both words and pictures verbally. These effects were not found for non-semantic stimuli (pronounceable non-words and nonsense pictures). Importantly, as expected, no individual differences in neural representation were found in a separate network of regions known to process semantic content independent of format. These results highlight inter-individual divergence and convergence in internal representations of encoded semantic content.

Significance Statement: This study shows how tendencies to attend to word representations is associated with individual differences in encoded neural representations. Individuals who selectively attend to words instead of pictures process semantically meaningful information in language regions of the brain, regardless of whether the information was originally presented as a word or a picture. Though all participants encoded words and pictures similarly in regions that are known to represent domain-general semantic information, only the individuals who were biased towards word representations additionally processed both words and pictures in modality-specific verbal regions. These results demonstrate both the convergence and divergence between individuals that occurs during encoding of meaningful information.

Imagine two students studying a figure from a textbook. Even though they are both presented with the same content, the two

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individuals might encode different representations of that information. One student might remember the steep sloping incline from the figure, while another student might remember the phrase "exponential growth" from the accompanying figure caption. Though this makes sense intuitively, a long-standing body of research indicates that words and pictures are processed separately in the brain. Evidence from early studies on the neural basis of encoding support the theory of material-specific encoding—that image and language representations are localized to separate hemispheres in the brain (Milner et al., 1991). For instance, lesions in the left medial temporal lobe interfere with verbal memory whereas lesions in the right temporal lobe interfered with memory for non-verbal material. Since then, a large body of work has examined the left-hemispheric association with language and the right-hemispheric association with visuospatial processing (Golby et al., 2001; Gross et al., 1972; Miller et al., 2012; Milner, 1971; Milner, 1972; Milner, 1982; Kelley et al., 1998; Kelley et al., 2002).

However, more recent research has revealed a high degree of inter-individual variation even at the level of basic information encoding (Casasanto et al., 2002; Kirchoff and Buckner, 2006; Miller et al., 2002; Miller et al., 2009). These patterns are stable across time, demonstrating systematic differences in how individuals encode and retrieve information (Miller et al., 2009; Miller et al., 2012). Behavioral and neural differences in information retrieval are additionally linked to self-reported visual and verbal habits of thought, e.g., using a word-based approach versus a mental-imagery-based approach during a memory task in which information is presented via words or pictures (Hsu et al., 2011; Kirchoff and Buckner, 2006; Kraemer et al., 2009; Kraemer et al., 2014; Miller et al., 2012).

The present study uses both words and pictures to examine how individual differences in attentional biases for words affects encoding of information in both formats. When encoding highly imageable words and easily nameable images, participants may encode the material according to their individual habits of thought, e.g., by using verbal labeling. Whereas the typical model of material-specific processing predicts that all participants encode verbal information in left hemispheric language regions and picture information in right hemispheric visual regions, the individual differences research cited above suggests that different patterns of activity may be observed between participants in addition to these group-level similarities. Specifically, we predict that individuals who attend to verbal representations will encode both verbal and visual content similarly, using verbally-associated regions, i.e., a cortical speech production network.

Whereas previous studies have focused on encoding of words (Miller et al., 2012) or pictures (Kirchoff and Buckner, 2006), participants in this study were presented with both words and picture stimuli, allowing for analysis of the representational similarities of meaningful content, regardless of original presentation format (word or picture). We used a novel behavioral task to measure individual habits of thought in terms of attentional bias to verbal information (similar to Amit and Greene, 2012). This Attentional Bias Task leverages conflicting verbal and pictorial information during a speeded judgment task to measure implicit bias for attending to word representations compared to picture representations. Participants preferentially attending to words is expected to correspond to a verbal internal representation of the material. Given that phonological processing casually influences language comprehension, we predict that participants who are more biased towards attending to words would show similar processing in language network regions for encoding meaningful words and pictures (Shomers and Pulvermüller, 2016).

In contrast to these individual differences predicted for modality-specific neural representations, activation patterns are expected to be more similar between individuals in a network of brain regions associated with semantic retrieval across content (Binder et al., 2005; Frankland and Greene, 2015; Shinkareva et al., 2011; Thompson-Schill, 2003). For example, Shinkareva et al. (2011) demonstrated multi-variate similarity between neural responses to object pictures and

object names, such that semantic category was accurately classified regardless of original presentation format. Therefore, a content-independent semantic processing network is expected to show similar representations across participants. Further, material-specific brain regions—specifically the speech production network—are predicted to reflect individual differences in representational format, regardless of how that content was originally presented.

1. Results

Attentional Bias Task. The task was designed to assess Word Attentional Bias based on the percentage of trials where, when given conflicting verbal and visual information, participants relied on the word to respond. A subtraction score was calculated for each participant comparing the percentage of trials participants responded to words versus pictures (Word Attentional Bias score: % Word trials – % Picture trials). This created single score for each participant, ranging from −1 (only selected pictures during incongruent trials) to 1 (only selected words during incongruent trials). These Word Attentional Bias scores indicated both the type of content that each participant selectively attended to as well as how consistently each participant was drawn to that type of content. Trials where participants gave an invalid response (e.g., pressing the "spade" key when the trial was a picture of "heart" labeled "club") were discarded. Though participants were split on whether they preferred words or pictures, each participant was relatively consistent in their Attentional Bias across trials (Fig. 1). Even the three participants with the least consistent Attentional Biases (closest to 0) still tended to choose one content type 10–20% more often than the other. Word Attentional Bias was significantly negatively correlated with higher accuracy during the picture memory test, r (26) = −0.44, p = .017. Importantly, neither verbal nor visual cognitive style significantly correlated with any behavioral measure in the intentional encoding task. This indicates that this measure of Attentional Bias was able to predict behavioral outcomes which were not predicted by any other measure

Representational Similarity Analysis Results: The searchlight representational similarity analysis (RSA) looked for regions of the brain where the neural signal reflecting semantic similarity (i.e., where words and object pictures are similar to each other but dissimilar to pseudo-words and abstract pictures; Fig. 6). Broad patterns of activity (Fig. 1B) clearly differed depending on whether a participant had a positive or negative Word Attentional Bias score. To determine how individual variation in Word Attentional Bias affected neural processing of meaningful words and pictures, the vector of each individual's Word Attentional Bias scores were correlated with each individual participant's permutation-corrected RSA Z-maps at each node (Fig. 2).

