Title: **Task-irrelevant semantic properties of objects impinge on sensory representations within the early visual cortex**

Authors: Joseph C. Nah[1], George L. Malcolm[2], and Sarah Shomstein[3]

Author affiliation: [1] University of California, Davis, 95618

[2] University of East Anglia, NR4 7TJ

[3] The George Washington University, 20052

Corresponding author:
Joseph C. Nah
Center for Mind and Brain
University of California, Davis
E-mail: josephcnah@gmail.com

Abstract

Objects can be described in terms of low-level (e.g., boundaries) and high-level properties (e.g., object semantics). While recent behavioral findings suggest that the influence of semantic relatedness between objects on attentional allocation can be independent of task-relevance, the underlying neural substrate of semantic influences on attention remains ill-defined. Here, we employ behavioral and functional magnetic resonance imaging (fMRI) measures to uncover the mechanism by which semantic information increases visual processing efficiency. We demonstrate that the strength of the semantic relatedness signal decoded from the left inferior frontal gyrus (IFG): (i) influences attention, producing behavioral semantic benefits; (ii) biases spatial attention maps in the intraparietal sulcus (IPS), subsequently modulating early visual cortex (EVC) activity; (iii) directly predicts the magnitude of behavioral semantic benefit. Together, these results identify a specific mechanism driving task-independent semantic influences on attention.

Keywords: early visual cortex, fMRI, parietal cortex, semantic influence, visual attention

The visual system extracts high-level semantic information from complex scenes early in the information processing stream (Potter, 1976; Potter, Wyble, Hagmann, & McCourt, 2014; Thorpe, Fize, & Marlot, 1996) and attentional allocation is then guided by more detailed semantic signal such as object and scene layout (Brockmole, Castelhano, & Henderson, 2006; Castelhano & Henderson, 2007; Loftus & Mackworth, 1978), the relationship between a scene and object (Malcolm & Henderson, 2010; Spotorno, Malcolm, & Tatler, 2014; Võ & Henderson, 2010), and the co-occurrence and spatial dependency between objects in scenes (Bar, 2004; Mack & Eckstein, 2011; Oliva & Torralba, 2007). Additionally, behavioral findings indicate that semantic relatedness of objects guides attention when task-relevant (Belke, Humphreys, Watson, Meyer, & Telling, 2008; Castelhano & Heaven, 2010; de Groot, Huettig, & Olivers, 2016; Moores, Laiti, & Chelazzi, 2003). Taken altogether knowledge-based information plays a crucial role in attentional guidance.

Despite repeated demonstrations that task-relevant information guides selective attention, most of the information in the environment is task-irrelevant. For instance, when stopped at the intersection, the color of the traffic light, vehicles, and pedestrians are immediately relevant. However, these task-relevant details of the scene explain only a fraction of the environment. Buildings, benches, mailboxes, etc., are all processed perceptually, while irrelevant to the task of driving. Whether these task-irrelevant aspects exert similar influence on attention, is unclear. If relevant and irrelevant semantic information guides attention, it suggests an automatic nature of such influence. Thus, once objects are processed, we are aware of and can be influenced by their high-level properties whether that information is directly relevant (Shomstein, Malcolm, & Nah, 2019). Recent evidence posits an influence of high-level properties of objects on attentional allocation when task-irrelevant. For instance, semantic relationships between objects bias spatial

attentional allocation (Malcolm, Rattinger, & Shomstein, 2016), out-of-place objects (e.g., toothbrush on desk) are fixated for longer than control items (Cornelissen & Võ, 2017), and meaningful regions within a scene are fixated more than salient regions (Peacock, Hayes, & Henderson, 2018). Combined with the speed at which high-level information is processed (Potter, 1976; Potter & Levy, 1969; Potter et al., 2014; Thorpe et al., 1996), these results demonstrate that semantic information has a continuous, and likely automatic, influence on attention (Shomstein et al., 2019).

In order to posit that object semantics influence attention, such information has to be computed and available. Recent neuropsychological and neuroimaging literature provides evidence that semantic information is derived by a broadly distributed neural network, lateralized towards the left hemisphere (Binder, Desai, Graves, & Conant, 2009). Specifically, the left inferior frontal gyrus (IFG) has been demonstrated to be crucial in the control of semantic information, including the retrieval and evaluation of meaning (Fiez, 1997; Gabrieli et al., 1996; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Wagner, Desmond, Demb, Glover, & Gabrieli, 1997; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001) and as a key region that computes semantic similarity (Carota, Kriegeskorte, Nili, & Pulvermuller, 2017). Additionally, the left posterior temporal lobe is implicated in storing object representations (Martin, 2007) with some claiming that the temporal lobe is the "hub" for semantic representations (Patterson, Nestor, & Rogers, 2007). Additionally, several recent studies point to the pervasiveness of task-relevant semantic information within the perceptual system (Bar & Aminoff, 2003; Binder et al., 2009; Brady & Oliva, 2008; Greene & Fei-Fei, 2014; Livne & Bar, 2016; Lupyan, Thompson-Schill, & Swingley, 2010; Thompson-Schill et al., 1997) with direct evidence of semantic

representations decoded throughout the ventral visual cortex, from the occipital to temporal pole (Çukur, Nishimoto, Huth, & Gallant, 2013).

While prior investigations identified brain regions sensitive to semantics and that semantics influence behavior, these two types of observations remained largely independent. Consequently, the precise mechanism of how this information influences attentional distribution remains ill-defined. In service of this question, we directly tested whether attentional benefit from task-irrelevant semantic information modulates sensory representations of objects in the early visual cortex (EVC) through facilitation of spatial representations in spatially-selective intraparietal sulcus (IPS) (Bisley & Goldberg, 2010; Shomstein & Gottlieb, 2016; Todd & Manaligod, 2017), or object representations derived in the object-selective lateral occipital complex (LOC), or possibly both (Figure 1). Thus, the present report: (i) establishes that semantic information influences behavior automatically, independent of task-relevance, and (ii) elucidates the neural mechanism through which task-irrelevant semantic information influences attentional selection.

Materials and Methods

Participants. Sample size was determined by adopting similar sample sizes used in previous neuroimaging studies (Bar & Aminoff, 2003; Livne & Bar, 2016; Walther, Caddigan, Fei-Fei, & Beck, 2009) combined with multiple trials (many observations, multiple scanning sessions) per experimental run for each participant. Twelve (four females; mean age 25.1, range 20–33) with normal or corrected-to-normal vision, and no history of neurological problems, participated in Experiment 1. One participant was removed from data analysis (chance level accuracy). Fourteen (ten females; mean age: 23.7, range: 19–29) with normal or corrected-to-normal vision, and no history of neurological problems, participated in Experiment 2. One

participant was removed from data analysis due to excessive head motion within the scanner.

