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The Neural Representation Of Duration In Event Concepts

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THE NEURAL REPRESENTATION OF DURATION IN EVENT CONCEPTS

by

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DEDICATION

This thesis is dedicated to our late son, Ezra Olsen Hackett (12/7/2014) who was born too early and left us too soon.

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ABSTRACT

Little is known about the neural basis of temporal concepts. Some have suggested that temporal concepts are grounded in spatial or temporal processes. Here we aimed to examine the representation of duration of event concepts, and compare them with judgments of object size, which may entail spatial processing. A 2x2 block design used event and object nouns as stimuli that were presented during functional imaging. Participants made judgments about event duration, object size, and event and object valence. In addition to whole-brain analyses, we examined activations in areas known to be involved in temporal processing and spatial processing. Knowledge of events compared to objects activated a distributed network with large clusters in bilateral angular gyri, precuneus, middle temporal lobules and prefrontal cortices in whole-brain analyses. The whole-brain analyses of duration minus valence revealed a right hemispheric preference for processing of semantic duration information compared to valence tasks. Peak activation of clusters for duration were located in the right dorsomedial prefrontal cortex, precuneus, lingual gyrus, SMG, left middle MTG/ITG, parahippocampal gyrus and bilateral angular gyri. ROI analyses of angular gyri suggested the processing of semantic information of duration occurred mainly the right AG and left PGp. ROI analyses of temporal perception areas suggested a role of the right SMG in the representation of duration. Additionally, temporal ROIs suggested that the right pSTS and left SMG were involved in event processing relative to objects. IPS ROI revealed that the right middle IPS was activated for event duration minus event valence

v

and object size minus object valance. Additionally, PPA ROI revealed that event duration compared to event valence and object size compared to object valence activated the PPA. Thus, we found that event concepts were supported by bilateral inferior parietal and anterior and middle temporal cortex, as well as precuneus and posterior cingulate. This is consistent with the role of AG in integrating temporal sequences. Conceptual duration processing is grounded in both temporal perception (right SMG) and space (IPS and PPA).

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ABBREVIATIONS

3T ....Three Tesla

AFNI ....Analysis of Functional NeuroImages

ATOM.. A Theory of Magnitude

BOLD...Blood Oxygenation Level Dependent

EDur..Event Duration

EEG...Electroencephalography

EVal ....Event Valence

FDR... False Discovery Rate

fMRI...functional Magnetic Resonance Imaging

FoV .... Field of View

FWHM .... Full Width Half Maximum

IFG ....Inferior Frontal Gyrus

IQR...Interquartile Range

IPL...Inferior Parietal Lobule

IPS... Intraparietal Sulcus

ms ....millisecond

MTG..Middle Temporal Gyrus

ObSz...Object Size

OVal..Object Valence

PET ....Positron Emission Tomography

PFC ....Prefrontal Cortex

CHAPTER 1

INTRODUCTION

Time is in a sense, an abstract concept as well as a concrete concept. We are able to perceive and discuss characteristics about time without being able to physically interact with it. Moreover, we use our knowledge about time to estimate the duration of events. Semantic knowledge pertaining to event duration is crucial to understanding many aspects of language. Indeed, the duration of events can be estimated without prior personal experience with a given event. For example, if we are on our lunch break and Tino the shoeshine guy asks us if we "have time for a shine?" we can appropriately reply "yes." Alternatively, if we have to be in a meeting in two minutes, we can appropriately reply "no." Our knowledge of an event such as a "shoeshine" and the components that make up an event can be used to estimate the duration of the event. In this case we might estimate that it will take at least a few minutes for Tino to find the correct color of shoe wax, apply the wax and effectively shine each shoe. Therefore we might estimate the total duration of a shoeshine to be about fifteen minutes. Despite the ubiquity with which time is used in thought and language, the representation of time is still being resolved.

1.1 Perception of Time

A meta-analysis by Weiner, Turkeltaub and Coslett (2010a) identified a number of coordinates involved in time perception. The analysis separately examined areas that were active while performing sub-second (less than one second) and supra-

second (greater than one second) timing. The neuroimaging experiments reviewed in this study tested for perception of intervals ranging from 200 ms to 24 seconds. A vast network was found to be involved in time perception. Sub-second timing chiefly activated sub-cortical regions such as the basal ganglia and cerebellum, while supra-second timing recruited more cortical areas such as the supplementary motor area (SMA) and prefrontal cortex. Overall, a number of significant correlates were found to be involved in timing. One region found to be activated during sub-second and supra-second tasks in the Weiner et al. (2010a) meta-analysis and a region that is a recurrent coordinate in time perception literature is the right inferior parietal lobule (IPL).

The right IPL includes the supramarginal gyrus (SMG) and the angular gyrus (AG), and this area has been indicated to be involved in temporal tasks by neuroimaging reviews (Harrington & Haaland, 1999; Lewis & Miall, 2003a; Weiner et al., 2010a). Moreover, damage to the right IPL in the form of brain lesions (Danckert et al., 2007; Harrington, Haaland & Knight, 1998) and following rTMS (repetitive transcranial magnetic stimulation) (Bueti, Bahrami, & Walsh, 2008; Wiener, Hamilton, Turkeltaub, Matell, & Coslett, 2010b; Wiener et al., 2012) has altered temporal perception. One recent study reported that activity in the right SMG decreased when participants were presented with repeated visual stimuli of the same duration (Hayashi et al., 2015). In addition to the right IPL, some suggested that networks in the right prefrontal hemisphere might be involved temporal perception (Lewis & Miall, 2006).

Lewis and Miall (2006) noticed a trend in previously published neuroimaging studies utilizing discrete timing tasks. The authors found that discrete timing tasks, involving breaks in between trials, activated the right prefrontal and parietal cortices

while continuous timing trials that involved a repeated task such as finger tapping involved a different network consisting of a portion of the motor system (Lewis & Miall 2003a; Lewis & Miall, 2006). The reanalysis by Lewis and Miall (2006) found corroborating results in that the right prefrontal cortex and anterior insula were involved in time perception of both sub and supra-second durations. A more lenient threshold also revealed the parietal cortex (including the AG) and anterior cingulate for both sub and supra-second timing tasks. The function of the right hemisphere in processing information about temporal concepts may not be limited to duration but rather, duration may be processed as part of a magnitude system.

1.2 Relationship Between Time and Space Perception

Walsh's ATOM (A Theory of Magnitude) provided evidence for a generalized magnitude system, where the right parietal lobules are activated during spatial tasks and certain number tasks as well as during temporal processing (Walsh, 2003). Moreover, ATOM suggested that comparison or estimation number tasks are located in the right parietal lobe, whereas the left parietal lobule computes exact calculations, perhaps because of the left hemisphere being involved in language (Bueti & Walsh, 2009; Walsh, 2003). In addition to proposed hemispheric differences in processing estimations and exact calculations of magnitude, a review by Jager and Postma (2003) suggested a hemispheric dissociation of spatial processing.

Jager and Postma (2003) proposed a dissociation between the type of spatial relations and the preferred hemispheric representation. This review split the data into categorical spatial relations, which consisted of a general spatial layout of a visual stimulus (e.g., left of/right of, above/below) and coordinate spatial relations, which

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identified specific spatial locations of objects in terms of metric units (e.g., three inches away). This review of spatial perception studies found that categorical spatial relations were suggested to involve the left hemisphere and specifically the left IPL, while coordinate spatial relations were represented in the right hemisphere. Despite support for a general hemispheric dichotomy between categorical and coordinate spatial relations as reported in the review by Jager and Postma (2003), a recent study has suggested a more complex representation of spatial relations.

Amorapanth, Widick and Chatterjee (2010) employed two experiments to test the hemispheric separation of spatial relations found in the literature. The authors used fMRI of healthy participants and voxel-based lesion symptom mapping (VLSM) in brain-damaged and healthy participants. All participants viewed pictures of objects with different spatial relationships to each other. FMRI of healthy participants and residual analyses of brain-damaged patients revealed the left IPL was involved to a greater extent in categorical spatial relations than the right IPL. The VLSM analysis indicated that damage to the left superior temporal gyrus (STG) affected categorical deficits, but no areas were identified in the right hemisphere. Coordinate spatial relations were impaired in patients with damage to the right middle temporal gyrus (MTG) and in patients with left hemispheric damage to the AG and inferior frontal gyrus (IFG). The results of this study suggested that the correlates of categorical and coordinate spatial processing might be arranged in a more complex fashion, rather than being represented by a dissociation between hemispheres.

1.3 Time and Space in Language

The right hemisphere has been suggested to be involved in time perception and generalized magnitude processing, whereas the left hemisphere has been associated with exact calculation and also spatial relations through language (Damasio et al., 2001). Damasio et al. (2001) used positron emission tomography (PET) to examine the retrieval of action words and words indicating spatial relations between objects. The authors found that the left frontal and parietal regions were activated in actions and spatial relations. A recent review of linguistically encoded categorical spatial relations (Kemmerer, 2006) also found support for IPL structures such as the SMG and AG in representing categorical spatial relations. Interestingly, the left SMG has also been implicated in categorical relations via locative prepositions, such as 'to the left of' and 'to the right of' (Noordzij, Neggers, Ramsey & Postma, 2008). Despite an accumulating amount of data examining spatial relations in language, less is known about regions activated during temporal processing of language.

Lai and Desai (2016) recently provided the first evidence that temporal language activated coordinates involved in temporal perception. The authors examined activation during fMRI while participants read temporal, spatial literal or a control fictive motion sentence. This study used whole-brain analyses as well as ROIs (region of interest) centered around supra-second coordinates found to be involved in time perception from the Weiner et al. (2010a) meta-analysis. The ROI analysis found greater activation in the left insula and right claustrum for temporal metaphors compared to controls. Additionally a whole-brain analysis suggested greater activation in the left posterior middle temporal gyrus (pMTG), IFG, right anterior insula and STG for temporal

metaphors compared to controls. Overall this study concluded that the perisylvian regions, involved in time perception, were activated during temporal sentences. Aforementioned studies suggested that time and space were processed in distinct coordinates but others have proposed that language might be a vehicle by which time and space interact.

Time and space have been proposed to interact through language. The conceptual metaphor theory (Lakoff & Johnson, 1999) was proposed to explain this interaction by suggesting that we use a more concrete entity such as space to understand a less concrete concept such as time. A number of behavioral and psychophysical studies have found strong support for the conceptual metaphor theory of using spatial metaphors to understand time (e.g., Wednesday's meeting has been moved to Monday; Christmas is coming up) but not the other way around (Boroditsky, 2000; Casasanto & Boroditsky, 2008; Matlock, Ramscar, & Boroditsky, 2005). Studies have also reported that time and space interacts to the extent of a mental time line where events are linearly represented (for a review see Bonato, Zorzi, & Umilta, 2012). This has been found in healthy controls (Arzy, Adi-Japha & Blanke, 2009) and in patients with left spatial neglect, where these patients had difficulty assessing past events that would be located on the left side of a mental time line (Saj, Fuhrman, Vuilleumier, & Boroditsky, 2014). Other have failed to find strong support for a time and space interaction through language.