In order to determine whether the regions of high semantic content for participants with positive Word Attentional Bias include linguistic processing regions for items presented in both word and picture format, a network of regions of interest was isolated using the NeuroSynth (www.neurosynth.org; Yarkoni et al., 2011) reverse inference map for "speech production". This map can be used to indicate areas that are selectively active for speech production (created through meta-analysis of 86 studies, thresholded at FDR corrected 0.01), and it is an alternative method to generate networks based on keywords rather than selecting anatomical ROIs. These masks were used to identify networks of regions used in material-specific processing to determine if there are significant differences in how similarly words and pictures are represented in those regions depending on a preference for verbal or visual information. The "speech production" network map was overlaid onto each participant's permutation-corrected z-map from their individual RSAs with the semantic model, and the average permutation-corrected z-value from within that mask was taken from each participant. These values were then correlated with their Word Attentional Bias subtraction score, (the degree to which a participant is more biased towards words over pictures). This correlation was significant, r
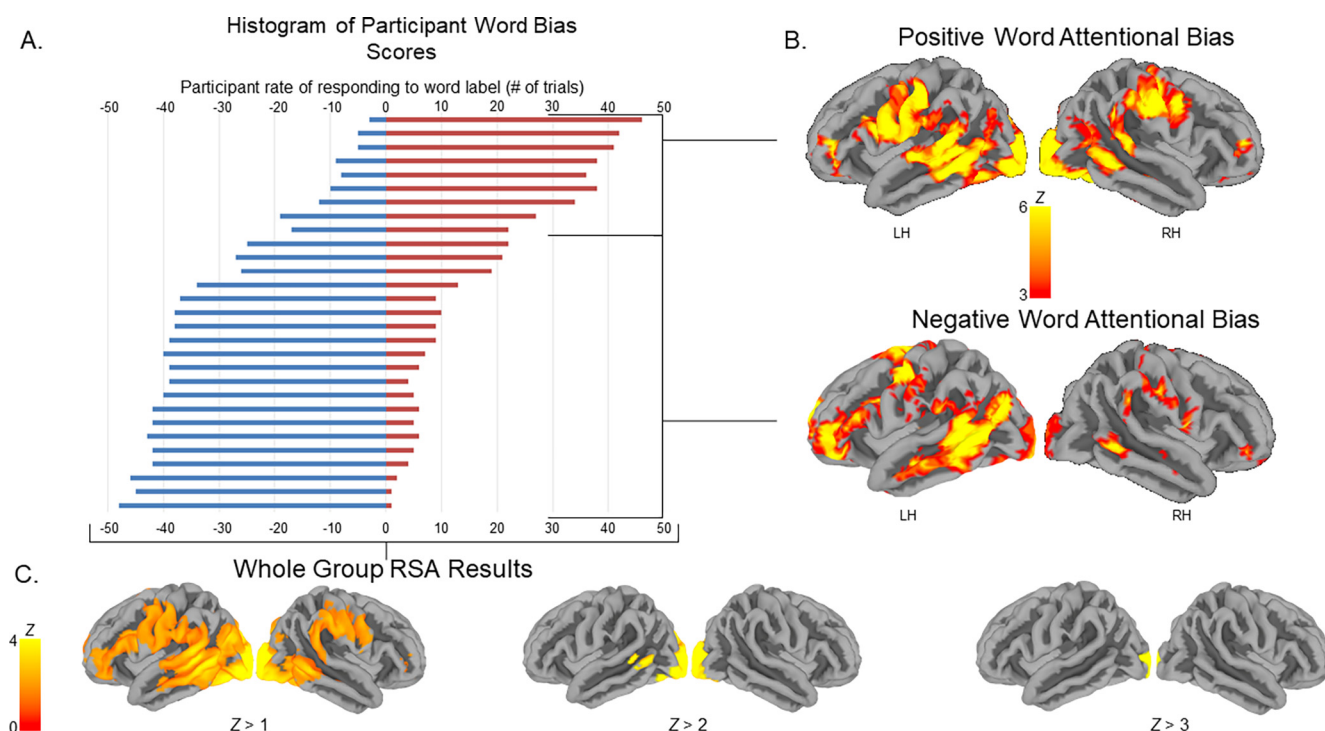
Fig. 1. There are distinct patterns of neural activity depending on the level of Word Attentional Bias. A. Histogram of Word Bias by participant, indicating on how many trials individual participants responded to the picture or to the word. Word Attentional Bias were calculated by subtracting the percentage of trials that participants responded to pictures from the percentage of trials participants responded to words, such that a Word Attentional Bias score of 1 indicated that participant always responded to words. B. Averaged individual permutation-corrected semantic model RSA Z-maps, split at the 0 mark between positive and negative Word Attentional Bias. These groupings are solely displayed to demonstrate broad patterns of RSA results, particularly in peri-sylvian language regions. Participants are analyzed as individuals in all further analyses. C. Whole brain RSA results for the whole group. Unlike when participant results were considered based on Word Attention Bias scores, permutation-corrected Z values were lower across the whole brain. The broad pattern of results resembles an average of the two groups when thresholded at $Z > 1$ (not significant), only a small occipital cluster remains at $Z > 3$. All maps are thresholded at $Z > 3$, except where otherwise indicated.
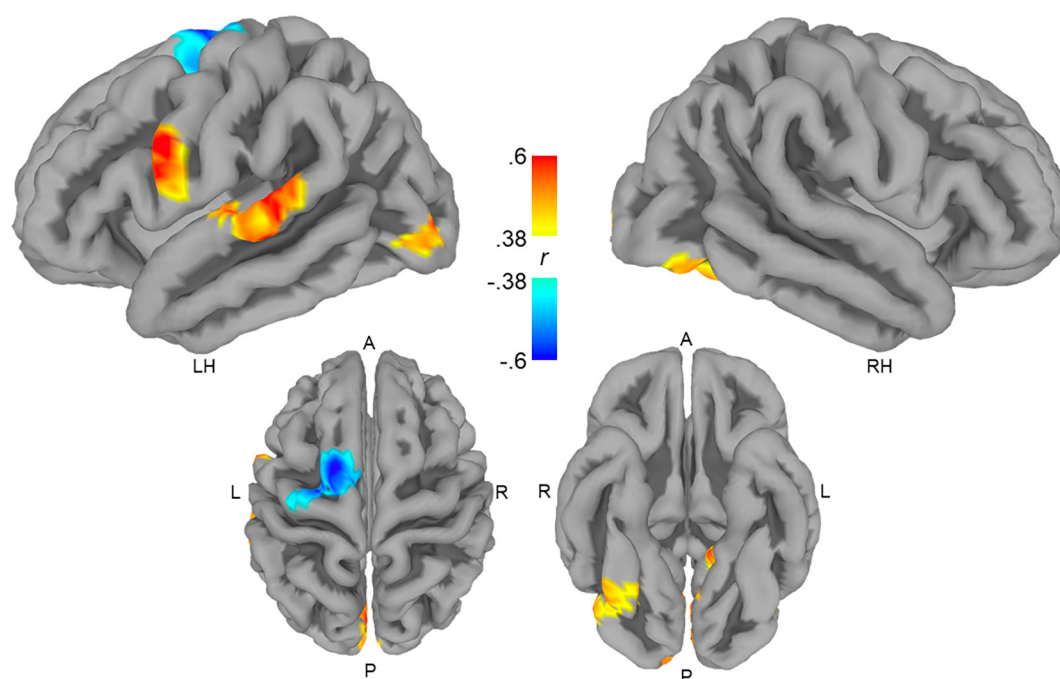