Four participants took part in both Experiment 1 and 2. All participants gave informed consent

and the study was approved by the Institutional Review Board of The George Washington and

Georgetown Universities.

Statistical analysis. All statistical analyses were performed in SPSS or MATLAB using

custom code. Behavioral data within the manuscript are presented as the mean or accuracy ± 1

standard error of the mean (SEM) corrected for within-subjects variance (Cousineau (2005)),

unless otherwise noted. Since the current experiment had a specific directional hypothesis based

on a previous study, behavioral data obtained from the scanner were analyzed using a paired

sample t-test. Unless otherwise noted, all fMRI analyses were corrected for multiple comparisons

by using whole-brain False Discovery Rate (FDR) of $q < 0.05$.

Experimental Procedure. Experiment 1. Each trial began with a reference object

presented just above the central fixation cross (Figure 2A). After 1,000 ms, two objects appeared

in each periphery below the midline creating a triangle, or "triad." Critically, one of the

peripheral objects was always semantically-related (SR; objects that frequently co-occur in the

real-world or functionally go together) to the central object while the other was not-related (NR)

(e.g., if the central object was a lamp, peripheral objects were a light bulb and an envelope).

Participants were instructed to maintain fixation and to prioritize speed of response (focusing on

accuracy analysis). No other eye movement controls were included in Experiment 1 (but later

controlled for in Experiment 2). After the triads remained on screen for 1,000 ms, a target letter

(T or L) along with two distractor characters (T/L hybrids) were superimposed on top of the

objects (one on each object). The long object exposure was intended to allow sufficient time to

fully process the object information as well as any semantic association between them. The aim

is to test whether semantic relatedness of fully recognized yet task-irrelevant objects has consequences for attentional allocation. Participants then performed a target discrimination task while maintaining fixation on the central cross. Most importantly, the target appeared on the three objects with equal probability, rendering the semantic information between objects irrelevant to the task at hand (i.e., actively attending to the semantically related object would not be beneficial in performing the task). Participants had 3,000 ms to respond, after which the triad was removed from screen. The inter-trial stimulus interval (ISI) was jittered between 2,000 – 6,000 ms in 250 ms steps for an average of 4,000 ms to allow for BOLD deconvolution. Participants completed a total of 7 experimental blocks (runs) intermixed between functional localizer scans.

Experiment 2. Each trial began with two objects appearing on either side of a center fixation for 750 ms. A vertical Gabor patch rotated 45° horizontally in either the left or right direction, was then overlaid on top of each object for 100 ms followed by an ISI of 5,150 ms (Figure 2B). Participants were instructed to report whether the two Gabor patches were identical in orientation. The two objects on the screen were either semantically-related or not-related to one another (e.g., a makeup brush and lipstick or a makeup brush and salt shaker; Figure 2C). Participants performed a total of 48 trials per run, for a total of 8 runs, with an equal number of trials for each condition. Participants were instructed to respond as fast as possible without sacrificing accuracy (focusing analyses on RTs).

fMRI Acquisition Parameters.

MRI scanning was conducted at the Center for Functional and Molecular Imaging (CFMI) at the Georgetown University Medical Center on a Siemens 3-Tesla scanner equipped with a 12-channel head coil. All functional data during the experimental as well as localizer runs

were acquired in 38 transverse slices covering occipital and parietal cortices (TR: 2000 ms, TE: 30 ms, matrix size: 64 x 64, FoV: 192 mm, acquisition voxel size: 3 x 3 x 3 mm). High-resolution anatomical images (1 mm^3) were also acquired for each participant using MPRAGE T1-weighted sequence (TR: 1900 ms, TE: 2.5ms, matrix size: 256 x 256, FoV: 250 mm). In both experiments, each participant completed a single 1.5-hour long session which included either 7 (Experiment 1) or 8 (Experiment 2) experimental runs and functional localizers (5 runs). Custom E-Prime (Sharpsburg, PA) scripts were used to generate the main experimental task of Experiment 1 and custom python code using the PsychoPy library (Peirce, 2007, 2009) were used to generate Experiment 2 and for the localizer scans for both experiments. The display was then back projected onto a screen mounted at the rear end of the scanner, which participants viewed via a mirror attached to the head coil (distance from screen to mirror: 80 cm, average distance from participant's face to mirror: 10 cm).

fMRI preprocessing and analysis.

All data were preprocessed using BrainVoyager QX (version 2.8.0, Brain Innovation, Maastricht, The Netherlands) along with custom MATLAB (Natick, MA) and Python scripts. All functional data were slice time corrected, motion corrected, and temporally high-pass filtered using a general linear model containing a Fourier basis set (2 sines and cosines) to remove low- and high-frequency noise in the functional time series. All EPI and anatomical images were then normalized into Talairach space (Talairach & Tournoux, 1988) and interpolated into 1 mm isotropic voxels. Localizer data as well as data used for univariate analysis were spatially smoothed with a 3 mm FWHM kernel. A segmented white matter mask generated from FreeSurfer (recon-all function) was imported into BrainVoyager to segment white matter from

gray matter. Afterwards, the cortical surface for each hemisphere was inflated and all analysis was conducted on the inflated surface.

Experiment 1 - Univariate Analysis. Within each region of interest (ROI), the average Blood Oxygenation Level-Dependent (BOLD) response magnitude across was calculated for each condition (SR, NR). Triad-related activity (1TR), time-locked to the onset of the completion of object triads (i.e., once all three objects were presented on screen), was deconvolved to estimate the hemodynamic response function for each event type. The BOLD response was estimated at the onset of the triad and at each of the next 12 time points, 0-24s after stimulus. The BOLD peak response for each condition was calculated by averaging coefficients at time point 6.

Preliminary analysis was conducted separately for each hemisphere, consistent with the experimental design. For instance, if a SR object appeared on the left side of fixation, a NR object would appear simultaneously on the right. Thus, the neural activity for SR was examined within the right hemisphere ROI while the neural activity for NR was examined within the left hemisphere. Semantic relationship beta coefficients were extracted separately from each ROI by using a general linear model and a design matrix that modeled the response.