Three other studies failed to find strong support for a connection between time and space in language processing. Kemmerer (2005) used prepositions to examine spatial and temporal processing in patients with lesions to their left perisylvian cortex. Conflicting results were found in this study as two of the four patients performed better

on spatial than temporal tests while the other two patients performed better on temporal

rather than spatial tests. More weak support for an asymmetric time–space relationship

was described in a review by Kranjec, Cardillo, Schmidt, and Chatterjee (2010a) who

suggested that time and space have separate representations and spatial thought may

influence temporal thought but space is not necessary to think about time. Additionally

Kranjec, Cardillo, Schmidt, Lehet and Chatterjee (2012) examined interactions between

time, space and causality during events as described in sentences. The authors found that

time and causality were closer associated than time and space. Overlapping areas for

time and causality as revealed by fMRI analysis included the left middle frontal gyrus

and SMA. A recent review attempted to reconcile the previous data involving space and

time interactions and suggested that the domain-general magnitude system as outlined in

ATOM and the conceptual Metaphor Theory should be interpreted as complementary

theories (Winter, Marghetis, & Matlock, 2015).

1.4 Event Nouns

Here we aimed to extend upon previous findings concerning the representation of

duration. Instead of using sentences or verbs to denote events, we used event nouns.

Atypical nouns such as event nouns have been utilized to a lesser extent in experiments

than typical object-denoting nouns. One notable study that employed event nouns

attempted to clarify correlates involved in actions compared to objects (Peelen, Romagno

& Caramazza, 2012). This study compared activation during event words (verbs and

event nouns) to words denoting a state of being (verbs and object nouns) as well as action

verbs to object nouns. State-denoting and action verbs were found to activate the left

pMTG and superior temporal sulcus (STS), whereas object nouns were found to activate

the left fusiform gyrus, relative to action verbs. Another notable study examined representation of grammatical class (verbs vs. nouns) and semantic category (events vs. objects) during neuroimaging (Bedny, Dravida & Saxe, 2014). Verbs compared to nouns activated left pMTG and superior STG. Interestingly, Bedny et al. (2014) also found the left pMTG to be activated more during processing of event nouns compared to object nouns. Overall, the authors concluded that processing event and object nouns are represented in partially dissociable networks.

The primary aim of this study was to determine the representation of conceptual processing of duration. It has been previously suggested that the perisylvian cortex is involved in semantic representation of temporal concepts (Kranjec & Chatterjee, 2010b; Kremmer 2005; Lai & Desai, 2016). Therefore we expect to find similar areas within the perisylvian cortex to display greater activation for duration judgments compared to valence or size judgments. A secondary aim of this study was to further examine the question; are temporal concepts grounded in spatial perception areas, temporal perception areas or are temporal concepts not grounded in perceptual areas? (Kranjec & Chatterjee, 2010b). Theories of grounded cognition assume that processing of semantic knowledge of concepts in language is achieved through motor and sensory systems corresponding to the concepts (Gallese & Lakoff 2005; Barsuola, 2007). Support for grounded cognition have been previously demonstrated in a number of studies across a number of categories, including action, audition, color, emotion, gustation, motion and olfaction (Binder & Desai, 2011). Lai and Desai (2016) provided the first evidence that temporal concepts are at least partially grounded in temporal perception areas.

We aimed to test our questions by examining activation in healthy participants comparing durations of two event nouns while undergoing fMRI. We use event and object nouns, as it allows us to match the grammatical class of words with non-temporal objects thereby avoiding grammatical and lexical confounds and thus examining semantic rather than lexical factors (Metusalem et al., 2012). Additionally, we are able to contrast activation of the same event nouns during different tasks (i.e., duration and valence judgment). This allowed us to measure duration processing while the valence task controlled for general processing of event nouns. Additionally, the object size task provided an analogous magnitude based task for conceptual spatial processing. Therefore these manipulations allowed us to compare temporal and spatial processing of event nouns. In order to accomplish the aims of this study, we used whole-brain analyses and ROIs. Coordinates associated with perceptual temporal processing as defined by Weiner et al. (2010a) served as ROIs. We also defined bilateral angular gyri ROIs and areas PGa and PGp in order to further examine differences in role of the left and right AG in temporal tasks involving events. A number of studies have found the AG to be involved in processing temporal sequences as well as event words (Binder & Desai, 2011; Boylan, Trueswell, & Thompson-Schill, 2015; Lewis & Miall, 2003b). Bilateral regions in the IPL served as an additional ROI to examine event nouns and duration processing in this region. We defined an ROI in the left parahippocampal place area (PPA) and bilateral intraparietal sulcus (IPS) to further investigate the relationship between spatial processing of event nouns.

CHAPTER 2

METHODS

2.1 Participants

Twenty healthy adults (16 women) with a mean age of 19.75 years (SD = 2.29, range 18 – 26) participated in the fMRI experiment. The participants were native English speakers and right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971). All of the participants displayed normal or corrected-to-normal vision and none of participants indicated that they had a history of neurological disorders. Written informed consent was obtained from each adult prior to participation in the experiment. Participants were paid their choice of $25 or credits (if applicable) to be applied to an undergraduate psychology course. The Institutional Review Board at the University of South Carolina approved the protocol used in this study.

2.2 Stimuli

The stimuli used in this experiment consisted of 80 pairs of event nouns (e.g., "the avalanche", "the exam") and 80 pairs of object nouns (e.g., "the eel", "the moth") (Appendix A). Deverbal nouns denoting an activity (e.g., relaxation, jumping) were not used. Stimuli (object and event nouns) were matched on a number of psycholinguistic characteristics including: number of nouns also classified as verbs, log verb frequency, log noun frequency (WebCelex; http://celex.mpi.nl) word frequency, log of the word frequency, number of letters, number of syllables (Balota et al., 2007), concreteness (Brysbaert, Warriner, & Kuperman, 2014), imageability (Wilson, 1988), semantic

diversity (Hoffman, Ralph, & Rogers, 2013) and valence (Warriner, Kuperman, & Brysbaert, 2013), all $p > 0.05$ (table 2.1).

2.3 Task

The experiment was arranged in a 2 x 2 factorial design. Each participant judged 40 pairs of events nouns on duration (e.g., which event is typically greater in duration or are the events about the same duration) and a unique set of 40 event nouns on valence (e.g., which event is typically more pleasant or are the two events equally as pleasant). Additionally the same participant judged 40 pairs of object nouns on size (e.g., which object is typically greater in size or are the objects about the same size) and a unique set of 40 object nouns on valence (e.g., which object is typically more pleasant or are the two objects equally as pleasant). The same 80 pairs of event nouns and 80 pairs of object nouns were judged by all participants but the condition in which the specific noun pair was presented, was counterbalanced between participants. This ensured that the participants were not previously exposed to stimuli from an earlier block. Additionally, this design allowed all event nouns to be judged on duration and valence. Likewise, our design allowed all object nouns to be judged on size and valence. Each noun was preceded by "the" in order to disambiguate grammatical class.

The "correct answer" for valence conditions was determined by the Warriner, Kuperman and Brysbaert (2013) ratings, despite the highly subjective nature of valence judgments. If the difference in the valence rating between a pair of nouns was greater than 0.25, then the noun with the larger valence rating was determined to be more pleasant. If the difference in the valence rating between a pair of nouns was less than 0.25, then those nouns were considered to be equivalent in valence. The experimenters

Table 2.1 Characteristics of Stimuli

Characteristic	Event nouns (n = 160)	Object nouns (n = 160)	p value
# of Nouns also classified as verbs	73(45.6)	73(45.6)	1.00[a]
Verb Frequency	0.67±0.58	0.64±0.55	0.71[b]
Noun Frequency	0.87±0.70	0.91±0.65	0.60[b]
Word Frequency	2249[658 – 11081]	3358[610 – 14123]	0.59[c]
Log Frequency	7.92±1.90	8.05±1.93	0.56[b]
# of Letters	6.27±1.95	6.12±1.99	0.50[b]
# of Syllables	1.88±0.80	1.89±0.99	0.90[d]
Concreteness	4.05±0.48	4.09±0.42	0.40[b]
Imageability	5.12±0.72	5.11±0.83	0.89[b]
Semantic Diversity	1.50±0.25	1.50±0.32	0.98[d]
Valence	5.24±1.60	5.36±1.06	0.43[d]

All values are number of occurrences(percent), mean±SD or median[IQR]
[a]Chi–Square test for Independence
[b]T–Test equal variances assumed
[c]Mann–Whitney U Test
[d]T–Test equal variances not assumed

determined correct responses for the event duration and the object size conditions with at least 90% agreement between experimenters. In order to reduce the effects of spatial priming, the location of the correct judgment was balanced. The correct response for 16 of the 40 noun pairings in each of the conditions was the noun on the left. Likewise, the

noun on the right was considered correct in 16 of the 40 pairings. Eight of the forty pairings in each of the four conditions were considered to be judgments of equivalence.

2.4 Stimulus norming

Twenty healthy adults (18 women) with a mean age of 21.3 years (SD = 5.81, range 18 – 41) participated in the norming task. All participants were native English speakers and right-handed as determined by the Edinburgh Handedness Inventory (Oldfield, 1971). All of the participants displayed normal or corrected-to-normal vision and none of participants indicated that they had a history of neurological disorders. None of the participants in this norming study participated in the fMRI study. Written informed consent was obtained from each participant prior to inclusion in the experiment. Participants were paid in credits (if applicable) to be applied to an undergraduate psychology course. The Institutional Review Board at the University of South Carolina approved the protocol used in this study.

Participants completed at least three practice trials (mimicking the experiment but where feedback was given by an experimenter) for each of the four conditions. The order of the stimuli in the practice trials and experiment was randomized for each participant. Participants decided which noun was greater or if the nouns were about the same, for each of the four conditions, by pressing a key on a laptop. To avoid effects of laterality, participants were instructed to respond with either their left or right hand for entire experiment. The specific hand (left or right) was determined before participation and was alternated between participants. Therefore the number of participants who responded with their left hand was equal to the number of participants who responded with their right hand.

The stimuli were presented visually in a block design (Figure 2.1).
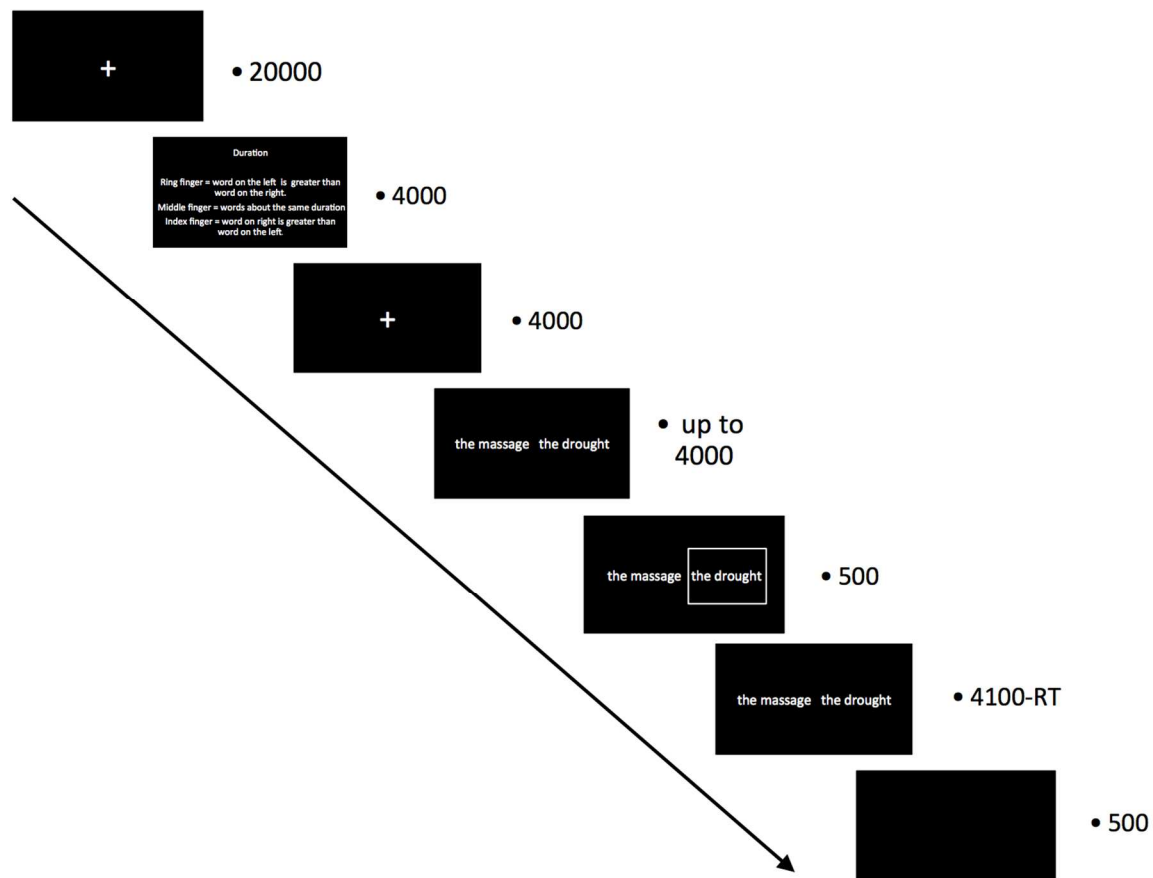
Figure 2.1 Experimental Block Set-up. This is an example of the experiment block set-up. Each block began with a 20000 ms fixation cross followed by the condition and instructions (Duration task, in this case) for 4000ms. Next a fixation cross for 4000 ms was presented. The stimuli followed and participants were allowed up to 4000 ms to respond. The participants' response was indicated by a white rectangle enclosing the chosen stimuli and this was displayed for 500 ms. The participants were then shown the original stimuli for the remainder of 4100 ms minus their reaction time. Lastly a blank screen appeared for 500 ms before the next trial in the block began.