Fig. 2. Positive Word Attentional Bias scores correlate with the semantic RSA model in language regions and Negative Word Attentional Bias scores correlate with the semantic RSA in the frontal eye field. At each node, each participant's permutation-corrected Z for the semantic RSA was Pearson correlated with their Word Attentional Bias score. The resultant correlation map was further bootstrap cluster corrected (for clusters significant at $p < .001$, $\geq 189\,mm^2$ per cluster) and the map was thresholded at nodes that are significant, $p < .05$.
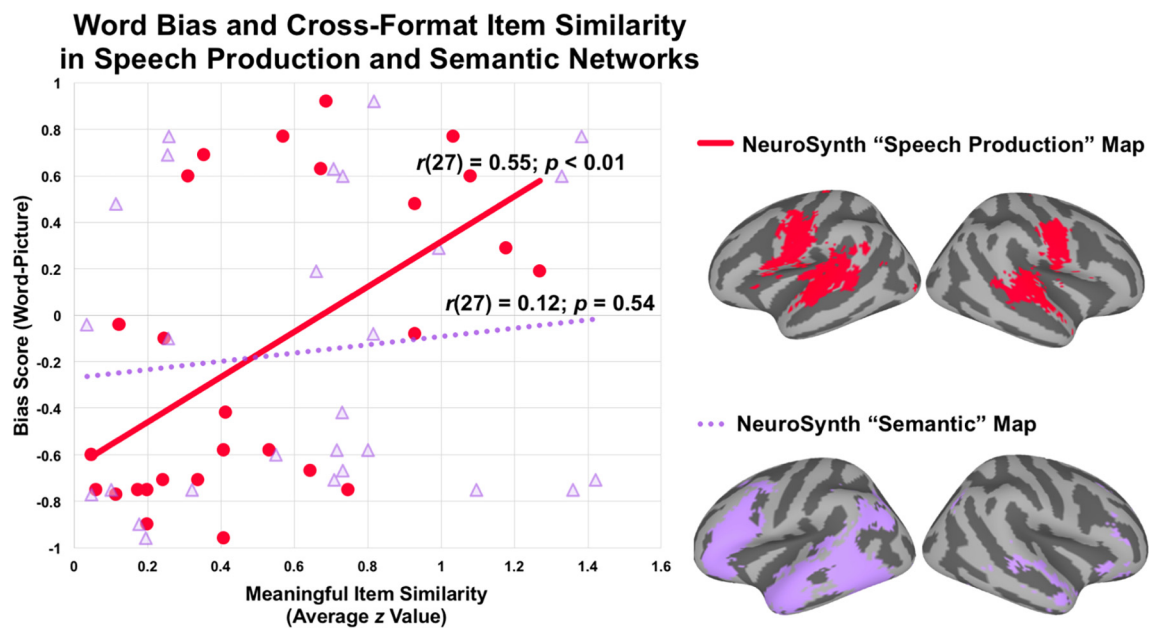
Fig. 3. Correlations between average permutation-corrected *z*-value in "speech production" and "semantic" reverse inference maps and Word Attentional Bias score. The more biased a participant was towards verbal information, the more similarly words and pictures were represented in areas selectively active during speech production. This relationship was not seen with the semantic network, used as a control.