Experiment 2 - Multivariate Analysis. Multivariate pattern analysis was conducted to assess changes in the pattern of activity of each EVC ROI modulated by task-irrelevant semantic information. Custom MATLAB code using LIBSVM (Chang & Lin, 2011) as well as BrainVoyager's MVPA module was utilized to conduct these analyses. For each individual trial in each condition, t-values (Misaki, Kim, Bandettini, & Kriegeskorte, 2010) were extracted by fitting a canonical two-gamma HRF in a standard general linear model (GLM) regression analysis and z-score normalized to control for differences in baseline activity (Kravitz, Peng, &

Baker, 2011). The resulting t-values were then used as feature vectors for that trial or block and used to train a linear support vector machine (SVM). To assess classification performance, the leave-one-run-out cross-validation was utilized. On each iteration, 7 experimental runs were used to train the classifier and the remaining run was used to test the classifier's performance. The classification performance was then averaged across all cross-validation loops to obtain average classification accuracy for each ROI and condition. This accuracy was then compared with chance performance (25%) as well as between SR and NR conditions.

Functional localizers and retinotopic mapping. For each participant, separate sets of functional localizers were conducted to define regions of interest (ROIs): 1) meridian localizer to delineate borders between early visual cortex dorsal regions V1, V2, and V3 (and an additional stimuli position localizer for Experiment 1 to identify patches of cortex responsive to the object locations); 2) LOC localizer to identify object-selective regions of cortex; and 3) IPS localizer to define spatially-selective regions of cortex (see Table 1 and Table 2 in supplementary materials for ROI coordinates and size).

1. Meridian and stimuli position localizer: Retinotopic areas (V1, V2, V3) were defined using flashing checkerboard stimuli presented in a bowtie shape that flipped between blocks of vertical and horizontal meridians. Each half of the bowtie was a 16° wedge flickering at 5 Hz. This allowed delineation of borders between dorsal and ventral retinotopic regions of the visual cortex. Concurrently, participants fixated on a central black fixation square that randomly dimmed to gray for variable durations. Participants were informed to hold down a button every time the black fixation square dimmed to gray and release it when black. Each meridian was presented 8 times for 12 s starting with the horizontal meridian and was bookended by 8 s fixations for a total scan time of 208 s. An additional stimuli position localizer was conducted to

define the spatial locations (bottom left and bottom right) occupied by the objects in the experimental task and increase the selectivity of voxels. Participants maintained fixation at the center of the display and pressed a button whenever a small gray dot appeared in the middle of the fixation cross. Concurrently, flashing checkerboard stimuli (2.7° x 2.1°) flickering at 5 Hz was presented in one of the three possible stimuli location (above fixation, lower-left, lower-right) for 12 s. The initial fixation duration was 10 s, and each location block lasted 12 s, with an 8 s interblock fixation and a final fixation of 6 s for a total scan time of 256 s. The spatial location of the stimuli was then functionally defined with a lower-left > lower-right contrast for the left object and lower-right > lower-left for right object). Final EVC ROIs were determined by restricting the voxels to the overlapping activations from both the meridian and position localizer. ROIs were drawn for each participant for each hemisphere.

2. LOC localizer: All stimuli were presented at the center of the screen, with a fixation overlaid on top of all objects. A stream of 16 stimuli was presented one at a time for 500 ms with an interstimulus interval of 500 ms for a total of 8 s per block. Participants were informed to maintain fixation and perform a one-back task, identifying repeated images via a button press.

3. IPS localizer: Spatially selective regions (IPS: IPS0, IPS1, IPS2) were defined using a random dot movement change detection task. Two circles (3°) in opposite corners (upper left & lower right, lower left & upper right) were displayed simultaneously with the circle pairs alternating each block. Within the circles were dynamic random dot stimuli (RDS) moving horizontally. Concurrently, participants fixate on a central cross which indicated a direction either up or down with a change in color in one of the arms (e.g., the upper half of the vertical line would change from gray to green to indicate the direction, up). After a random interval between 500 and 1500 ms, the RDS in one of the two circles changed directions to either up or

down. Participants were instructed to indicate with a button press whether the change in direction matched the direction displayed on the fixation cross. Contrasting the two conditions approximately portrays the full array of visual space. IPS0, IPS1, and IPS2 were demarcated by visually inspecting reversals in activation as well as anatomical guidelines. (Sheremata, 2019).

     Stimuli & low-level control analysis. *Experiment 1*. Stimuli were directly adopted from a previous study which were controlled for low-level differences (Malcolm et al., 2016). To quantitatively measure the semantic similarity between objects, all object relationships were analyzed through the linguistics-based computational method known as latent semantic analysis (LSA) (Landauer & Dumais, 1997). LSA extracts the contextual meaning of words by statistical computations applied to a large body of text and assumes that words with similar meanings occur more frequently together (Landauer, Foltz, & Laham, 1998). A high dimensional semantic matrix is then constructed from the large body of text and a technique known as singular value decomposition (SVD) is applied to simplify the matrix. Afterwards, the semantic similarity between two terms is calculated as the cosine value between the two corresponding terms in the semantic matrix. A cosine value closer to 1 indicates that two terms are highly semantically related with one another while a value closer to 0 indicates that the two terms are semantically non-related. For the current study, LSA was applied to the stimuli combinations represented in text form to compute the semantic similarity using the LSA@CU text/word latent semantic analysis tool developed by the University of Colorado at Boulder. The semantic similarity between objects in the SR condition (0.32) was significantly greater than that between objects in the NR condition (0.05), $t(19) = 4.37$, $p < .001$, *Cohen's d* = .98. Additionally, a separate set of participants (n = 28) participated in a semantic rating survey. Participants were presented with images of all possible object pairs from both SR and NR conditions and were asked to rate how

related the two objects are on a scale of 1 (not related) to 6 (very related). Paired samples t-test revealed that the semantic relatedness between objects in the SR condition ($M = 5.28$) was significantly greater than that between objects in the NR condition ($M = 1.48$), $t(19) = 30.98$, $p < .001$, *Cohen's d* $= 6.93$.

Experiment 2. To rule out the possibility that any semantic influence was confounded by low-level factors (i.e., color and size), the feature space between the main object and their respective SR objects was compared with the differences between the main object and their respective NR objects (Malcolm et al., 2016). First, each object was converted into LAB color space, breaking down pixel information into luminance, green–red, and blue–yellow color channels. For each channel of each object, histograms were created and bin-to-bin comparisons were conducted by comparing the differences between the main object and its respective SR and NR object. Thus, low-level information in a specific location of the main object was directly compared to the corresponding location of the SR or NR object. Smaller differences between objects represented greater similarity in that specific channel. Thus, if the semantic influence was confounded by low-level similarities, significantly smaller differences in one or more channels between the main and SR objects than between the main and NR objects should be observed. However, paired t-tests for all three channels did not reveal any significant differences (ts < 1), suggesting that the observed semantic effect was not a byproduct of low-level similarities. Lastly, each object image was converted into number of pixels and compared across conditions to test whether there was a significant difference in the retinal size of the objects. Again, a paired t-test did not reveal any significant difference ($t < 1$) between the two conditions, suggesting that the objects used in both conditions were of similar sizes.