There were five runs in this experiment, each with four blocks (one block per condition).

The order of the blocks was randomized for each participant. Each block was comprised

of eight trials. Every block began with a 20,000 ms fixation cross that was centered on

the screen, which was followed by an instruction screen. The instruction screen displayed

the specific judgment that the participants would be performing (i.e, "Duration", "Size" or "Pleasant") with a reminder as to which keys/fingers corresponded with the judgments (i.e., word on the left is greater than word on the right; words are about the same; word on the right is greater than word on the left). A fixation cross, centered on the screen with duration of 4000 ms followed the instruction screen. Then, the pair of nouns was presented for up to 4000 ms. Once a participant responded, their choice was displayed on the screen for 500 ms and a white rectangle surrounded the chosen noun. If the participant determined that the nouns were about the same in a given condition, then both nouns would be surrounded by white rectangles to reflect the participant's judgment. After the participant's choice was displayed, the original noun pairing was shown for the remainder of the 4100 ms minus the reaction time. This ensured that each participant experienced the same amount and duration of visual stimuli. Lastly, a blank screen was presented for 500 ms before the next trial was presented.

We conducted item and subject analyses to examine differences in mean RT (Reaction Time) across the four conditions. A one-way ANOVA was conducted on the mean RTs of the 80 pairs of nouns for each of the four conditions. This item analysis suggested that there were no significant differences in the RT of the noun pairs across conditions, $F(3, 316) = 2.52$, $p = 0.06$ (Table 2.2).

Table 2.2 Item Analysis of the Norming Experiment

Condition	n	Reaction Time	Accuracy
Event Duration	80	2060[1990, 2131]	75.6[69.6, 81.6]

Event Valence	80	2075[2007, 2143]	56.9[49.9, 63.9]
Object Size	80	2058[1977, 2138]	78.4[72.8, 84.0]
Object Valence	80	2178[2109, 2247]	56.4[49.1, 63.8]

All values are mean[95% Confidence Interval].
All accuracy values are percentages.
n indicates the number of unique pairs of nouns in each condition.

We also conducted a one-way ANOVA on the mean RT for each participant across the four conditions. This subject analysis suggested no significant difference in RT across conditions, $F(3, 76) = 1.07$, $p = 0.37$ (Table 2.3).

Table 2.3 Subject Analysis of the Norming Experiment

Condition	*n*	Reaction Time	Accuracy
Event Duration	20	2059[1943, 2175]	76.1[72.5, 79.8]
Event Valence	20	2078[1955, 2200]	56.9[53.3, 60.5]
Object Size	20	2061[1940, 2183]	78.6[74.3, 82.8]
Object Valence	20	2184[2062, 2306]	56.8[53.9, 59.7]

All values are mean[95% Confidence Interval].
All accuracy values are percentages.
n indicates the number of participants.

Accuracy is not a meaningful measure in these tasks, especially the valence task, which is highly subjective and dependent on personal experiences. Nonetheless, we analyzed "accuracy" based on normative ratings. Heterogeneity of variances between groups was found, so a Brown-Forsythe test for equality of means was used in the item analysis of mean accuracy for noun pairings. The item analysis suggested a significant difference in

the accuracy ratings of noun pairs between conditions, $F(3, 302) = 12.95$, $p < 0.001$ (Table 2.2). Post-hoc item analysis using a bonferroni correction revealed significant pairwise differences between event duration and event valence; event duration and object valence; event valence and object size; and object size and event valence judgments (all $p < 0.001$). There were no significant differences between event duration and object size or event valence and object valence (all $p > 0.9$). A one-way ANOVA conducted for the subject analysis suggested there were significant differences in participants' accuracy between conditions, $F(3, 76) = 74.88$, $p < 0.001$ (Table 2.3). Post-hoc subject analysis using a bonferroni correction suggested significant pairwise differences between event duration and event valence; event duration and object valence; event valence and object size; and object size and event valence (all $p < 0.001$). The mean accuracy of the other two pairwise conditions, event duration and object size; event valence and object valence, were not significantly different (all $p > 0.25$).

2.5 fMRI Procedure

The stimuli in the fMRI procedure were presented as in the norming study. Instead of participants responding via key presses as in the norming study, participants responded via a response glove, using the same three fingers (index, middle and ring) as the norming study. The stimuli were presented in five runs (identical to the norming study) and 375 images were collected during each run.

2.6 Image Acquisition and Analysis

Imaging data was collected at the McCausland Center for Brain Imaging, Palmetto Health Richland Memorial Hospital in Columbia, SC. A Siemens Magnetom 3T Prism (Siemens, Erlangen, Germany) was used to acquire imaging data. Anatomical

imaging was collected using a multi-echo T1 scan of the whole brain, which produced a

1mm isotropic voxel size (TR = 2250 ms, TE = 4.11 ms, TI = 925 ms, flip angle = 9 °,

FoV = 256 mm). Functional imaging was collected using a multiband echo, which

produced echo-planar images (TR = 800 ms, TE = 37 ms, flip angle = 51°, FoV = 220

mm). Volumes were composed of 44 slices with a 10% slice gap and a slice thickness of

2.5 mm that were axially oriented and each volume covered the whole brain. The

resulting voxel size was 2.75 x 2.75 x 2.5 mm^3.

Image analysis was performed using the AFNI software package (Cox, 1996).

The standard afni_proc.py processing script was utilized for within-subject analysis,

which included spatial co-registration (Cox & Jesmanowicz, 1999) followed by

registration of functional images to the anatomy (Saad et al., 2009) and projection of

images to standard stereotaxic space (Talairach & Tournoux, 1988). The normalized

images were smoothed with a Gaussian filter of 6 mm FWHM and the run mean for each

voxel was scaled to 100.

The preprocessed fMRI time series was analyzed with the program *3dREMLfit*,

using reference functions that represented each condition convolved with a standard

hemodynamic response function. *3dREMLfit* performed a voxel-wise multiple linear

regression with covariates of interest for each of the four conditions (event duration,

event valence, object size and object valence). Six motion parameters, the signal

extracted from the ventricles, the manual response and presentation of the instructions

were included as covariates of no interest. General linear tests were performed to

examine contrasts between the covariates of interest.

A random effects analysis was conducted by creating group maps that compared activation against a constant value of 0. A voxel-wise threshold was applied to the group maps at $p < 0.001$. The group maps were corrected for multiple comparisons by removing clusters smaller than threshold size to achieve a two-tailed map-wise correction of $p < 0.05$. The program *3dClustSim* was used with 10,000 iterations to determine the cluster threshold. Monte Carlo simulations estimated the chance probability of spatially contiguous voxels exceeding the voxel-wise p threshold. The *3dClustSim* analysis used a mask that excluded areas outside of the brain, locations of deep white matter and areas pertaining to the ventricles.

In addition to the whole-brain analysis, a hypothesis-driven ROI analysis was conducted to determine if event nouns activated areas associated with time perception. A previous meta-analysis found 27 coordinates associated with supra-second temporal processing, in perceptual or motor timing tasks (Wiener et al., 2010a). Of these 27 coordinates, we selected areas within the perisylvian cortex as part of our *a priori* hypothesis given the results from previous experiments (Kranjec & Chatterjee, 2010b; Kremmer 2005; Lai & Desai, 2016). These areas included one coordinate in the right posterior STS (pSTS; 54, -38, 4) two in the claustrum (32, 16, 4; 34, 12, 6), two in the left insula (-40, 18, 0; -36, 12, 4), bilateral IFG (-40, 14, -6; 46, 8, 22) and SMG (-50, -48, 28; 50, -46, 44). The 18 remaining coordinates were examined in an *a posteriori* analysis, including five coordinates in the bilateral precentral gyrus, three coordinates in the right IPL, three locations in the middle frontal gyrus, three locations in the bilateral cingulate gyrus and one coordinate in each of the following locations: right SMA, SMA, left putamen and the left superior frontal gyrus. ROIs were defined by placing a sphere of

10mm in diameter circumscribing each of the 27 coordinates. Corrections for multiple comparisons were performed using the False Discovery Rate (FDR) correction (Benjamini & Hochberg, 1995).

A priori ROIs of the bilateral AG and PGa/PGp division of the IPL was performed in order to examine the semantic representation of events and duration. The AG has been found to be activated when processing temporal and spatial information related to events (Binder & Desai, 2011; Boylan, Trueswell & Thompson-Schill, 2015; Lewis & Miall, 2003a). We defined bilateral ROIs using masks from the probability atlas, *TT_desai_ddpmaps* (Destrieux, Fischl, Dale, & Halgren, 2010), with a probability threshold of 0.40. We also performed an *a posteriori* ROI of areas in the bilateral IPL (PF, PFm and PFcm) to further investigate the role of the IPL in processing event nouns and duration. The regions of the IPL were defined by bilateral ROIs that used masks from the maximum probability atlas, *TT_caez_mpm_18* (Caspers et al., 2008). Multiple comparisons were corrected by using the FDR correction (Benjamini & Hochberg, 1995).

An *a priori* ROI examining divisions of the bilateral IPS was performed to examine the relationship between event nouns, duration and spatial processing. Here three areas per hemisphere served as ROIs corresponding to middle, anterior and posterior regions of the IPS. The IPS ROIs used masks derived from the probability atlas *TT_caez_pmaps_18* (Eickhoff et al., 2005) with a probability threshold of 0.30. Lastly, an *a posteriori* PPA ROI analysis was performed to elucidate the relationship between event nouns and space. Epstein and Kanwisher (1998) found that an area on the parahippocampal gyrus was activated when participants made judgments about places. We used the same coordinate (-28, -39, -6) as found by Epstein & Kanwsiher (1998) to

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be the average coordinate of all subjects for the PPA. A sphere of 10mm in diameter

centered on the left PPA coordinate defined the ROI. Corrections for multiple

comparisons were performed using the FDR correction (Benjamini & Hochberg, 1995).