(26) = 0.55; $p < .001$, Cohen's $d = 1.32$ (Fig. 3), indicating that being more biased towards verbal information predicts higher levels of semantic processing in regions of the brain associated with speech production.

As a control, the NeuroSynth reverse inference map for "semantic" (844 studies) was used to get the average permutation-corrected *z*-value for each participant within that region. Notably, this meta-analytic map highlights, among other regions, a large portion of lateral mid-temporal cortex which has been implicated across a number of studies as playing a critical role in the retrieval of semantic information (Binder et al., 2005; Frankland and Greene, 2015; Shinkareva et al., 2011; Thompson-Schill, 2003). RSA results within this network were expected to show equal correlation with the semantic dissimilarity matrix for all subjects, and therefore should not correlate with a positive Word Attentional Bias. As expected, the semantic map did not significantly correlate with positive Word Attentional Bias, $r(26) = 0.12$, $p = .54$, in contrast to the significant correlation between the speech production map and Word Attentional Bias (Fig. 3). Further, a slope test revealed that the two correlations are significantly different from each other, $z = 5.233$, $p < .001$. This reinforces the result that the participants who are more biased towards words show a higher level of similarity in processing words and pictures in regions known to selectively process speech production.

2. Discussion

Regardless of whether information was originally presented as words or pictures, that information is represented in the same way in areas related to speech production in participants with verbal habits of thought. This study contributes to a growing body of work that shows that habits of thought have a sizeable effect on cognitive processes (Kraemer et al., 2009; Kraemer et al., 2014; Shin and Kim, 2015; Thomas and McKay, 2010; Zarnhofer et al., 2012; Zarnhofer et al., 2013). Even further, the relationship between patterns of neural activity while studying meaningful words and pictures and Word Attentional Bias score is specific to the speech production NeuroSynth map; there was no such relationship within the semantic NeuroSynth map. The regions contained in the semantic map, specifically across a large area of the lateral mid-temporal cortex, has been previously implicated

as being central to the retrieval of semantic information (Binder et al., 2005; Frankland and Greene, 2015; Shinkareva et al., 2011; Thompson-Schill, 2003). Because there is no correlation between Word Attentional Bias score and the patterns of activity for meaningful words and pictures in this region, this effect is not simply due to participants with a stronger Word Attentional Bias processing words and pictures more similarly than participants with a weaker Word Attentional Bias. In other words, whereas all participants encode words and pictures similarly in semantic processing regions, participants with a strong Word Attentional Bias encode words and pictures more similarly in speech production regions compared to participants with a weak Word Attentional Bias.

Further, Word Attentional Bias influenced the localization of semantic similarity between participants. Clusters for participants with a positive Word Attentional Bias were centered around the left supramarginal gyrus (SMG) and insula as well as left primary visual cortex. The left SMG has previously been reported as important for people with a verbal cognitive style during a picture memory task that involved translating pictures into word labels (Kraemer et al., 2014). The stronger a person's verbal cognitive style, the more impaired they were by the repetitive Transcranial Magnetic Stimulation to this region. The left insula has also previously been shown to be associated with language, such as with speech production (Ackermann and Riecker, 2004; Ardila, 1999) which was commonly reported by participants with a positive Word Attentional Bias during the debriefing after the memory task. Conversely, clusters for the participants with negative Word Attentional Bias were evident in the left IT and frontal eye fields. Inferior temporal cortex is strongly associated with object recognition and processing in the ventral visual stream, necessary for processing semantically relevant objects (Mishkin et al., 1983; Kriegeskorte et al., 2008; Ungerleider and Haxby, 1994). Frontal eye fields have previously been shown to be associated with visual attention and planned saccades to details in an image (Fischer and Breitmeyer, 1987; Muggleton et al., 2003).

Attentional bias, like cognitive style, falls under the broader umbrella of an individual's habits of thought- the way that an individual consistently experiences and represents the world. When an individual attempts to commit information to memory, what is ultimately encoded depends on what the individual attends to. While habits of thought refer

to the internal representation that an individual constructs, this representation is made up of the information that the individual selectively pays attention to. Both Attentional Bias and internal preferences are part of an individual's habits of thought, and these constructs have been shown to interact in previous research. For example, a related line of research has examined how the construct of cognitive style, which refers to ways that individuals consistently prefer to process material (e.g., visually or verbally), is in turn linked to inter-individual differences in the modality in which information is encoded (Kraemer et al., 2009; Kraemer et al., 2014; Miller et al., 2012). Participants' cognitive styles influence whether participants attend to (and therefore, encode) nameable landmarks or spatial information (relative directions) while navigating a virtual environment (Kraemer et al., 2017). Landmarks were easier to label verbally than judgments of relative direction, and therefore participants with a more verbal cognitive style were also more likely to focus their attention on landmarks. This interaction between cognitive style and Attentional Bias demonstrates that individuals have consistent habits of thought that both changes what sorts of information an individual focuses on, as well as the internal representation they build of that information.

Alternative methods to access individual differences in habits of thought, such as the Attentional Bias task that we introduce here, are a promising way to study what information participants are actually relying on. Although a large body of work has highlighted individual differences in verbal and visual processing (see Alfred and Kraemer, 2017 for review), self-report measures can be unreliable. Behavioral measures, such as measuring preferential attending to a particular material type, allow for the ability to capture these habits of thought directly. These results using Attentional Bias to reflect these habits of thought lend further support to the argument that differing preferences for verbal or visual material can lead to significant changes in neural patterns of activity during intentional memory encoding tasks.