Semantic similarity between objects were measured using both LSA and the semantic rating survey. The LSA analysis revealed that the semantic similarity between objects in the SR condition (.52) was greater than that between objects in the NR condition (.10), $t(3) = 6.42$, $p = .008$, *Cohen's d* = 3.21. The semantic rating survey also demonstrated that the semantic similarity between objects in the SR condition ($M = 5.17$) was also significantly greater than that between objects in the NR condition ($M = 1.41$), $t(3) = 20.42$, $p < .001$, *Cohen's d* = 10.21.

Results

Experiment 1: Task-irrelevant semantic relationships modulate spatial attention

The influence of task-irrelevant semantic knowledge on selective attention was examined through a combination of behavioral and fMRI methods. A key feature of this design is that semantic relationship did not predict the location of the target letter (Fig. 2A). Considering the difficulty of the task based on the distance of objects from fixation, participants were instructed to maintain fixation and to respond without sacrificing accuracy.

Behavioral data acquired during the neuroimaging scan provides strong evidence for task-irrelevant semantic guidance of attention independent of task-relevance. Examination of accuracy rates revealed that participants were significantly more accurate at identifying the target when it appeared on a SR object than when it appeared on a NR object, $t(10) = 2.21$, $p = .052$, Cohen's $d = .665$ (Figure 2D). These results are consistent with previous findings reported by our lab (Malcolm et al., 2016) as well as others (Cornelissen & Võ, 2017; Peacock et al., 2018), demonstrating that the task-irrelevant semantic relationship between objects influences attentional allocation. Examination of the response time (RT) data revealed no significant difference between the two conditions $t < 1$, $p > .4$, providing evidence against speed accuracy

tradeoffs. The presence of a behavioral effect is an important starting point for the subsequent neuroimaging analyses.

Semantic relationship modulates IPS and EVC activity

Having demonstrated the influence of task-irrelevant semantic relationships on attentional allocation, we examined the underlying neural mechanism. We hypothesized that semantic information either: 1) influences the spatial representations in the IPS, or 2) object representations in the LOC. To distinguish between these two mechanisms, we first tested whether semantic information modulates BOLD responses in the EVC, IPS, and LOC using univariate methods. If task-irrelevant semantic information facilitates neural responses in accordance with the behavioral profile reported above, we expect a greater target-evoked BOLD response for the SR than NR object.

A three-way repeated measures ANOVA was conducted with semantic relationship (SR, NR), hemisphere (left, right), and externally functionally-defined ROIs (V1, V2, V3; see Methods) as within-subject factors to test whether task-irrelevant semantic information influences cortical activity in the early sensory regions. Given absence of main effects or interactions involving hemisphere and ROI (Fs < 1), data were collapsed over these factors. Consistent with effects of semantic bias, there was a significant main effect of semantic relationship on BOLD signal, with greater BOLD responses for SR than NR objects ($F(1,10) =$ 16.44 , $p = .002$, $\eta_p^2 = .62$; Figure 3, EVC). The robust effect of semantic information on cortical activity in the EVC suggests that task-irrelevant high-level information spatially biases attention towards the SR object, resulting in signal enhancement in the early sensory regions, thereby increasing efficiency of visual processing. These results corroborate the behavioral

findings reported above and provide strong support for an automatic influence of semantic processing on efficiency of perception.

Next, to determine whether the modulation of EVC activity is accompanied by spatial attentional modulation or direct enhancement of object representations, we investigated whether semantic information modulates activity in the spatially-selective IPS and the object-selective LOC. First, a three-way repeated measures ANOVA with semantic relationships (SR, NR), hemisphere (left, right) and externally functionally defined IPS ROIs (IPS0, IPS1, IPS2; see Methods) was conducted. Again, no main effects or interactions involving hemisphere or ROIs reached significance (Fs < 1), thus data were collapsed over these factors. Similar to the results of the EVC, there was a significant main effect of semantic relationships with greater peak BOLD responses for SR than NR objects, ($F(1,10) = 5.55$, $p = .04$, $\eta_p^2 = .36$; Figure 3, IPS).

Activity in the externally functionally derived object-selective LOC was examined to determine whether object representations for semantically related objects were directly enhanced. A repeated measures ANOVA with semantic relationships (SR, NR) and hemisphere (left, right) as factors revealed no significant interactions or main effects (Fs < 1; Figure 3, LOC), offering no evidence that semantic information influences object representations in LOC. To test whether this difference between semantic relationships in IPS is significantly different from that in LOC, a repeated measures two-way ANOVA with ROIs (LOC, IPS), hemisphere (left, right), and semantic relationships (SR, NR) was conducted, revealing a significant interaction between semantic relationships and ROIs, $F(1,10) = 5.47$, $p = . 04$, $\eta_p^2 = .35$. Simple main effects analysis indicated that the interaction was driven by the significant difference between SR and NR conditions in the IPS ($F(1,10) = 5.48$, $p = . 04$, $\eta_p^2 = .35$). No other interaction or main effects were significant (Fs < 2.3, ps > .16). Combined, these results suggest

that the task-irrelevant semantic relationship between objects modulates neural activity in the EVC through attentional facilitation via the parietal cortex (IPS) rather than directly strengthening object representations in LOC.

Results of Experiment 1 show that semantic relationships influence spatial attentional maps in the parietal cortex and the relative salience of the space in which a semantically-related but task-irrelevant object is located. In contrast, no modulation was observed in the ventral processing region LOC, suggesting that semantic information influences activity in the IPS without directly influencing object representations. This finding aligns with previous research demonstrating that LOC is sensitive to the overall physical features of an object (e.g., shape), rather than higher-level semantic information (Chouinard, Morrissey, Kohler, & Goodale, 2008; Grill-Spector et al., 1999; Kim, Biederman, Lescroart, & Hayworth, 2009). These data provide the first neuroimaging evidence of the pervasive nature of semantic information on attentional allocation, with its influence observed to be independent of task-relevance. Thus the attentional priority map within the parietal cortex is composed of a multi-dimensional priority map that incorporates multiple factors in the natural environment to bias attentional allocation (Shomstein & Gottlieb, 2016), such as semantic relatedness or category membership (Freedman & Assad, 2006).