CHAPTER 3

RESULTS

3.1 Behavioral Results

Overall, participants responded in 99.5% of the trials. Participants' RTs in the scanner were similar to the norming study. In the fMRI item analysis, an ANOVA with equal variances assumed revealed that there were not significant differences in RT of noun pairings across conditions, $F(3, 316) = 2.20$, $p = 0.09$ (table 3.1).

Table 3.1 Item Analysis of the fMRI Experiment

Condition	*n*	Reaction Time	Accuracy
Event Duration	80	2127[2063, 2191]	76.9[70.5, 83.2]
Event Valence	80	2126[2061, 2191]	56.9[50.5, 63.3]
Object Size	80	2142[2068, 2215]	78.7[72.7, 84.7]
Object Valence	80	2229[2166, 2292]	52.4[45.8, 59.0]

All values are mean[95% confidence interval].
n indicates the number of unique pairs of nouns in each condition.

The fMRI subject analysis conducted with equal variances assumed one-way ANOVA also suggested no significant difference in the RT of participants across conditions, $F(3, 76) = 0.58$, $p = 0.63$ (table 3.2).

Table 3.2 Subject Analysis of the fMRI Experiment

Condition	*n*	Reaction Time	Accuracy
Event Duration	20	2127[1998, 2256]	76.9[74.5, 79.3]
Event Valence	20	2126[1992, 2261]	57.0[53.2, 60.8]
Object Size	20	2142[2022, 2261]	78.7[75.7, 81.6]
Object Valence	20	2228[2074, 2382]	52.5[48.8, 56.1]

All values are mean[95% confidence interval].
n indicates the number of participants.

Accuracy in the scanner was examined by conducting one-way ANOVA on the mean accuracy ratings for noun pairs within each condition (item analysis) and for participants within each condition. The item analysis revealed a significant difference in the accuracy of noun pairings between conditions, $F(3, 316) = 17.93$, $p < 0.001$ (table 3.1). Similar to the norming study, a bonferroni correction for multiple comparisons suggested that accuracy was significantly lower on valence judgments: event valence compared to event duration; event valence compared to object size; object valence compared to event duration; and object valence compared to object size (all $p < 0.001$). No other pairwise comparisons were significantly different in the item analysis (all $p = 1.00$). A similar profile of accuracy was found in the fMRI subject analysis, $F(3, 76) = 74.88$, $p < 0.001$ (table 3.2). Post-hoc comparisons using a bonferroni correction mirrored the item analysis where accuracy in the valence conditions was significantly lower than in magnitude conditions (all $p < 0.001$), with no other significant differences (all $p >$

0.25). There were no significant differences in accuracy between participants (all $p >$ 0.05) and all participants performed with accuracies better than chance for all conditions.

3.2 Event Duration Minus Event Valence

The whole-brain analysis suggested that the following areas displayed significantly greater activation for the duration task compared to the valence task: right middle frontal gyrus to superior frontal sulcus, precuneus, posterior ventral cingulate gyrus/ lingual gyrus, SMG, left middle MTG/inferior temporal gyrus (ITG), parahippocampal gyrus and bilateral angular gyri (figure 3.1 table 3.3).

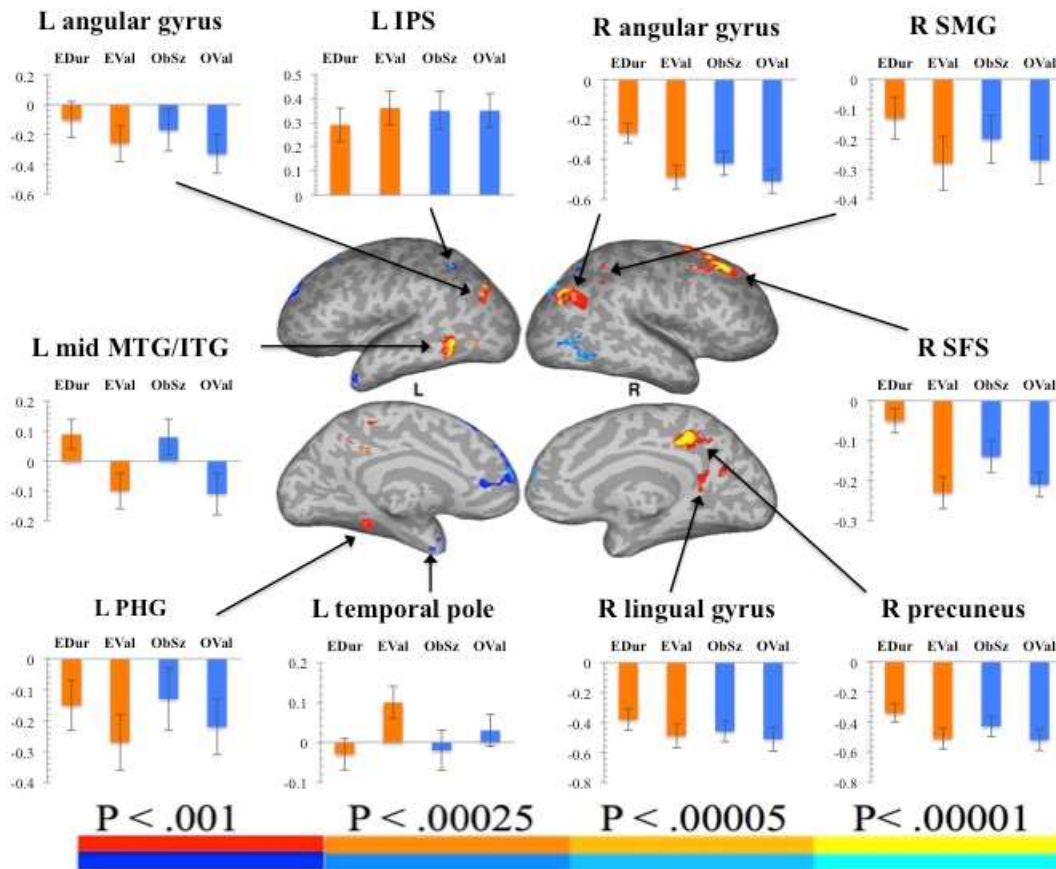Figure 3.1 Event Duration Minus Event Valence. Areas activated during whole-brain analysis of event duration minus event valence contrast. Red-yellow colors indicate greater activation for duration cyan-blue indicates greater activation for valence. Bar graphs of activation in each condition are shown. Y-axis indicates percent change in BOLD signal for each of the four conditions within select clusters indicated by the

whole-brain analysis. ITG indicates inferior temporal gyrus; L = left hemisphere; mid = middle; MTG = middle temporal gyrus; PHG = parahippocampal gyrus; R = right hemisphere; SFG = superior frontal gyrus; SFS = superior frontal sulcus; SMG = supramarginal gyrus.

Table 3.3 Whole-Brain Analysis for Main Contrasts of Interest

Volume	Mean	Max	x	y	z	Structure(s)
Event Duration > Event Valence						
4859	3.43	4.77	26	23	43	R superior frontal sulcus, middle frontal gyrus
3016	3.39	4.76	33	-78	38	R AG
2281	3.55	4.59	6	-43	36	R precuneus, middle cingulate cortex
1891	3.52	4.80	-53	-56	-3	L middle MTG/ITG
1344	3.40	4.48	-33	-73	31	L AG
609	3.14	3.47	8	-48	3	R posterior ventral cingulate gyrus, lingual gyrus
500	3.17	3.60	46	-46	41	R inferior parietal lobule, SMG
391	3.24	3.72	-28	-36	-8	L parahippocampal gyrus
Event Valence > Event Duration						
5312	-3.31	-4.72	-8	53	18	L superior frontal gyrus
1625	-3.30	-4.16	-41	16	-23	L temporal pole
1062	-3.26	-4.12	41	-63	-11	R inferior occipital gyrus
766	-3.33	-4.13	-13	28	51	L superior frontal gyrus
688	-3.30	-4.01	23	-68	23	R superior occipital gyrus, cuneus
500	-3.25	-3.96	-31	-48	43	L IPS
406	-3.20	-3.63	18	-63	43	R superior parietal lobule, precuneus
Event Duration > Object Size						
8297	3.53	5.54	-51	-58	21	L AG/SMG
6359	3.35	4.55	-8	-58	28	L precuneus
5391	3.43	4.36	48	-61	23	R AG
4500	3.24	4.13	-61	-11	-6	L STS/MTG
3078	3.39	4.89	-18	48	31	L middle frontal gyrus, superior frontal gyrus
2641	3.29	4.22	58	1	-11	R anterior STG/MTG
1359	3.48	4.64	-38	8	53	L middle frontal gyrus
1312	3.29	4.10	28	21	41	R superior frontal sulcus, middle frontal gyrus
1078	3.28	3.97	38	13	51	R middle frontal gyrus
422	3.02	3.31	-1	-51	13	L precuneus
Object Size > Event Duration						
1719	-3.19	-3.79	-41	1	31	L inferior precentral sulcus
1406	-3.17	-3.78	-26	-63	23	L middle occipital gyrus
1031	-3.34	-4.52	8	6	-3	R caudate nucleus
812	-3.37	-4.50	43	-48	-8	R inferior temporal gyrus
812	-3.27	-3.98	21	-73	31	R superior occipital gyrus, cuneus
641	-3.13	-3.63	-28	-28	-18	L lateral fusiform gyrus
609	-3.31	-3.99	21	-3	-8	R amygdala
516	-3.12	-3.61	-48	-68	-11	L inferior occipital gyrus
438	-3.29	-3.92	3	-38	-3	R cerebellar vermis
391	-3.14	-3.62	46	6	-3	R IFG (pars opercularis), insula
375	-3.04	-3.37	-36	-41	33	L inferior parietal lobule
Events > Objects						

13703	3.82	5.49	-51	-58	23	L AG/SMG
8953	3.45	4.82	-8	-61	31	L precuneus
5016	3.47	5.03	-46	16	-28	L anterior STG/MTG/TP
3875	3.44	4.63	48	-6	-13	R anterior STG/MTG/TP
3656	3.40	4.45	46	-66	28	R AG
2281	3.27	4.10	-8	31	51	L superior frontal gyrus
1578	3.33	4.20	-61	-43	1	L pMTG
1484	3.45	5.17	-18	48	33	L middle frontal gyrus
1453	3.31	4.16	-41	8	51	L caudal middle frontal gyrus
703	3.31	4.34	21	21	53	R superior frontal gyrus
562	3.11	3.73	-56	-28	-3	L middle STS
406	3.28	3.95	41	11	51	R caudal middle frontal gyrus
Objects > Events						
2344	-3.36	-4.22	-33	-8	-21	L fusiform gyrus/ITG
1562	-3.37	-4.28	-46	-63	-6	L inferior temporal gyrus, inferior occipital gyrus and sulcus
1312	-3.19	-4.52	-33	3	33	L middle frontal gyrus, IFG (pars opercularis), L precentral gyrus
594	-3.10	-3.41	26	-61	38	R IPS, superior occipital gyrus
469	-3.19	-3.80	26	-88	-8	R inferior occipital gyrus

Cluster volume (mm^3), mean z score, peak z score, coordinates (in Talairach space) of peak voxel and corresponding structures for the whole-brain analysis of contrasts of interest, corrected to whole-brain $p < 0.05$. IFG = inferior frontal gyrus, IPS = intraparietal sulcus, ITG = inferior temporal gyrus, L = left hemisphere, MTG = middle temporal gyrus, R = right hemisphere, SMG = supramarginal gyrus STS = superior temporal sulcus; TP = temporal pole.