One limitation of the Attentional Bias task in the current design is that it does not separate between object visualizers and object spatializers—two distinct categories of people typically lumped together in the "visual" cognitive style (Blajenkova et al., 2006; Blajenkova and Kozhevnikov, 2009; Kozhevnikov et al., 2005). While this is not a problem for this study due to its focus on participants with verbal habits of thought, this may pose problems for further studies that attempt to use the task to study individuals with visual habits of thought. Further, Attentional Bias did not significantly correlate with cognitive style, ($r = 0.27$, $p = 0.15$), though this not necessarily problematic. Though both measures are attempting to tap into the same construct, Attentional Bias significantly correlates with performance on memory tasks, whereas cognitive style only correlates with itself. Therefore, it's not clear that cognitive style as measured by the VVQ is superior to the Attentional Bias measure of habits of thought. Further research can clarify the relationship between Attentional Bias and traditionally measured cognitive style, as well as try to build alternative behavioral measures of cognitive style.

It remains an open question whether having specific habits of thought would improve an individual's performance on a given task or make it worse. Benefits could potentially come from translating labels from the given format to the preferred format (Fiorella and Mayer, 2016). Even when a task can be completed solely through visual information (e.g. novel category learning), participants were faster to learn the categories when given a redundant verbal label (Lupyan et al., 2007). This relationship was beneficial only when assigning verbal labels to visual information and not vice versa (Lupyan et al., 2007). Alternatively, it is possible that verbal overshadowing could lead to worse performance on a task if a participant is creating verbal labels for visual material (Dodson et al., 1997; Meissner et al., 2001; Schooler and Engstler-Schooler, 1990), and that cognitive style may interact with the verbal overshadowing effect (Ryan and Schooler, 1998). While this study cannot make any specific claims about which is more likely, participants who were biased towards preferring words ultimately

performed slightly worse on the picture memory task. Ultimately, future work should continue to include a variety of individual difference measures, especially measures designed to capture the ways that individuals preferentially process different types of material. Not only can a preference for processing specific materials lead to processing other materials in the preferred format, these preferences can predict memory performance on tasks not in the preferred format. This study confirms that patterns of behavioral responses and neural activity are highly idiosyncratic and this variation should not be averaged away as noise. Rather, when the variation is studied and carefully parcellated, it can reveal consistent changes in the neural patterns of activity between participants, which are necessary for understanding the factors that contribute to individual differences in thought.

Finally, this study puts a finer point on the results of previous work demonstrating broad associations between left-hemispheric processing of verbal content and right-hemispheric processing of visuospatial content. It is not simply the case that visual information is processed in the right hemisphere. Rather, depending on that individual's bias towards processing verbal information, content originally presented in the form of a picture may be represented linguistically. This study demonstrates that material presented in a specific format is not necessarily represented in that format, but rather that processing of specific materials is dynamic and depends on individual differences in cognitive habits of thought. These individual differences must be accounted for when examining the neural representations of the concepts that comprise human thought.

3. Method

Participants. Twenty-eight (16 female, $M_{AGE} = 20.7$) undergraduate and graduate students at Dartmouth College, who were right-handed native English speakers with normal or corrected to normal vision took part in this study. None of the participants had any history of neurological or psychiatric disorders. All participants provided informed written consent and were compensated with a choice of cash or course credit for their participation, in accordance with the Dartmouth's Committee for the Protection of Human Subjects.

Measures of visual and verbal cognitive style. Visual and verbal cognitive styles were assessed through a computerized presentation of the revised Visualizer-Verbalizer Questionnaire (VVQ) (Kirby et al., 1988) during a post-scanner session that occurred a couple of days after the initial fMRI task. Cognitive style was measured on two separate dimensions for the degree to which a person had the verbal cognitive style and the degree to which a person had a visual cognitive style. Participants indicated how much they agreed with each of 20 statements on a 7-point Likert scale, from 1 (strongly disagree) to 7 (strongly agree). Half of the questions for each dimension were reverse scored. The "dream vividness" dimension of questions was omitted from the questionnaire because the positive correlation between the visual subscale and visuospatial abilities was only observed after elimination of the questions relating to dream vividness (Kirby, 1988).

Measures of visual and verbal cognitive abilities. Participants took the long form of the Automated Working Memory Assessment (AWMA; Alloway et al., 2008) to obtain measures of visual and verbal working memory, as well as visual working memory. In addition, participants visual and verbal IQ scores (Verbal Comprehension Index (VCI) and Perceptual Reasoning Index (PRI) components respectively) were obtained through the Wechsler Abbreviated Scale of Intelligence (WASI; Weschler, 1999). All behavioral tests were taken out of the scanner and on a separate day from the fMRI task.