Experiment 2: Semantic relationships facilitate attentional allocation

Experiment 1 demonstrated that semantic information modulates a spatial attentional map within the parietal cortex, which in turn facilitates responses in the early sensory regions. Experiment 2 investigated the consequence of this spatial bias and the neural representation of task-irrelevant semantic relationships. The goals of Experiment 2 were to: (i) demonstrate that

the effects of semantic influence are not specific to a particular paradigm by internal replication

using a different paradigm and a different neuroimaging analysis method, (ii) investigate the

consequence of attentional bias on object representations in EVC, and (iii) examine whether

regions sensitive to task-relevant semantic information also exhibit sensitivity when object

meaning is task-irrelevant. The logic directly follows from Experiment 1: if spatial attention is

biased towards the SR object, the object should receive a benefit from the increased attentional

allocation, leading to a stronger neural representation. Thus, when two related objects are

presented simultaneously, the added attentional benefit should support and ultimately enhance

the representation of both objects. Comparatively, when the two objects are not related, the

object representations should be weaker. This design is a follow-up to Experiment 1 in which

this type of analysis was impossible, given that each object triad always contained one

semantically related and one non-related object. Additionally, unlike the task in Experiment 1,

where effect was focused towards accuracy, the task in Experiment 2 pushed the effect into RTs.

In Experiment 2, participants were presented with two objects on either side of fixation

that were either SR or NR (Figure 2B) and performed a fixation task. We predicted a behavioral

benefit when both objects are semantically related than when not and hypothesized that the

increased attentional allocation from task-irrelevant semantic information will facilitate the

strength of an object's neural representation, leading to significantly higher classification

accuracy of the object identity. Internally replicating previous behavioral findings, participants

were significantly faster at performing the task when both objects were SR than NR ($t(12) =$

2.51, $p = 0.028$, *Cohen's d* = .70 ; Figure 2E) suggesting that attentional facilitation is directed

by task-irrelevant semantic relationship between objects. Accuracy data between the SR (M =

96.8%) and NR (M = 95.6%) conditions also showed similar patterns as Experiment 1 but did

not reach significance, t(12) = 1.65, p = .12. These behavioral results replicate our previous results and demonstrates the robustness of the influence of task-irrelevant high-level semantic relationship between objects on attentional allocation.

Semantic information modulates object representations in the EVC

Using multivariate pattern analysis (MVPA), we reasoned that if semantic information increases attentional allocation to an object, the strength of the object's neural representation should be enhanced when paired with a SR object than a NR object. To test this, a linear support vector machine (SVM) classifier was trained to discriminate between the 4 reference objects used in the experiment (Figure 4A) with the prediction that decoding accuracy would be greater when a reference object was paired with a SR object than with a NR object, reflecting a less noisy representation supported by semantic influence from the frontal cortex. Classification performance of the SVM was tested against chance performance of 25% within the EVC (Figure 4B). A three-way repeated measures ANOVA was conducted with hemisphere (left, right), ROI (V1, V2, V3), and semantic relationships (SR, NR) as within-subjects variables. There was a main effect of ROI, (F(1, 24) = 5.27, p = .013, η_p^2 = .305) with post hoc tests showing significantly higher decoding accuracy for V1 compared to V2, t(12) = 3.62, p = .01 (Bonferroni corrected). When compared against chance, both the SR ($t(12)$ = 5.65, p < .001) and the NR condition, ($t(12)$ = 2.94, p = .01) were significantly greater than chance. Critically, a significant main effect of semantic relationships was observed, with decoding accuracy significantly higher for the SR than NR condition ($F(1,12)$ = 5.69, p = .034, η_p^2 = .332), suggesting that the benefit conveyed by an object's presence to the neural representation of another object is greater when the objects are semantically related to one another. No other main effect or interaction reached significance (Fs < 1). Consistent with the previous findings, our results demonstrate that the

increased attentional allocation leads to a robust effect of task-irrelevant semantic information on the neural pattern of the objects represented in the EVC.

Overall semantic facilitation in left IFG predicts behavioral benefit

Thus far, we provide evidence that task-irrelevant semantic information influences the efficiency of sensory processes in EVC through altering spatial priority maps in IPS. The consequence of which is enhanced representation of the objects in EVC. We next investigated how this high-level semantic information is represented in the brain. The left IFG has been implicated as central to the processing of task-relevant semantic information (Binder et al., 2009; Lupyan et al., 2010; Thompson-Schill et al., 1997; Wagner et al., 2001), with it playing a pivotal role in the selection of semantic knowledge. Considering the speed at which semantic information is processed (Potter, 1976; Potter & Levy, 1969; Potter et al., 2014; Thorpe et al., 1996) and its ubiquitous nature (Shomstein et al., 2019), we hypothesized that semantic information should be represented in the brain regardless of its task relevance. Thus, if attention is enhanced towards the semantically related object, the left IFG mechanism will be more engaged in the presence of an SR object than NR object

Given two types of trials, one in which the object pair was either SR or NR, Experiment 2 allowed for a direct SR vs. NR whole brain contrast to identify regions in the brain selective towards semantic information. For all participants, a whole brain univariate SR vs. NR contrast was conducted, revealing the left IFG, which was then individually defined with a threshold of $p < .05$. For each individual, the strength of semantic facilitation was calculated as the difference between BOLD responses of SR and NR trials in the defined left IFG, with a more positive value representing stronger facilitation. To determine whether neural activity predicts behavior, the

strength of semantic facilitation was again correlated with the difference in behavioral semantic facilitation (RT; NR - SR) revealing a significant positive correlation ($r = .595$, $p = .032$; Figure 4C). This result demonstrates that the strength of neural semantic facilitation is directly connected to the strength of behavioral semantic influence.

Discussion

All real-world objects in our environment are complex entities, described by basic physical properties and high-level semantic meaning. There has been an increasing interest to understand the role of semantic information in attentional guidance. Accordingly, it has been identified that semantic information is rapidly extracted and processed by a broadly distributed network (Binder et al., 2009), and that semantic relationships influence attentional allocation (Malcolm et al., 2016; Moores et al., 2003). However, the two types of findings remained largely independent, thus the mechanism of semantic influence on attentional distribution remained ill-defined. Three key findings for the current investigation demonstrate that we have, for the first time, provided a potential mechanistic explanation of semantic influence on attentional allocation.

First, we provide evidence that even task-irrelevant semantic information impacts visual processing. Target discrimination performance was significantly more accurate for targets embedded within an object that was semantically related to the reference object than targets within a non-related object. This effect was internally replicated using a different paradigm in which participants were tasked to discriminate the orientation of Gabor patches embedded within a pair of semantically related or non-related objects. Performance was modulated by semantic relatedness, such that task performance was significantly faster when the objects were semantically related, demonstrating an increased efficiency in processing of visual information.