The following areas were activated for valence: right inferior occipital gyrus, superior occipital gyrus/cuneus, superior parietal lobe/precuneus, left superior frontal gyrus, temporal pole and IPS (figure 3.1; table 3.3).

3.3 Event Duration Minus Object Size

The following areas were activated for duration compared to size judgments: right AG, anterior superior temporal gyrus (STG)/MTG, left AG/SMG precuneus, STG/MTG, and bilateral middle frontal to superior frontal gyri (figure 3.2; table 3.3).
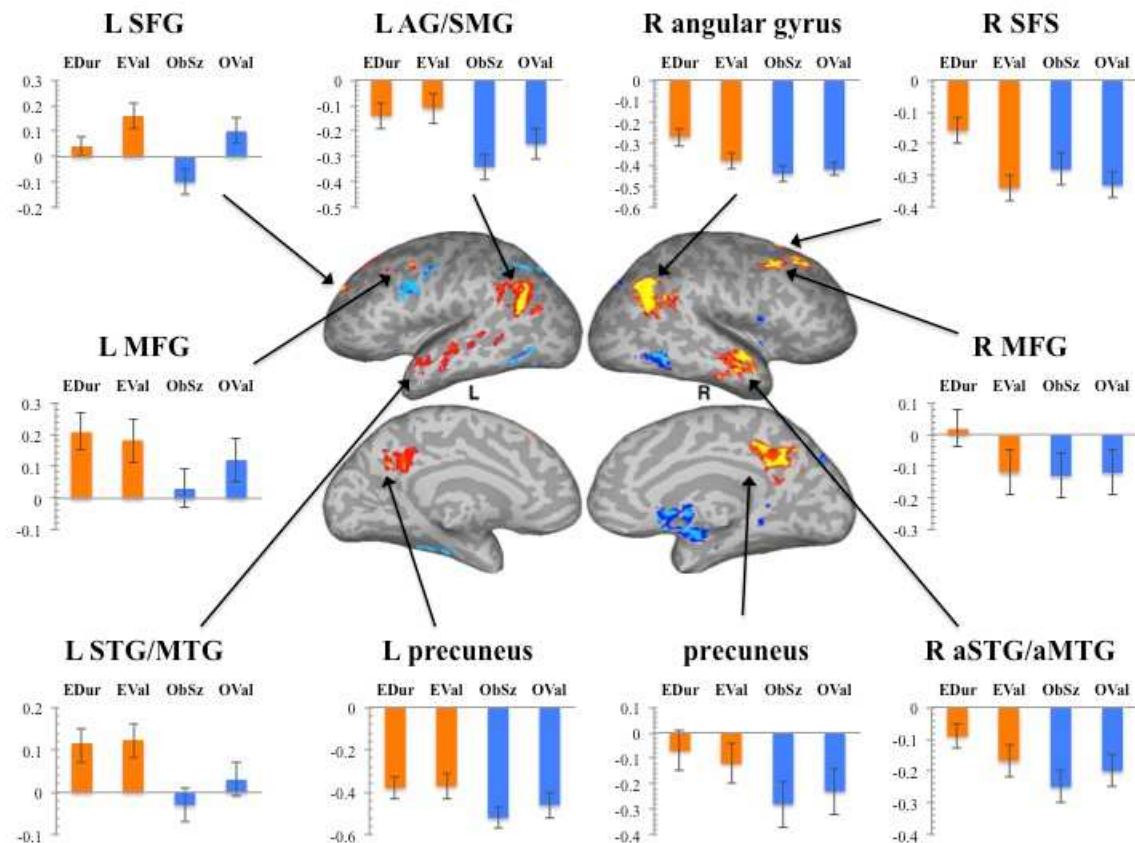
Figure 3.2 Event Duration Minus Object Size. Areas activated during whole-brain analysis of event duration minus object size contrast. Red-yellow colors indicate greater activation for duration cyan-blue indicates greater activation for size. P values are the same as the key in figure 3.1. Bar graphs of activation in each condition are shown. Y-axis indicates percent change in BOLD signal for each of the four conditions within select clusters indicated by the whole-brain analysis. aMTG indicates anterior middle temporal gyrus; aSTG= anterior superior temporal gyrus; MFG = middle frontal gyrus.

The following structures were found to display greater activation for size relative to duration: right caudate nucleus, ITG, superior occipital gyrus/cuneus, amygdala, cerebellar vermis, IFG (pars opercularis)/insula, left inferior precentral sulcus, inferior and middle occipital gyrus, lateral fusiform gyrus, AG and SMG (figure 3.2; table 3.3).

3.4 Event Valence Minus Object Valence

The following areas were significantly activated for event valence: left

AG/SMG/pSTS, pMTG, posterior cingulate cortex, bilateral anterior STG/anterior STS

and temporal poles (figure 3.3; table 3.4).
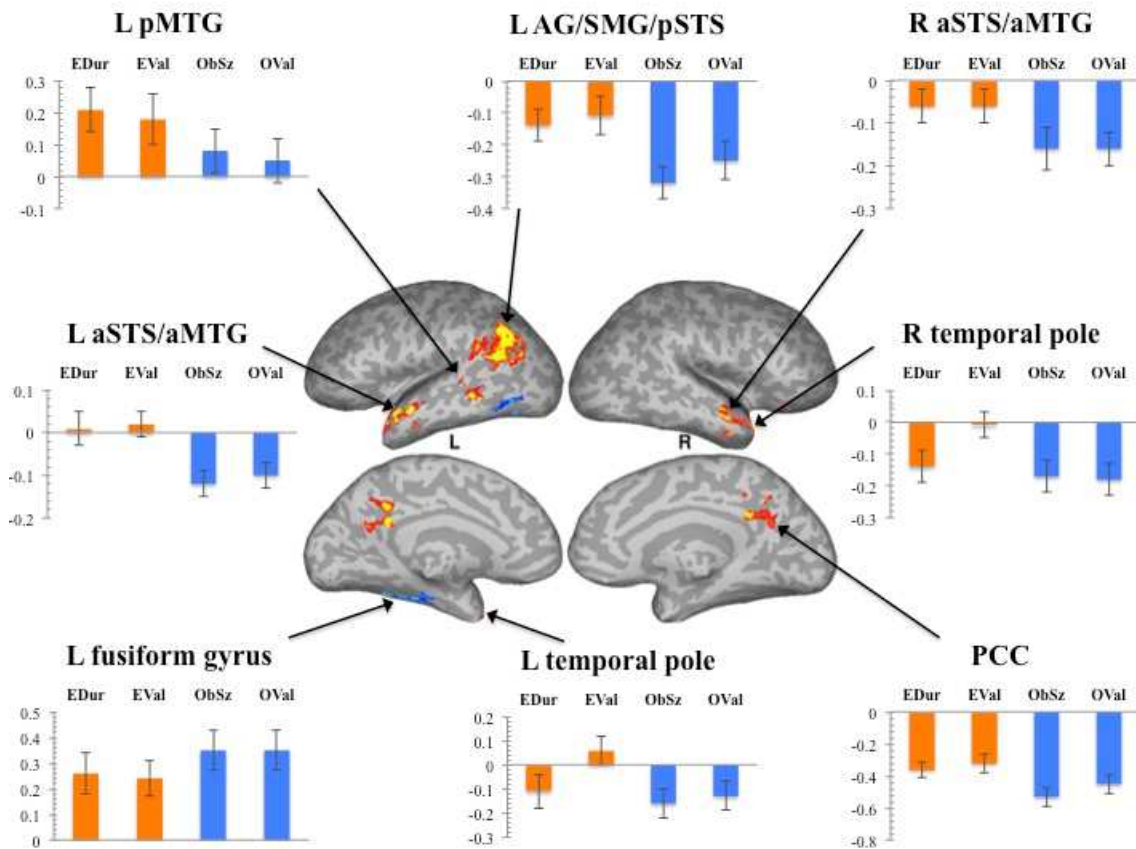
Figure 3.3 Event Valence Minus Object Valence. Areas activated during whole-brain analysis of event valence minus object valence contrast. Red-yellow colors indicate greater activation for event valence cyan-blue indicates greater activation for object valence. P values are the same as the key in figure 3.1. Bar graphs of activation in each condition are shown. Y-axis indicates percent change in BOLD signal for each of the four conditions within select clusters indicated by the whole-brain analysis. AG indicates angular gyrus; aSTS = anterior superior temporal sulcus; PCC = posterior cingulate cortex; pMTG = posterior middle temporal gyrus; pSTS = posterior superior temporal sulcus.

Table 3.4 Whole-Brain Analysis for Additional Contrasts

Volume	Mean	Max	x	y	z	Structure(s)
Event Valence > Object Valence						
7953	3.39	4.47	-46	-56	18	L pSTS/AG/SMG
2094	3.35	4.51	-1	-46	28	L posterior cingulate cortex
1781	3.29	4.24	-51	8	-16	L anterior MTG/STG
938	3.31	4.03	48	-6	-18	R anterior STS/MTG
844	3.27	3.99	-58	-43	-1	L posterior MTG
703	3.24	4.05	46	23	-18	R lateral STG, temporal pole
438	3.17	3.93	-33	23	-31	L temporal pole
Object Valence > Event Valence						
1172	-3.30	-4.31	-31	-43	-16	L fusiform gyrus
516	-3.23	-3.71	-46	-66	-6	L inferior occipital gyrus and sulcus
Object Size > Object Valence						
1547	3.46	4.66	-33	-78	28	L AG
1281	3.64	4.84	3	-43	38	R precuneus
1172	3.27	3.93	-56	-58	-3	L middle MTG
1078	3.36	4.90	13	3	-6	R putamen, caudate nucleus
828	3.35	4.09	36	-76	26	R middle occipital gyrus
781	3.32	4.25	21	18	43	R superior frontal sulcus
578	3.28	3.89	-31	-41	-6	L parahippocampal gyrus, L lingual sulcus
484	3.15	3.76	51	-38	51	R SMG/IPS
Object Valence > Object Size						
9219	-3.38	-4.81	-1	38	21	L anterior cingulate cortex
7000	-3.58	-5.67	-16	46	36	L superior frontal gyrus
2172	-3.59	-4.80	-28	13	-6	L anterior insula
1547	-3.42	-4.49	16	51	33	R superior frontal gyrus
1422	-3.13	-3.52	6	-46	26	R posterior cingulate cortex
1062	-3.10	-3.54	-51	21	13	L IFG (pars triangularis)
922	-3.11	-3.51	-1	-18	38	L posterior cingulate cortex
641	-3.13	-3.61	48	28	3	R IFG (pars triangularis)
594	-3.37	-4.12	8	18	58	R superior frontal gyrus
531	-3.35	-4.15	-46	16	-28	L temporal pole
531	-3.22	-3.66	-51	-36	1	L middle STS
484	-3.14	-3.57	-23	48	13	L middle frontal suclus
453	-3.12	-3.52	31	21	-1	R anterior insula
438	-3.34	-4.01	13	11	13	R caudate
Magnitude > Valence						
4891	3.50	4.99	28	26	46	R middle frontal gyrus, superior frontal sulcus
2750	3.66	5.06	-31	-76	36	L AG
2406	3.52	4.44	-56	-48	-3	L middle MTG/ITG
2219	3.54	4.63	33	-81	36	R AG
2188	3.83	5.26	1	-38	38	R posterior cingulate
1266	3.25	4.12	43	-46	41	R SMG/IPS
1172	3.21	3.83	66	-46	-1	R middle MTG
844	3.38	4.30	-28	-33	-11	L fusiform gyrus, L parahippocampal gyrus
594	3.47	4.45	31	-28	-11	R hippocampus, parahippocampal gyrus