Verbal Attentional Bias task. This novel behavioral task measured the degree to which participants attended to visual and verbal information. In each trial, participants were shown a card suit symbol and an accompanying text label, and were asked to press a key to identify whether they were being shown club, spade, or heart (Fig. 4A). The specific instructions provided to participants were as follows, "Please respond
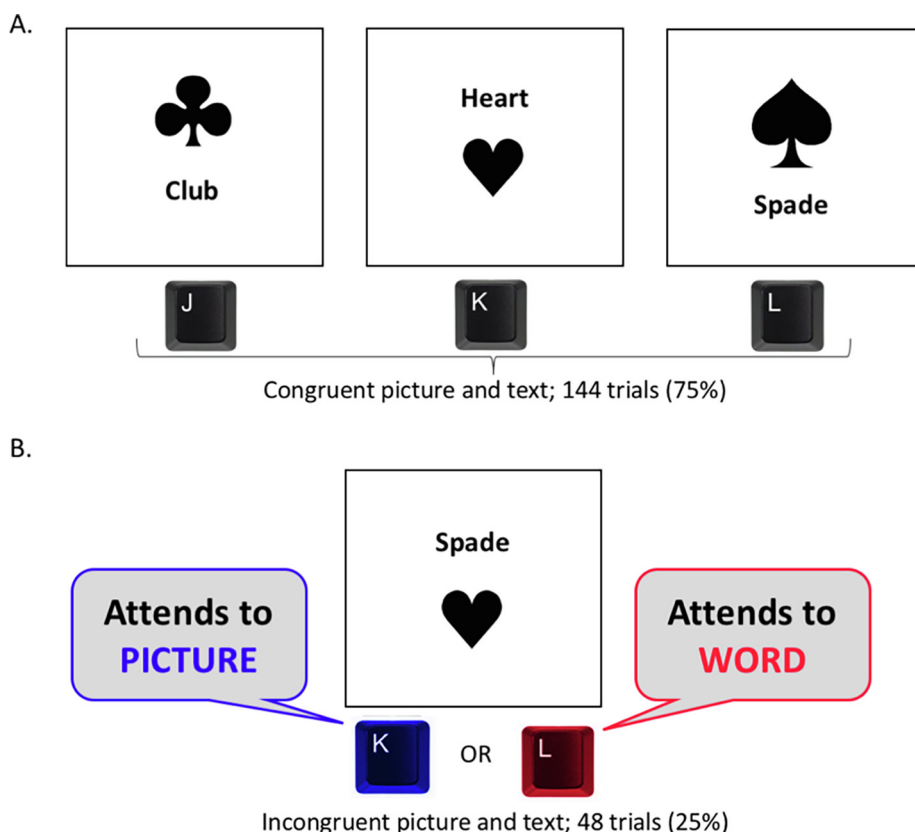
A.

B.

Fig. 4. Attentional Bias task structure. A. Participants were instructed to press J when shown club, K for heart, and L for spade and respond as quickly and accurately as possible. Most trials (75%) presented congruent word and picture information. B. Some trials (25%) unexpectedly presented a word and picture that were incongruent. Participants had to rapidly decide to select the key corresponding to the picture (in this case, responding K for heart) or word (in this case, responding L for spade).

as quickly and as accurately as you can. Use three fingers on J, K, L pressed by the index, middle, and ring fingers respectively. 'J' corresponds to club. 'K' corresponds to heart. 'L' corresponds to spade (in alphabetical order). Open the door and get me when the experiment is complete."

Out of a total of 192 trials, 144 (75%) presented congruent information—i.e., the text labels matched the symbols shown. In 48 (25%) of the trials, however, participants were shown incongruent information, where the picture and the text label had conflicting information (e.g., a picture of a club with text that says "spade"). Participants were not informed that there would be any incongruency between the picture and word presented. The experimenter was present for a set of practice trials that were only congruent trials, and then left the room so the participant would need to determine which piece of information was most salient. Word Attentional Bias was calculated as the percentage of incongruent trials for which the participant pressed the key for the verbal label (Fig. 4B). Each of the three suits was the target image an equal number of times, and the location of the text was counterbalanced for presentation above and below the picture. The center of the screen was always centered between the picture and the text. This task was completed in an out-of-scanner behavioral session within a week after the fMRI task, in one session along with the other behavioral measures.

Word and picture intentional encoding task (fMRI task). During fMRI scanning, participants were presented with a series of items to memorize. The items were presented in blocked lists of words, pseudowords, pictures, and abstract pictures to measure neural activity during intentional encoding processes (Fig. 5). Participants were instructed to pay attention to the stimuli for a later test using the specific instructions, "In this section you will see a series of words. Pay attention to each word and try to remember it - your memory for these words will be tested later. You should also pay attention to when an item has been presented more than once. When you see a word appear for the second time, press the button with your right index finger. Otherwise do not