Altogether, these results directly replicate findings that semantic relationships of task-irrelevant objects guide attention (Cornelissen & Võ, 2017; Malcolm et al., 2016; Peacock et al., 2018) and provide strong evidence that objects' semantic properties continuously influence visual attention allocation even when the information is not task-relevant. Importantly, these findings demonstrate that semantic information is processed obligatory and continually influences attention.

Second, this behavioral modulation is accompanied by changes in the overall response and strength of object representations in early visual cortices. BOLD activity in early visual sensory areas (V1-V3) were modulated by task-irrelevant semantic information, demonstrating that associative knowledge between objects modulates neural activity in the EVC. Additionally, using multivariate measures, we revealed that an object's neural representation was enhanced when supported by a semantically-related object. These results provide the first demonstration that the semantic context of an object (i.e., its relationship to other non-retinotopically coincident objects) affects its representation at the earliest stages of visual processing.

Finally, we show that the same regions known to mediate spatial attentional shifts (IPS) (Corbetta & Shulman, 2002; Serences & Yantis, 2007; Shomstein, 2012; Silver & Kastner, 2009) and process semantic information (left IFG) (Binder et al., 2009; Thompson-Schill et al., 1997; Wagner et al., 2001) are modulated by semantic relationships. In the case of left IFG, these modulations strongly predict the strength of semantic behavioral facilitation. BOLD response in spatially-selective IPS was modulated by task-irrelevant semantic information, suggesting that the modulation of sensory representations of objects in the early visual cortex is accomplished through facilitation of spatial representations. While left IFG has been demonstrated to be involved in processing of semantic information (Fiez, 1997; Gabrieli et al., 1996; Thompson-

22

Schill et al., 1997; Wagner et al., 1997; Wagner et al., 2001), the current study demonstrates that

its involvement is not restricted to task-relevant situations. Thus, the results offer evidence that

high-level semantic influence on attentional allocation is achieved through the processing of

semantic relationships in the left IFG, which modulates spatial priority maps in IPS, and

ultimately influences early sensory representations. The task-irrelevant aspect of this modulation

show that this process is not susceptible to task demands, and rather is ongoing and automatic.

A possible alternative explanation of the semantic benefit can be found in the

configuration of the objects. Semantically related objects were arranged in a manner often

encountered in the real-world (e.g., raincoat is more likely to be found next to an umbrella than a

spoon). Studies have provided evidence that object configuration influences object perception

and attention (Green & Hummel, 2006; Roberts & Humphreys, 2011) as well as decrease neural

interference (Kaiser, Stein, & Peelen, 2014). However, semantic similarity can be defined as the

repeated co-exposure of visual objects that are physically proximal and are meaningfully related

within a specific scenario or event (in fact, the concept literature defines this as thematic

similarity; see Mirman, Landrigan, & Britt, 2017 for review). The semantic effect observed in

the current study is investigating the influence objects that functionally belong with each other

and also co-occur in the real-world have on attentional allocation. Thus, frequently co-occurring

objects in the real-world (e.g., lipstick and make-up brush, a violin and drum) are considered to

be semantically related and is a defining feature of the two objects' relationship.

Our findings provide both behavioral and neural evidence uncovering a link between

task-irrelevant conceptual information and the perceptual system (Greene & Fei-Fei, 2014).

While recent neuroimaging studies have provided evidence that semantic and visual information

can coexist within the same brain region (Walther et al., 2009), these studies were mainly

restricted to task-relevant semantic information, thus offering no insight to the important question of whether semantic influence on perception is automatic. There has also been a recent effort to understand how semantic information affects attention and perception even in task-irrelevant situations (Cornelissen & Võ, 2017; Greene & Fei-Fei, 2014; Malcolm et al., 2016), given the ubiquitous nature of semantic information. In summary, we identified, and describe, a potential neural network through which high-level information increases efficiency within sensory processing regions in the brain. Task-irrelevant semantic information is processed in the left IFG, altering the priority weightings in the spatial attention maps within the parietal cortex, which in turn modulate activity in the early visual cortex. Thus, these results provide converging behavioral and neuroimaging evidence that the impact of task-irrelevant semantic information extends to the lowest and highest levels of visual processing.

Uncategorized References

Bar, M. (2004). Visual objects in context. *Nat Rev Neurosci, 5*(8), 617-629. doi:10.1038/nrn1476

Bar, M., & Aminoff, E. (2003). Cortical analysis of visual context. *Neuron, 38*(2), 347-358. doi:http://dx.doi.org/10.1016/S0896-6273(03)00167-3

Belke, E., Humphreys, G. W., Watson, D. G., Meyer, A. S., & Telling, A. L. (2008). Top-down effects of semantic knowledge in visual search are modulated by cognitive but not perceptual load. *Percept Psychophys, 70*(8), 1444-1458. doi:10.3758/PP.70.8.1444

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19*(12), 2767-2796. doi:10.1093/cercor/bhp055

Bisley, J. W., & Goldberg, M. E. (2010). Attention, intention, and priority in the parietal lobe. *Annu Rev Neurosci, 33*(1), 1-21. doi:10.1146/annurev-neuro-060909-152823

Brady, T. F., & Oliva, A. (2008). Statistical learning using real-world scenes: extracting categorical regularities without conscious intent. *Psychol Sci, 19*(7), 678-685. doi:10.1111/j.1467-9280.2008.02142.x

Brockmole, J. R., Castelhano, M. S., & Henderson, J. M. (2006). Contextual cueing in naturalistic scenes: Global and local contexts. *J Exp Psychol Learn Mem Cogn, 32*(4), 699-706. doi:10.1037/0278-7393.32.4.699

Carota, F., Kriegeskorte, N., Nili, H., & Pulvermuller, F. (2017). Representational Similarity Mapping of Distributional Semantics in Left Inferior Frontal, Middle Temporal, and Motor Cortex. *Cereb Cortex, 27*(1), 294-309. doi:10.1093/cercor/bhw379

Castelhano, M. S., & Heaven, C. (2010). The relative contribution of scene context and target features to visual search in scenes. *Attention, Perception, & Psychophysics, 72*(5), 1283-1297. doi:10.3758/APP.72.5.1283

Castelhano, M. S., & Henderson, J. M. (2007). Initial scene representations facilitate eye movement guidance in visual search. *J Exp Psychol Hum Percept Perform, 33*(4), 753-763. doi:10.1037/0096-1523.33.4.753

Chang, C. C., & Lin, C. J. (2011). LIBSVM: A Library for Support Vector Machines. *Acm Transactions on Intelligent Systems and Technology, 2*(3), 27-27. doi:Artn 27 10.1145/1961189.1961199