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391	3.17	3.80	56	-33	-16	R inferior temporal gyrus

Valence > Magnitude

16797	-3.50	-5.56	-16	46	41	L superior frontal gyrus
3469	-3.25	-4.19	-48	18	11	L IFG (pars opercularis)
1859	-3.54	-5.78	-43	18	-23	L temporal pole
1203	-3.27	-4.51	-3	-46	23	L posterior cingulate gyrus
1172	-3.47	-4.39	1	-21	28	R posterior cingulate cortex
1047	-3.39	-4.33	13	48	33	R superior frontal gyrus
656	-3.43	-4.70	-66	-16	-8	L middle MTG
656	-3.29	-4.71	-6	-3	11	L thalamus, caudate nucleus
625	-3.17	-3.67	6	23	23	R anterior cingulate cortex
562	-3.24	-3.79	-48	-38	3	L middle STS
516	-3.37	-4.39	-3	-21	11	L thalamus
500	-3.15	-3.81	-48	28	-6	L inferior orbital frontal gyrus
500	-3.18	-3.74	18	-66	46	R superior parietal gyrus
438	-3.07	-3.71	-51	-63	31	L AG

(Event Duration > Event Valence) > (Object Size > Object Valence)

1578	3.29	4.48	28	21	41	R superior frontal sulcus, middle frontal gyrus
656	3.09	3.51	46	-58	21	R AG

(Object Size > Object Valence) > (Event Duration > Event Valence)

438	-3.16	-3.66	-26	8	-26	L medial temporal pole

Cluster volume (mm^3), mean z score, peak z score, coordinates (in Talairach space) of peak voxel and corresponding structures for the remaining whole-brain analyses, corrected to whole-brain p < 0.05. IFG = inferior frontal gyrus, L = left hemisphere, MTG = middle temporal gyrus, R = right hemisphere, SMG = supramarginal gyrus, pSTS = posterior superior temporal sulcus.

Two clusters were found to be significantly activated by object valence: left fusiform gyrus and posterior ITG/inferior occipital gyrus/sulcus (figure 3.3; table 3.4).

3.5 Object Size Minus Object Valence

The following areas showed significantly greater activation for the size task: right precuneus, putamen/caudate nucleus, middle occipital gyrus, superior frontal sulcus, SMG/IPS, left AG, middle MTG and parahippocampal gyrus/ lingual sulcus (figure 3.4; table 3.4).

Figure 3.4 Object Size Minus Object Valence. Areas activated during whole-brain analysis of object size minus object valence contrast. Red-yellow colors indicate greater activation for size cyan-blue indicates greater activation for valence. P values are the same as the key in figure 3.1. Bar graphs of activation in each condition are shown for select clusters. Y-axis indicates percent change in BOLD signal for each of the four conditions within cluster indicated by the whole-brain analysis. ACC indicates anterior cingulate cortex; IPS = intraparietal sulcus; MOG = middle occipital gyrus.

Object valence relative to object size activated: right posterior cingulate cortex, caudate, left anterior to posterior cingulate cortex, temporal pole, middle STS, middle frontal sulcus, bilateral superior frontal gyri, anterior insula and IFG (pars triangularis) (figure 3.4; table 3.4).

3.6 Main Effect of Noun Type

Event nouns relative to object nouns activated: right AG, anterior STG/MTG/TP, posterior middle frontal gyrus, left AG/SMG, precuneus, temporal pole that extends through anterior STG to anterior MTG, pMTG, anterior and posterior middle frontal gyri, middle STS, and bilateral superior frontal gyri (figure 3.5; table 3.3).
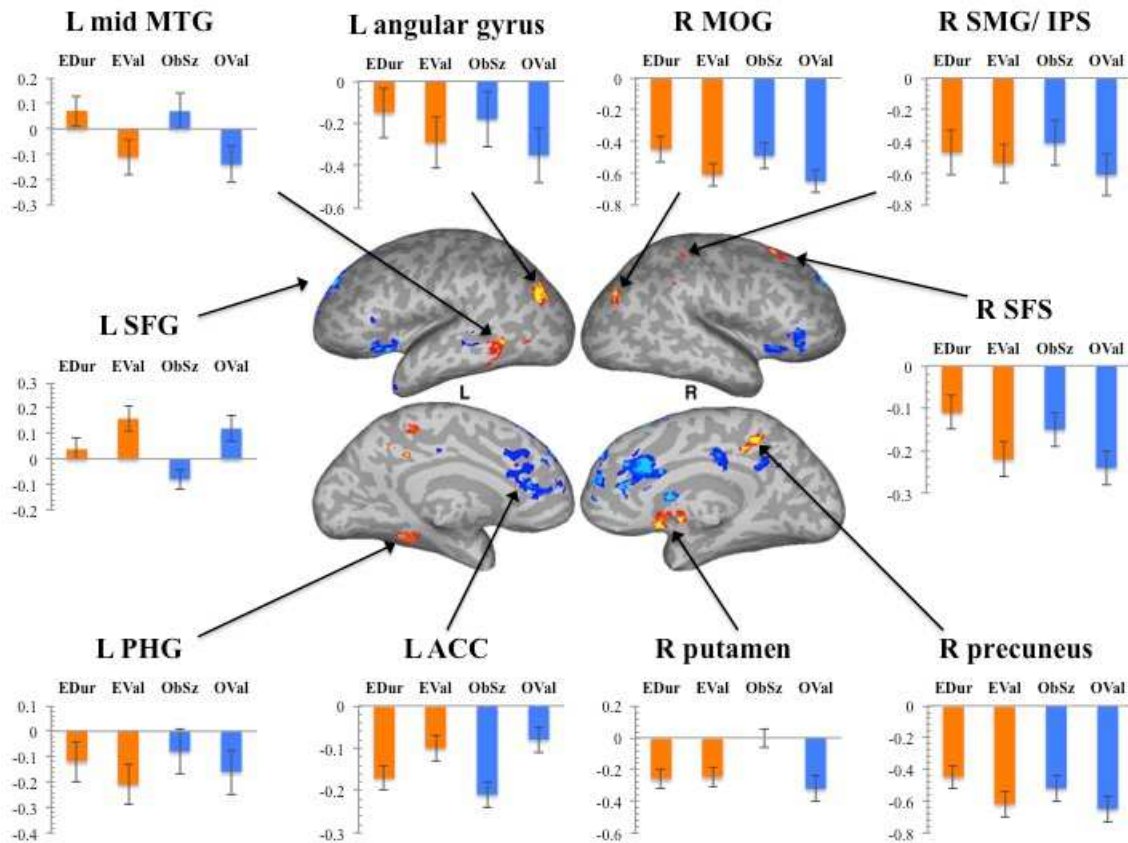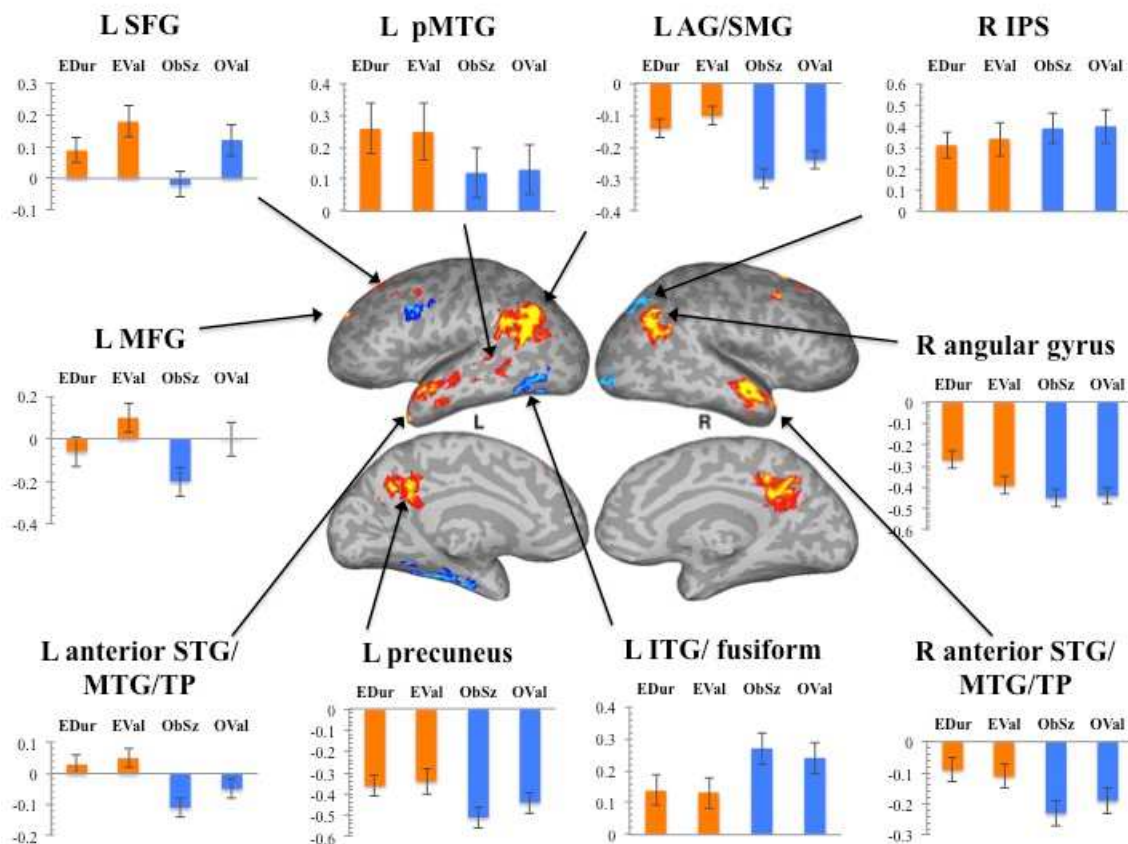

Figure 3.5 Events Minus Objects. Areas activated during whole-brain analysis of events minus object contrast. Red-yellow colors indicate greater activation for events cyan-blue indicates greater activation for objects. P values are the same as the key in figure 3.1. Bar graphs of activation in each condition are shown. Y-axis indicates percent change in BOLD signal for each of the four conditions within select clusters indicated by the whole-brain analysis.

Object nouns compared to event nouns activated: right IPS/superior occipital gyrus, inferior occipital gyrus, left fusiform gyrus/ITG, inferior occipital gyrus and

sulcus, middle frontal gyrus/IFG (pars opercularis)/precentral gyrus (figure 3.5; table 3.3).