press a button." These instructions were used for the Object Name and Pseudo Word conditions. In conditions with Object Pictures and Abstract pictures, the word "word" in the instructions was changed to say "picture". Each participant completed a total of 4 study blocks and 2 test blocks. During study blocks, participants studied a set of words, pseudowords, pictures, or pseudo-pictures while watching for repeated items. After memorizing a list of real (English) words and a list of pseudowords, participants took a test on the real words they had studied. Tests were comprised of 120 trials, and participants had to indicate if an item was studied or new. Half of the trials contained the 60 items studied in the word block, and 60 items were new. After each response, participants rated their confidence as "high", "low", or "guess". During the test runs, anatomical and diffusor tensor imaging sequences were collected instead of functional scans. In the pictures block, participants studied one set each of object pictures and abstract pictures, then took a test on the object pictures. Participants were not given tests on pseudowords or abstract pictures. Each block contained a total of 60 items that would later appear on the test for that block (2.5 s each), 6 repeat items that were shown twice (2.5 s each), and fixation crosses (72 fixation periods, 2.5 s each, with up to 3 fixation periods in a row) interleaved together. In the word block, the words were the names of pictures from the Snodgrass item set (Snodgrass and Vanderwart, 1980). In the picture block, the critical items were easily nameable black line drawings from the same item set. Abstract pictures were black line drawings with both straight and curved lines, but did not resemble an object that could be named. Non-words were drawn from the Deacon (2004) set of non-words without English roots. Repeat items were the same type of stimuli, but were not present in the test, and were used to check for continued attention during study phases. Results from the n-back attention checks for each condition can be found in the Supplementary Materials. Although participants may have become aware that they were not going to be tested on Abstract Picture/Pseudoword blocks after not being tested on the presentation of the first of those two blocks, this did not affect participant engagement in the
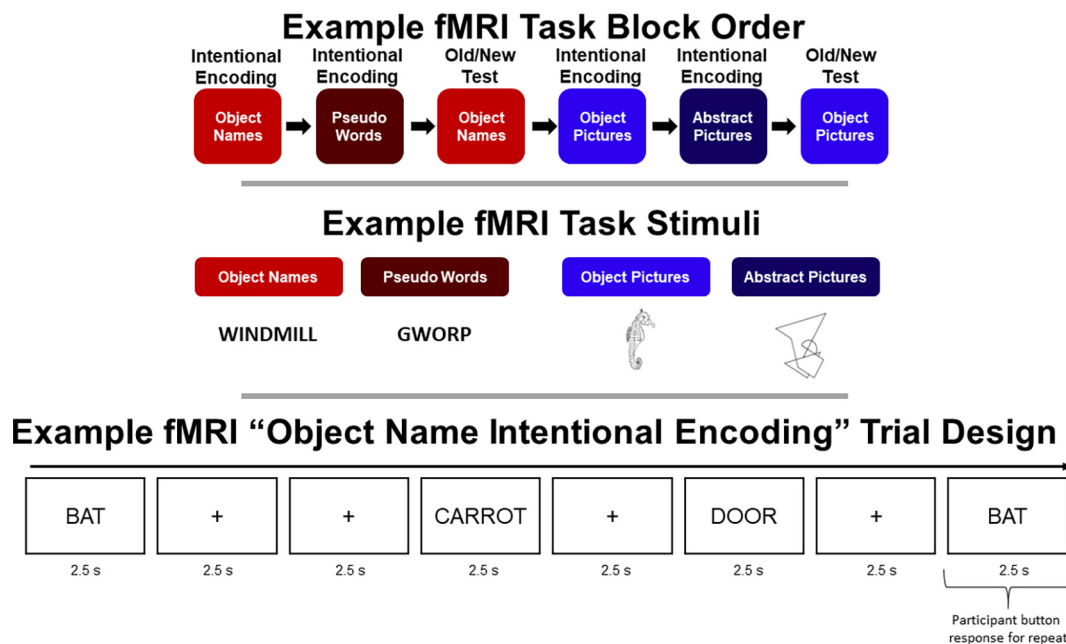
Fig. 5. Overview of fMRI task design. Participants were first presented with an intentional encoding task block with object names, such as "windmill", followed by a block of pseudo-words, such as "gworp". Participants were then tested on the object names they had studied. The procedure was repeated with object pictures and abstract pictures, and a test on the object pictures. Word and picture block order was counterbalanced between participants.

encoding task. Regardless of which of the two abstract blocks participants were exposed to first, participants had nearly identical signal detection rates for repeated items, indicating engagement in the encoding process especially given most of the repeated trials had a large number of items between the initial presentation and the repeat. Overall, participants showed nearly identical signal detection rates for both first and second presentations of both conditions: the pseudoword condition ($d'_{first-pres.}$: $M = 2.48$, $SD = 0.78$; $d'_{second-pres.}$: $M = 2.56$, $SD = 0.83$), $t(26.5) = -0.24$, p = 0.81; and the abstract picture condition ($d'_{first-pres.}$: $M = 1.47$, $SD = 0.90$; $d'_{second-pres.}$: $M = 1.55$, $SD = 0.64$), $t(25.3) = -0.28$, p = 0.79. Due to a low number of attention check trials per participant, these data were not used for individual differences analyses. With the exception of repeat trials, none of the words or pictures were repeated between conditions (i.e., a word studied in one block would not be the name of a picture studied in a later block). The task was counterbalanced both for the half of the stimuli used first as well as the material format (word/picture) that set was presented in. In total, the fMRI session lasted approximately two and a half hours, including all anatomical and functional scans. An overview of the fMRI design can be seen in Fig. 5.

Scanner information. All scans took place at the Dartmouth Brain Imaging Center. The scanner used to obtain the imaging data was a Phillips 3 T Achieva Intera with a 32 channel sense head coil. For the functional runs, there were four runs of 150 volumes per run for a total of 600 functional (T2*) volumes with a TR of 2.5 s. The functional scans were a gradient-echo EPI with 42 transverse slices at 3 mm per slice. TE was 35, flip angle was 90 degrees. The scan acquisition order was Philips interleaved.

Univariate functional imaging analysis: Neural data were preprocessed with FSL tools for motion correction and registration (Jenkinson et al., 2002). Each participant's neural data set was modeled using the canonical 6 s HRF epoch after onset of the display of the items (words, pseudo-words, pictures, or abstract pictures) during the encoding task, and were smoothed using a 5 mm FWHM Gaussian kernel. Regressor covariance estimates generated by FSL confirmed that these portions of the trial were statistically separable due to the jittered fixation periods inserted in between sections of each trial. The beta values used in the representational similarity analysis (described below) were drawn from

the contrast of studied item (separated by study block) compared to jittered fixation baseline. Anatomical data for the searchlight portion of the analysis were prepared from participants' T1 1 mm images using FreeSurfer (Fischl, 2012).

Searchlight Representational Similarity Analysis: We used a 10 mm radius surface-based searchlight mapping technique with white matter excluded (Oosterhof et al., 2011) to produce a whole-brain map for each subject (previously registered to MNI space) that reflected the Pearson correlation between local neural representational structure and a target similarity structure. The target similarity structure was created to probe for semantic similarity, looking for brain regions that process meaningful words and pictures similarly (in the vein of Shinkareva et al., 2011). Specifically, a dissimilarity matrix (DSM) for the stimuli was created using the similarity of semantic content with the diagonal values discarded and not used in further analyses (Fig. 6). Each run was broken into 4 chunks that contained interleaved items from the run (e.g. chunk 1 contained items 1, 5, 9, etc. and chunk 2 contained 2, 6, 10 etc.) Similar to the diagonal, each chunk from any given run was assigned 0 dissimilarity to the other chunks from the run. That is, Picture Chunk 1 has no dissimilarity to Picture Chunk 2. While the off-diagonal 0 values remained in the model, the diagonal where each chunk was compared to itself was not included in the RSA. Words and pictures were modeled with a low level of dissimilarity with each other (1), given that they were not identical to each other, but both contained semantically meaningful content. All other comparisons were modeled as highly dissimilar from each other, as words have very little similarity to pseudowords (for example) in terms of semantically meaningful content. The values chosen are category markers- that is, the values were chosen to indicate low and high levels of dissimilarity, but do not represent a strict 4 units of dissimilarity between them.