Chouinard, P. A., Morrissey, B. F., Kohler, S., & Goodale, M. A. (2008). Repetition suppression in occipital-temporal visual areas is modulated by physical rather than semantic features of objects. *Neuroimage, 41*(1), 130-144. doi:10.1016/j.neuroimage.2008.02.011

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci, 3*(3), 201-215. doi:10.1038/nrn755

Cornelissen, T. H., & Võ, M. L. (2017). Stuck on semantics: Processing of irrelevant object-scene inconsistencies modulates ongoing gaze behavior. *Atten Percept Psychophys, 79*(1), 154-168. doi:10.3758/s13414-016-1203-7

Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutorials in Quantitative Methods for Psychology, 1*(1), 42-45. doi:10.20982/tqmp.01.1.p042

Çukur, T., Nishimoto, S., Huth, A. G., & Gallant, J. L. (2013). Attention during natural vision warps semantic representation across the human brain. *Nature neuroscience, 16*(6), 763-770. doi:10.1038/nn.3381

de Groot, F., Huettig, F., & Olivers, C. N. (2016). When meaning matters: The temporal dynamics of semantic influences on visual attention. *J Exp Psychol Hum Percept Perform, 42*(2), 180-196. doi:10.1037/xhp0000102

Fiez, J. A. (1997). Phonology, semantics, and the role of the left inferior prefrontal cortex. *Human Brain Mapping, 5*(2), 79-83. doi:10.1002/(sici)1097-0193(1997)5:2<79::Aid-hbm1>3.0.Co;2-j

Freedman, D. J., & Assad, J. A. (2006). Experience-dependent representation of visual categories in parietal cortex. *Nature, 443*(7107), 85-88. doi:10.1038/nature05078

Gabrieli, J. D. E., Desmond, J. E., Demb, J. B., Wagner, A. D., Stone, M. V., Vaidya, C. J., & Glover, G. H. (1996). Functional Magnetic Resonance Imaging of Semantic Memory Processes in the Frontal Lobes. *Psychological Science, 7*(5), 278-283. doi:10.1111/j.1467-9280.1996.tb00374.x

Green, C., & Hummel, J. E. (2006). Familiar interacting object pairs are perceptually grouped. *J Exp Psychol Hum Percept Perform, 32*(5), 1107-1119. doi:10.1037/0096-1523.32.5.1107

Greene, M. R., & Fei-Fei, L. (2014). Visual categorization is automatic and obligatory: evidence from Stroop-like paradigm. *J Vis, 14*(1). doi:10.1167/14.1.14

Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzchak, Y., & Malach, R. (1999). Differential Processing of Objects under Various Viewing Conditions in the Human Lateral Occipital Complex. *Neuron, 24*(1), 187-203. doi:10.1016/s0896-6273(00)80832-6

Kaiser, D., Stein, T., & Peelen, M. V. (2014). Object grouping based on real-world regularities facilitates perception by reducing competitive interactions in visual cortex. *Proc Natl Acad Sci U S A, 111*(30), 11217-11222. doi:10.1073/pnas.1400559111

Kim, J. G., Biederman, I., Lescroart, M. D., & Hayworth, K. J. (2009). Adaptation to objects in the lateral occipital complex (LOC): shape or semantics? *Vision Res, 49*(18), 2297-2305. doi:10.1016/j.visres.2009.06.020

Kravitz, D. J., Peng, C. S., & Baker, C. I. (2011). Real-world scene representations in high-level visual cortex: it's the spaces more than the places. *J Neurosci, 31*(20), 7322-7333. doi:10.1523/JNEUROSCI.4588-10.2011

Landauer, T. K., & Dumais, S. T. (1997). A solution to Plato's problem: The latent semantic analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review, 104*(2), 211-240. doi:Doi 10.1037/0033-295x.104.2.211

Landauer, T. K., Foltz, P. W., & Laham, D. (1998). An introduction to latent semantic analysis. *Discourse Processes, 25*(2-3), 259-284. doi:10.1080/01638539809545028

Livne, T., & Bar, M. (2016). Cortical Integration of Contextual Information across Objects. *Journal of Cognitive Neuroscience, 28*(7), 948-958. doi:10.1162/jocn_a_00944

Loftus, G. R., & Mackworth, N. H. (1978). Cognitive determinants of fixation location during picture viewing. *J Exp Psychol Hum Percept Perform, 4*(4), 565-572. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/722248

Lupyan, G., Thompson-Schill, S. L., & Swingley, D. (2010). Conceptual penetration of visual processing. *Psychol Sci, 21*(5), 682-691. doi:10.1177/0956797610366099

Mack, S. C., & Eckstein, M. P. (2011). Object co-occurrence serves as a contextual cue to guide and facilitate visual search in a natural viewing environment. *Journal of Vision, 11*(9), 1-16. doi:10.1167/11.9.9

Malcolm, G. L., & Henderson, J. M. (2010). Combining top-down processes to guide eye movements during real-world scene search. *Journal of Vision, 10*(2), 4 1-11. doi:10.1167/10.2.4

Malcolm, G. L., Rattinger, M., & Shomstein, S. (2016). Intrusive effects of semantic information on visual selective attention. *Atten Percept Psychophys, 78*(7), 2066-2078. doi:10.3758/s13414-016-1156-x

Martin, A. (2007). The representation of object concepts in the brain. *Annu Rev Psychol, 58*, 25-45. doi:10.1146/annurev.psych.57.102904.190143

Mirman, D., Landrigan, J. F., & Britt, A. E. (2017). Taxonomic and thematic semantic systems. *Psychol Bull, 143*(5), 499-520. doi:10.1037/bul0000092

Misaki, M., Kim, Y., Bandettini, P. A., & Kriegeskorte, N. (2010). Comparison of multivariate classifiers and response normalizations for pattern-information fMRI. *Neuroimage, 53*(1), 103-118. doi:10.1016/j.neuroimage.2010.05.051

Moores, E., Laiti, L., & Chelazzi, L. (2003). Associative knowledge controls deployment of visual selective attention. *Nature neuroscience, 6*(2), 182-189. doi:10.1038/nn996

Oliva, A., & Torralba, A. (2007). The role of context in object recognition. *Trends Cogn Sci, 11*(12), 520-527. doi:10.1016/j.tics.2007.09.009

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci, 8*(12), 976-987. doi:10.1038/nrn2277

Peacock, C. E., Hayes, T. R., & Henderson, J. M. (2018). Meaning guides attention during scene viewing, even when it is irrelevant. *Atten Percept Psychophys*. doi:10.3758/s13414-018-1607-7