3.7 Main Effect of Judgment Type

Magnitude (object size or event duration) judgments activated the following areas: right middle frontal gyrus/superior frontal sulcus, posterior cingulate cortex, SMG/IPS, middle MTG, hippocampus/parahippocampal gyrus, ITG, left middle MTG/ITG, fusiform gyrus/parahippocampal gyrus, bilateral AG (figure 3.6; table 3.4).
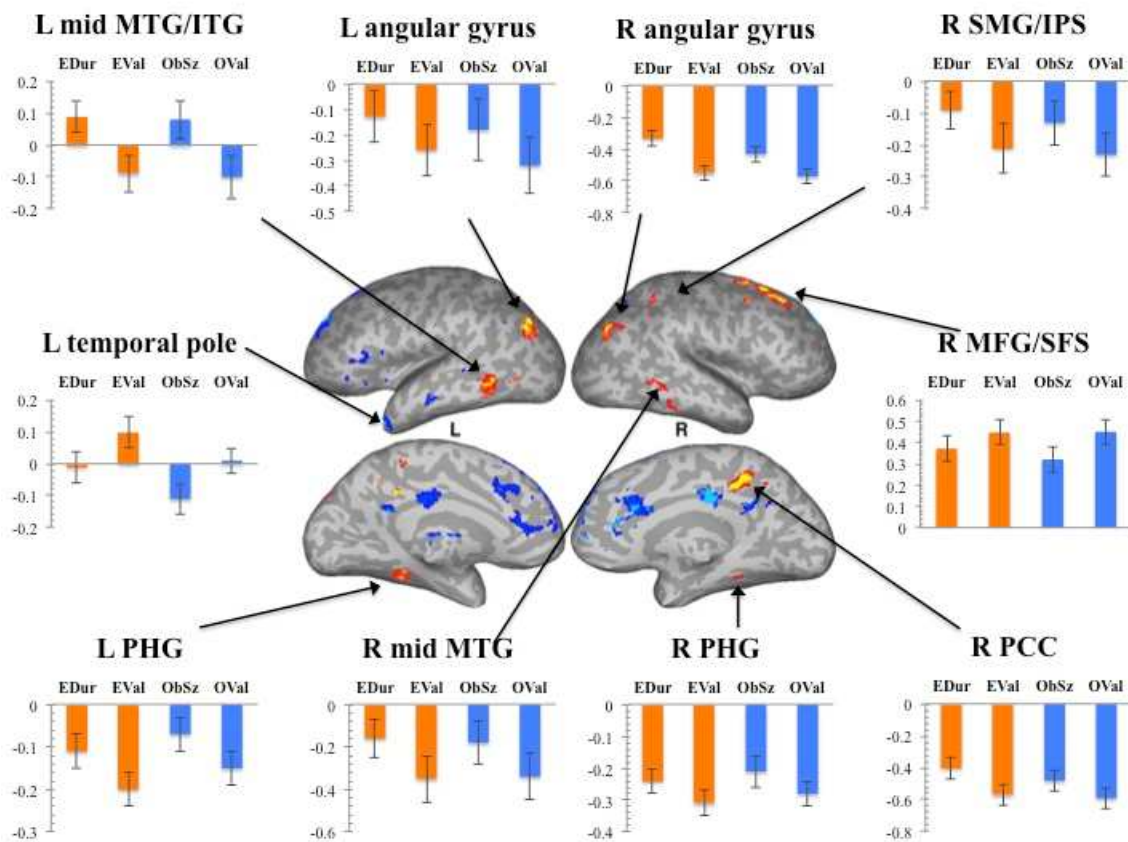
Figure 3.6 Magnitude Minus Valence. Areas activated during whole-brain analysis of magnitude minus valence contrast. Red-yellow colors indicate greater activation for magnitude (duration and size) cyan-blue indicates greater activation for valence. P values are the same as the key in figure 3.1. Bar graphs of activation in each condition are shown. Y-axis indicates percent change in BOLD signal for each of the four conditions within select clusters indicated by the whole-brain analysis.

The following areas were activated for valence judgments right anterior cingulate cortex, superior parietal gyrus, left IFG (pars opercularis), temporal pole, middle MTG, thalamus, caudate nucleus, middle STS, inferior orbital frontal gyrus, AG, bilateral superior frontal gyri, and posterior cingulate cortices (figure 3.6; table 3.4).

3.8 Interaction

The contrast of (event duration – event valence) – (object size – object valence) in the whole-brain analysis revealed two peak positive activations. The positive activations for the interaction were reported in the right superior frontal sulcus and the AG (figure 3.7; table 3.4).
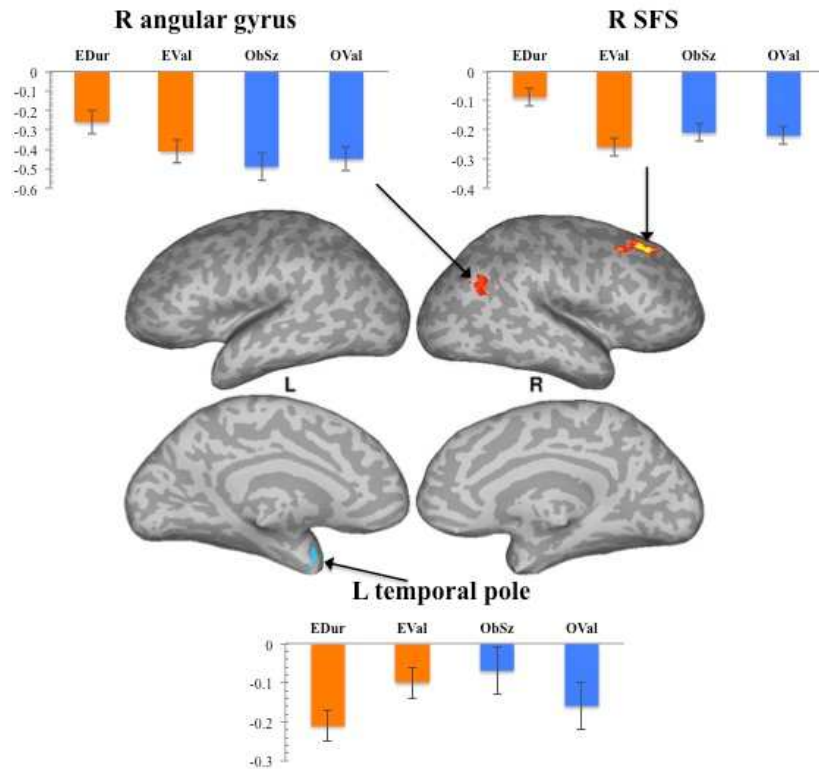
Figure 3.7 Interaction. Areas activated during whole-brain analysis of (event duration – event valence) – (object size – object valence) contrast. Red-yellow colors indicate

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greater activation for event duration and object valence cyan-blue indicates greater activation for event valence and object size. P values are the same as the key in figure 3.1. Bar graphs of activation in each condition are shown. Y-axis indicates percent change in BOLD signal for each of the four conditions within each cluster indicated by the whole-brain analysis.

Additionally one region survived the whole-brain analysis of interaction, suggesting a negative activation for a cluster with the peak value stemming from the left medial temporal pole (figure 3.7; table 3.4).

3.9 Temporal ROI Analysis

Analysis of the perisylvian ROIs resulted in greater activation for event duration > event valence in the right SMG [$t(19) = 3.17$, $p = 0.003$, Cohen's $d = 0.70$]. Event duration > object size revealed that the left SMG [$t(19) = 3.36$, $p = 0.002$, Cohen's $d = 0.78$] and right SMG [$t(19) = 2.28$, $p = 0.02$, Cohen's $d = 0.53$] displayed significantly greater activation for event duration. Event valence > object valence suggested that only the left SMG displayed significant activation for the event valence [$t(19) = 3.74$, $p < 0.001$, Cohen's $d = 0.85$]. No areas of activation survived the object size > object valence contrast in the temporal ROIs. Events were found to activate temporal ROIs greater than objects in the left SMG [$t(19) = 9.02$, $p < 0.001$, Cohen's $d = 1.99$] and right pSTS [$t(19) = 2.87$, $p = 0.005$, Cohen's $d = 0.60$]. Magnitude > valence judgments activated the R SMG [$t(19) = 3.00$, $p = 0.004$, Cohen's $d = 0.66$] (figure 3.8). Additionally, the right claustrum displayed significant activation for the contrast of (event duration > event valence) > (object size > object valence), [$t(19) = 2.15$, $p = 0.02$, Cohen's $d = 0.47$]. No other contrasts of the right claustrum revealed significant differences.
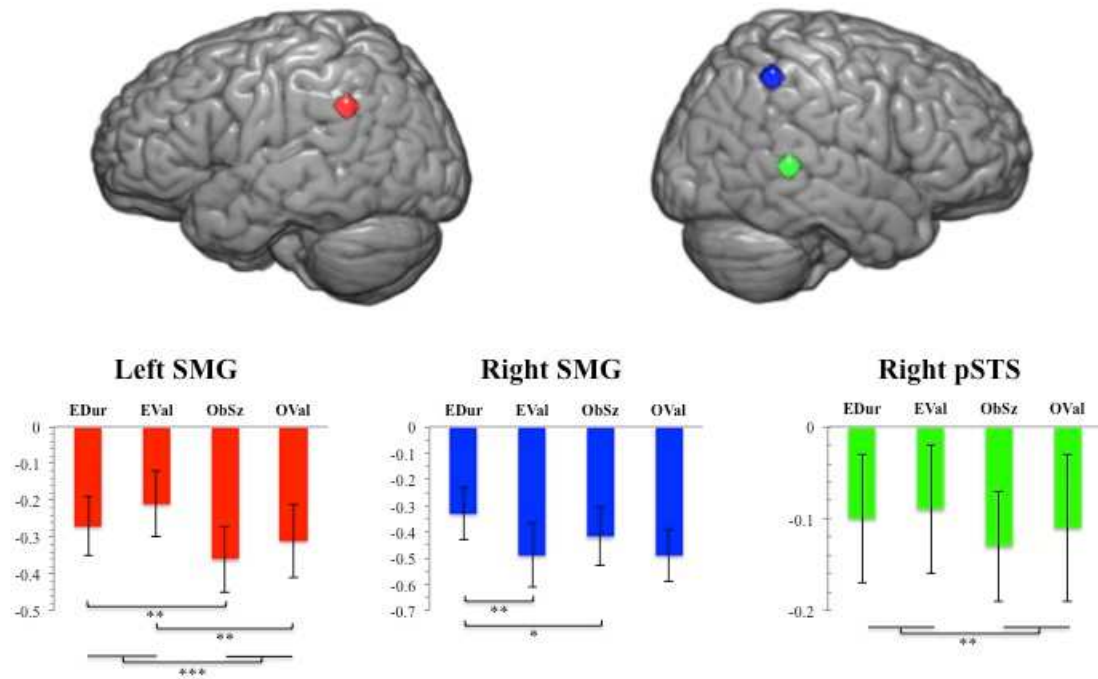
Figure 3.8 Temporal ROI Analysis. Activation in temporal ROIs within the perisylvian cortex. Coordinates with significant differences in contrasts are shown. Left SMG (red, on the left), right SMG (blue, on the middle) and right pSTS (green, on the right). Y axis symbolizes the average percent signal change within the ROI. The error bars are the standard error of the mean for each of the four conditions (EDur, EVal, ObSz and OVal). An interaction in the right claustrum also displayed significant activation at a $p < 0.01$ (not shown). After correcting for multiple comparisons no other coordinates suggested significant differences of percentage signal change between groups. * < 0.05, ** < 0.01, *** < 0.001.

3.10 Angular Gyrus ROI Analysis

ROI analysis of bilateral angular gyri suggested that the right AG [$t(19) = 3.29$, $p = 0.002$, Cohen's $d = 0.77$] was significantly activated for the event duration > object valence task. The contrast of the duration > valence suggested no difference in activation of the left AG [$t(19) = 0.02$, $p = 0.49$, Cohen's $d = 0.01$]. Event duration > object size

found the left AG [$t(19) = 5.42$ $p < 0.001$, Cohen's $d = 1.21$] and right AG [$t(19) = 5.38$, $p < 0.001$, Cohen's $d = 1.23$] to have significant activation in these regions for event duration judgments. Event valence > object valence revealed the left [$t(19) = 4.86$, $p < 0.001$, Cohen's $d = 1.07$] but not the right AG [$t(19) = 0.91$, $p = 0.19$, Cohen's $d = 0.21$] displayed greater activation for event valence. No areas of activation survived the object size > object valence contrast in the angular gyri ROI analysis. Event nouns were found to significantly activate the angular gyri in contrast to object nouns; left [$t(19) = 7.68$, $p < 0.001$, Cohen's $d = 1.68$] and right [$t(19) = 4.45$, $p < 0.001$, Cohen's $d = 0.95$]. Magnitude > valence suggested that the right AG [$t(19) = 2.09$, $p = 0.03$, Cohen's $d = 0.46$] but not the left [$t(19) = -0.63$, $p = 0.73$, Cohen's $d = -0.14$] resulted in greater activation for the magnitude. Lastly, there was significant activation in the right [$t(19) = 2.80$, $p = 0.006$, Cohen's $d = 0.65$] but not the left AG [$t(19) = 0.45$, $p = 0.33$, Cohen's $d = 0.10$] for the interaction contrast (figure 3.9).