The local neural dissimilarity matrix for each participant at each location was computed using Euclidean correlation distance between activity patterns for all possible pairings of the 4 chunks for each of the 4 content type runs (120 pairwise distances total). Activity patterns were defined by the voxel-wise estimated hemodynamic responses from GLM analysis of the functional data collected during the four encoding sessions. These analyses were performed using Python and PyMVPA (http://www.pymvpa.org; Hanke et al., 2009), SciPy (http://scipiy.

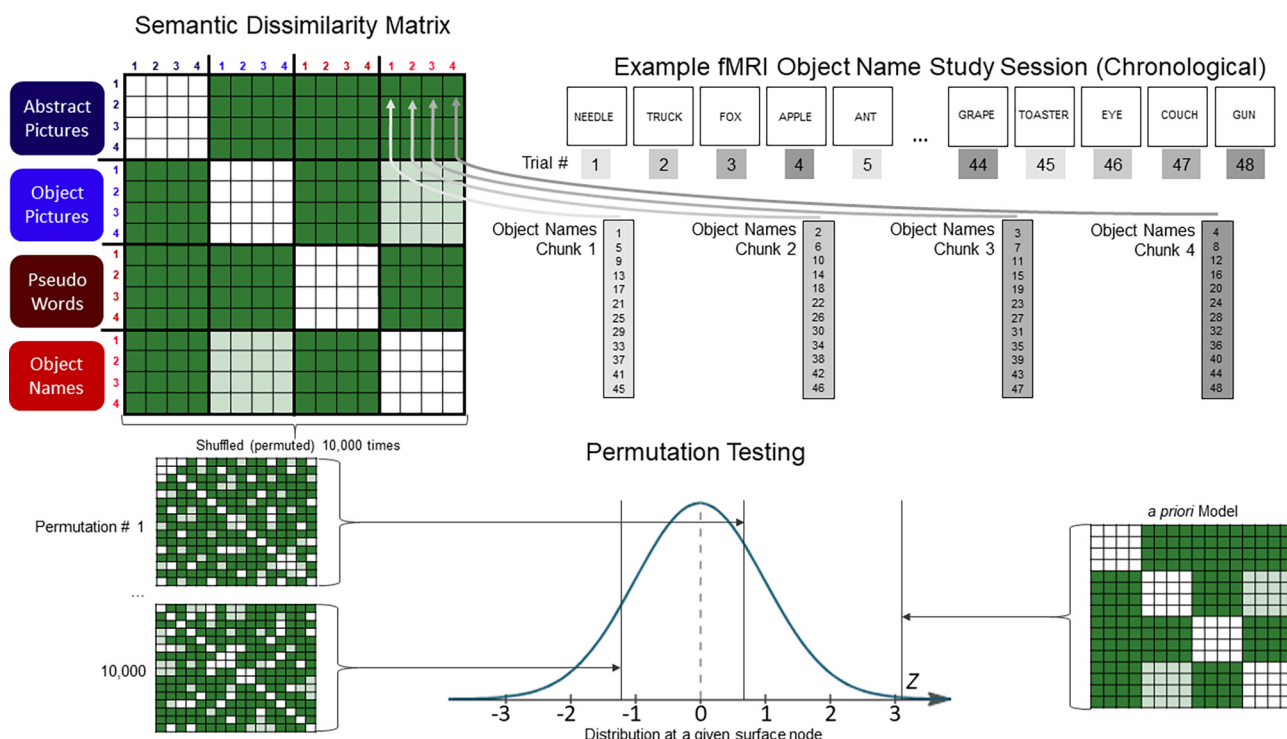## Semantic Dissimilarity Matrix

Fig. 6. *A priori* semantic model and permutation testing. The upper portion of the figure shows the *a priori* semantic dissimilarity matrix. Each row/column corresponds to 1 of 4 chunks for a particular content type. Items were sorted into the chunks in an interleaved way, so that chunks did not contain trials that were temporally adjacent, and no chunks contained only items from the last quarter of the run, for example. The *a priori* model shows that chunks from the same run were considered to be the same, items from word and picture runs were considered to have low dissimilarity (but were not identical) and all other items were highly dissimilar. All RSA analyses were permutation corrected on the node level for each participant. For every given node, a distribution was created but permuting (or shuffling) the data 10,000 times to see how well that artificial DSM correlates with the data. After the distribution was created, we calculated a one-sample *t* test at each node to compare the actual result to the distribution and identify how likely this was due to chance (e.g. was it greater than 3 standard deviations from the artificial distribution mean).

org), and NumPy (http://numpy.scipy.org). The resultant DSMs at each searchlight location were correlated with the semantic content model DSM, yielding a whole-brain correlation map for each participant. To determine the likelihood that the observed correlations occurred due to chance, we conducted a permutation test to compare our observed results to a distribution of possible results based on a distribution of 10,000 random permutations of the target labels. The probabilities associated with our results were thus calculated as the number of times the average correlation at a given searchlight across subjects for permuted observations exceeded the actual observed average correlation, divided by 10,000.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.brainres.2019.146483.

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