Peirce, J. W. (2007). PsychoPy--Psychophysics software in Python. *J Neurosci Methods, 162*(1-2), 8-13. doi:10.1016/j.jneumeth.2006.11.017

Peirce, J. W. (2009). Generating Stimuli for Neuroscience Using PsychoPy. *Front Neuroinform, 2*, 10. doi:10.3389/neuro.11.010.2008

Potter, M. C. (1976). Short-term conceptual memory for pictures. *J Exp Psychol Hum Learn, 2*(5), 509-522. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/1003124

Potter, M. C., & Levy, E. I. (1969). Recognition memory for a rapid sequence of pictures. *Journal of Experimental Psychology, 81*(1), 10-15. doi:10.1037/h0027470

Potter, M. C., Wyble, B., Hagmann, C. E., & McCourt, E. S. (2014). Detecting meaning in RSVP at 13 ms per picture. *Attention, Perception, & Psychophysics, 76*(2), 270-279. doi:10.3758/s13414-013-0605-z

Roberts, K. L., & Humphreys, G. W. (2011). Action relations facilitate the identification of briefly-presented objects. *Atten Percept Psychophys, 73*(2), 597-612. doi:10.3758/s13414-010-0043-0

Serences, J. T., & Yantis, S. (2007). Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cerebral Cortex, 17*(2), 284-293.

Sheremata, S. L. (2019). Topographic Mapping of Parietal Cortex. In *In: Pollmann S. (eds) Spatial Learning and Attention Guidance. Neuromethods* (Vol. 151): Humana, New York, NY.

Shomstein, S. (2012). Cognitive functions of the posterior parietal cortex: top-down and bottom-up attentional control. *Front Integr Neurosci, 6*, 38. doi:10.3389/fnint.2012.00038

Shomstein, S., & Gottlieb, J. (2016). Spatial and non-spatial aspects of visual attention: Interactive cognitive mechanisms and neural underpinnings. *Neuropsychologia, 92*, 9-19. doi:10.1016/j.neuropsychologia.2016.05.021

Shomstein, S., Malcolm, G. L., & Nah, J. C. (2019). Intrusive Effects of Task-irrelevant information on visual selective attention: semantics and size. *Current Opinion in Psychology*.

Silver, M. A., & Kastner, S. (2009). Topographic maps in human frontal and parietal cortex. *Trends Cogn Sci, 13*(11), 488-495. doi:10.1016/j.tics.2009.08.005

Spotorno, S., Malcolm, G. L., & Tatler, B. W. (2014). How context information and target information guide the eyes from the first epoch of search in real-world scenes. *Journal of Vision, 14*(2). doi:10.1167/14.2.7

Talairach, J., & Tournoux, P. (1988). Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: an approach to cerebral imaging.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc Natl Acad Sci U S A, 94*(26), 14792-14797. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/9405692

Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature, 381*(6582), 520-522. doi:10.1038/381520a0

Todd, R. M., & Manaligod, M. G. M. (2017). Implicit guidance of attention: The priority state space framework. *Cortex*. doi:10.1016/j.cortex.2017.08.001

Võ, M. L., & Henderson, J. M. (2010). The time course of initial scene processing for eye movement guidance in natural scene search. *Journal of Vision, 10*(3), 14 11-13. doi:10.1167/10.3.14

Wagner, A. D., Desmond, J. E., Demb, J. B., Glover, G. H., & Gabrieli, J. D. (1997). Semantic repetition priming for verbal and pictorial knowledge: a functional MRI study of left inferior prefrontal cortex. *J Cogn Neurosci, 9*(6), 714-726. doi:10.1162/jocn.1997.9.6.714

Wagner, A. D., Paré-Blagoev, E. J., Clark, J., & Poldrack, R. A. (2001). Recovering Meaning: Left Prefrontal Cortex Guides Controlled Semantic Retrieval. *Neuron, 31*(2), 329-338. doi:10.1016/s0896-6273(01)00359-2

Walther, D. B., Caddigan, E., Fei-Fei, L., & Beck, D. M. (2009). Natural scene categories revealed in distributed patterns of activity in the human brain. *J Neurosci, 29*(34), 10573-10581. doi:10.1523/JNEUROSCI.0559-09.2009

Figure Captions

*Figure 1. **Predicted pathway of semantic influence**. If semantic information biases spatial attention (green path + green bordered box): the space surrounding the semantically related object is preferably processed. If semantic information influences object representations (red path + red bordered box): the semantically related object itself is preferably processed.*

*Figure 2, **Experiment Paradigms & Behavioral Results**. A) Experiment 1 – Participants are presented with a reference object presented above the fixation cross. Next, two objects appeared in periphery below the midline creating an object triad. One of the peripheral objects is semantically related (SR) to the central object while the other is not (NR). After a 1s delay, a target letter (T or L) along with two distractor characters (T/L hybrids) appear superimposed on top of the objects. Participants then perform a target discrimination task. Semantic relatedness is not predictive of target location, thus task-irrelevant. B) Experiment 2 – Participants were presented with two objects appearing on either side of fixation. The objects were either semantically related to one another, or not. A rotated Gabor patch was overlaid on top of either object, with participants tasked to report whether the two Gabor patches matched in orientation. C) Example of semantically related (SR) and not-related (NR) pairs in Experiment 2. D) Experiment 1 Behavioral Results – Participants were significantly more accurate at identifying targets that appeared on top of an SR object. E) Experiment 2 Behavioral Results - Participants were more accurate and significantly faster at performing the task when the objects were SR (* p < . 05, and error bars represent ±1 standard error)*

*Figure 3. **Experiment 1 fMRI Results**. Semantic relationships significantly modulate activity in EVC and IPS, but not LOC. This suggests that high level semantic relationships facilitate activity in lower processing regions via an attentional, rather than object recognition mechanism. (* p < . 05, and error bars represent ±1 standard error)*

*Figure 4. **Experiment 2 Stimuli and fMRI Results**. A) Full example of the four main objects (left of each pair) when paired with a SR object or NR object. The object pairs in the blue background indicates SR condition, the object pairs in the yellow background indicates NR condition. B) Decoding accuracy performance of a linear classifier. Performance was only greater than chance (25%) in EVC. A main effect of semantic relatedness was also observed in EVC, with SR pairs having higher decoding accuracy than NR pairs. Small insert graph represents EVC data across V1, V2, V3, showing a main effect of ROIs, such that V1 decoding accuracy was greatest. C) Semantic facilitation in left IFG again predicted behavioral benefit (*p < . 05, and error bars represent ±1 standard error).*