3.11 Inferior Parietal Lobule ROI Analysis

Area PFm in the left IPL was significantly activated for events compared to objects [$t(19) = 5.71$, $p < 0.001$, Cohen's $d = 1.26$] as well as the separate contrasts of event duration > object size [$t(19) = 3.77$, $p = 0.004$, Cohen's $d = 0.86$] and event valence > object valence [$t(19) = 3.10$, $p = 0.02$, Cohen's $d = 0.68$]. Right PFm was significantly activated for event duration > object size [$t(19) = 2.81$, $p = 0.006$, Cohen's $d = 0.65$]. Left PGa revealed a main effect of events [$t(19) = 7.25$, $p < 0.001$, Cohen's $d = 1.66$]. Specific contrasts of event duration > object size [$t(19) = 4.15$, $p < 0.001$, Cohen's $d = 0.95$] and event valence > object valence [$t(19) = 4.31$, $p < 0.001$, Cohen's $d = 0.99$] also favored events. An interaction was found in the right PGa [$t(19) = 2.42$, $p = 0.01$,
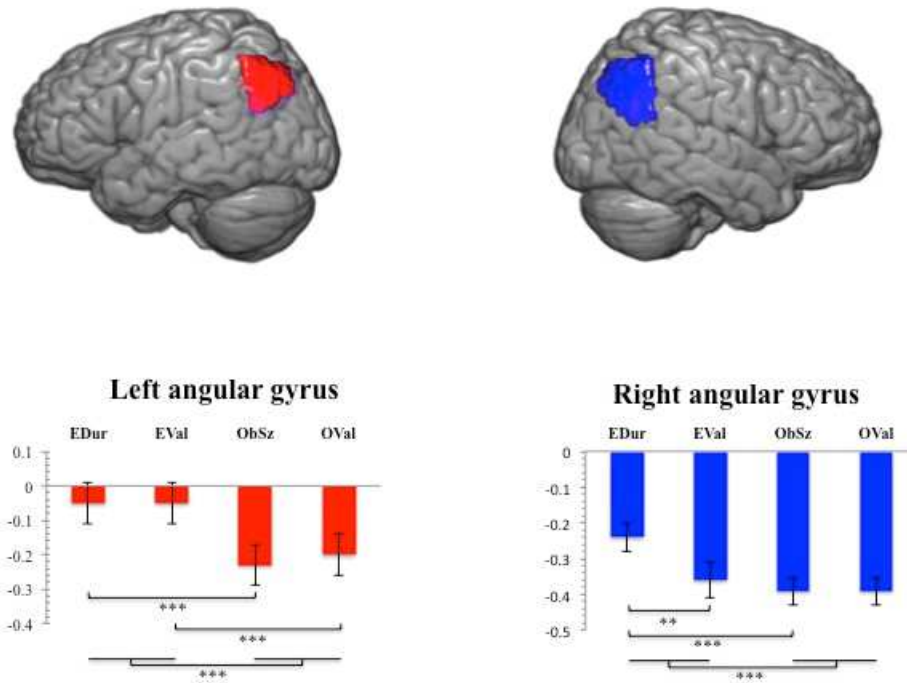
Figure 3.9 Angular Gyrus ROI Analysis. Activation in the left (red, on the left) and right (blue, on the right) AG ROIs. Y axis symbolizes the average percent signal change within the ROI. The error bars are the standard error of the mean for each of the four conditions (EDur, EVal, ObSz and OVal). $* < 0.05$, $** < 0.01$, $*** < 0.001$.

Cohen's $d = 0.55$] as well as a main effect of events [$t(19) = 3.72$, $p < 0.001$, Cohen's $d = 0.81$] that was aided by event duration. Event duration > event valence [$t(19) = 1.89$, $p = 0.04$, Cohen's $d = 0.42$] and event duration > object size [$t(19) = 4.63$, $p < 0.001$, Cohen's $d = 1.02$] also suggested the right PGa was activated to a greater extent for duration processing. The left PGp revealed a main effect of events [$t(19) = 4.98$, $p < 0.001$, Cohen's $d = 1.10$] and magnitude [$t(19) = 3.20$, $p = 0.002$, Cohen's $d = 0.74$]. Specific contrasts suggested event duration > event valence [$t(19) = 3.85$, $p < 0.001$, Cohen's $d = 0.84$], event duration > object size [$t(19) = 3.73$, $p < 0.001$, Cohen's $d =$

0.84] and event valence > object valence [t(19) = 5.22, $p < 0.001$, Cohen's d = 1.11]

activated the left PGp for events. An interaction [t(19) = 3.34, $p = 0.002$, Cohen's d =

0.76] was suggested for the right PGp as well as main effects for events [t(19) = 3.40, $p =$

0.002, Cohen's d = 0.76] and magnitude [t(19) = 3.74, $p < 0.001$, Cohen's d = 0.83].

Specific contrasts revealed that duration tasks activated the right PGp for event duration

> event valence [t(19) = 5.31, $p < 0.001$, Cohen's d = 1.21] as well as event duration >

object size [t(19) = 3.96, $p < 0.001$, Cohen's d = 0.93]. Bilateral areas PF and PFcm

suggested no difference in activation across conditions (Figure 3.10).

Figure 3.10 Inferior Parietal Lobule ROI Analysis. Activation in bilateral areas of the
IPL ROIs. Axial brain slices, numbers below brain indicate LPI coordinates from left to

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right: z = 20, 28, 40. Red is area PF, blue = PFm, violet = PGa, green = PGp, yellow = PFcm (is an area in the medial IPL, displayed on the surface) as defined by Casper et al., 2008. Y axis symbolizes the average percent signal change within the ROI. The error bars are the standard error of the mean for each of the four conditions (EDur, EVal, ObSz and OVal). * < 0.05, ** < 0.01, *** < 0.001.

3.12 Intraparietal Sulcus ROI Analysis

ROI analysis of the IPS revealed that the anterior area was activated bilaterally for object size compared to object valence, left [$t(19) = 2.79$, $p = 0.006$, Cohen's $d = 0.60$] and right [$t(19) = 2.84$, $p = 0.005$, Cohen's $d = 0.61$]. Magnitude > valence also reported greater activation for the right anterior IPS [$t(19) = 2.21$, $p = 0.02$, Cohen's $d = 0.50$]. No other contrasts in the anterior IPS were significantly different. Activation in the left middle IPS was not significantly different between groups. The right middle IPS was activated by Event duration > event valence [$t(19) = 2.63$, $p = 0.008$, Cohen's $d = 0.62$]; object size > object valence [$t(19) = 2.09$, $p = 0.03$, Cohen's $d = 0.46$] and magnitude > valence [$t(19) = 3.70$, $p < 0.001$, Cohen's $d = 0.87$]. There were no significant differences in the contrasts stemming from the posterior bilateral IPS (Figure 3.11).

3.13 Parahippocampal Place Area ROI Analysis

ROI analysis of left PPA revealed that the contrast of event duration minus event valence activated the left PPA to a greater extent for the event duration task [$t(19) = 3.31$, $p = 0.03$, Cohen's $d = 0.73$]. The contrast of event duration minus object size did not indicate a significant difference in activation [$t(19) = -2.04$, $p = 0.39$, Cohen's $d = -0.46$]. Similarly, there was no difference in the contrast of event valence minus object valence [$t(19) = -2.38$, $p = 0.20$, Cohen's $d = -0.52$]. Object size activated the left PPA to a greater extent than object valence [$t(19) = 3.92$, $p = 0.006$, Cohen's $d = 0.84$]. There was not a main effect of noun type [$t(19) = -2.59$, $p = 0.13$, Cohen's $d = -0.59$] but there was a
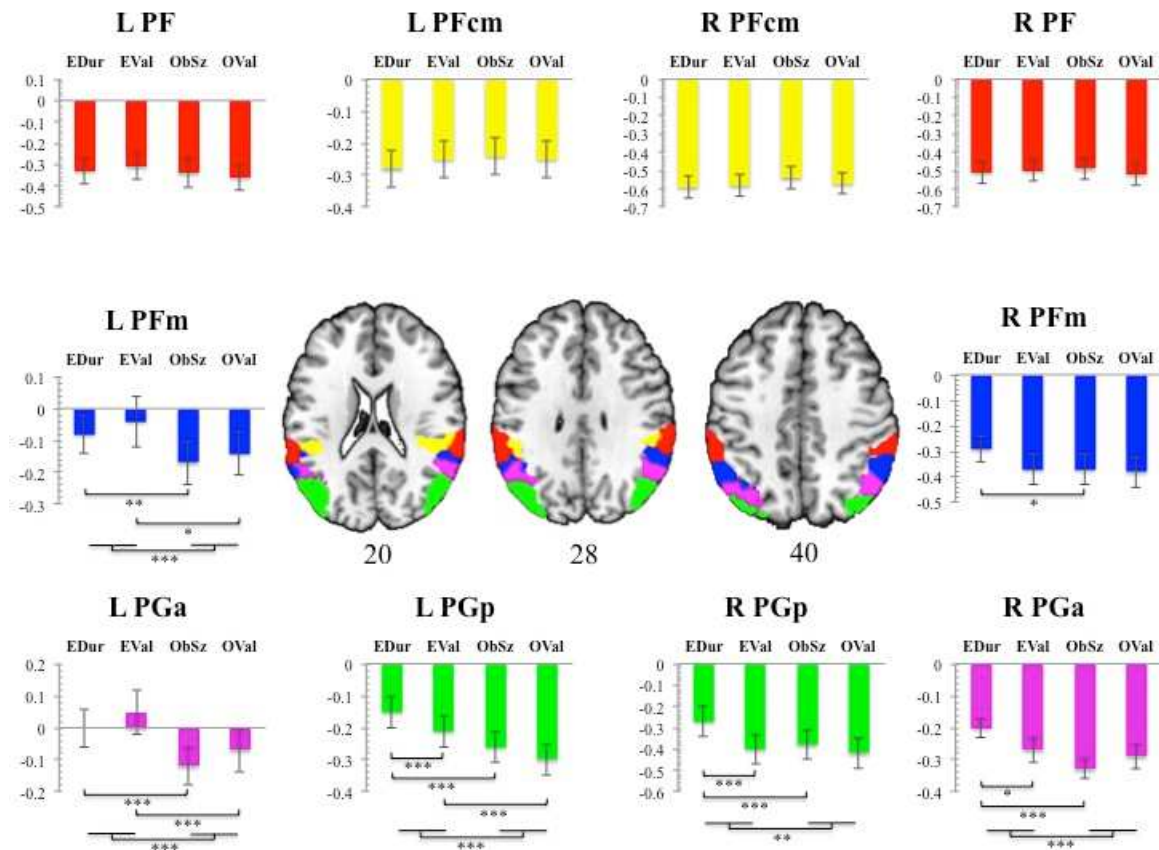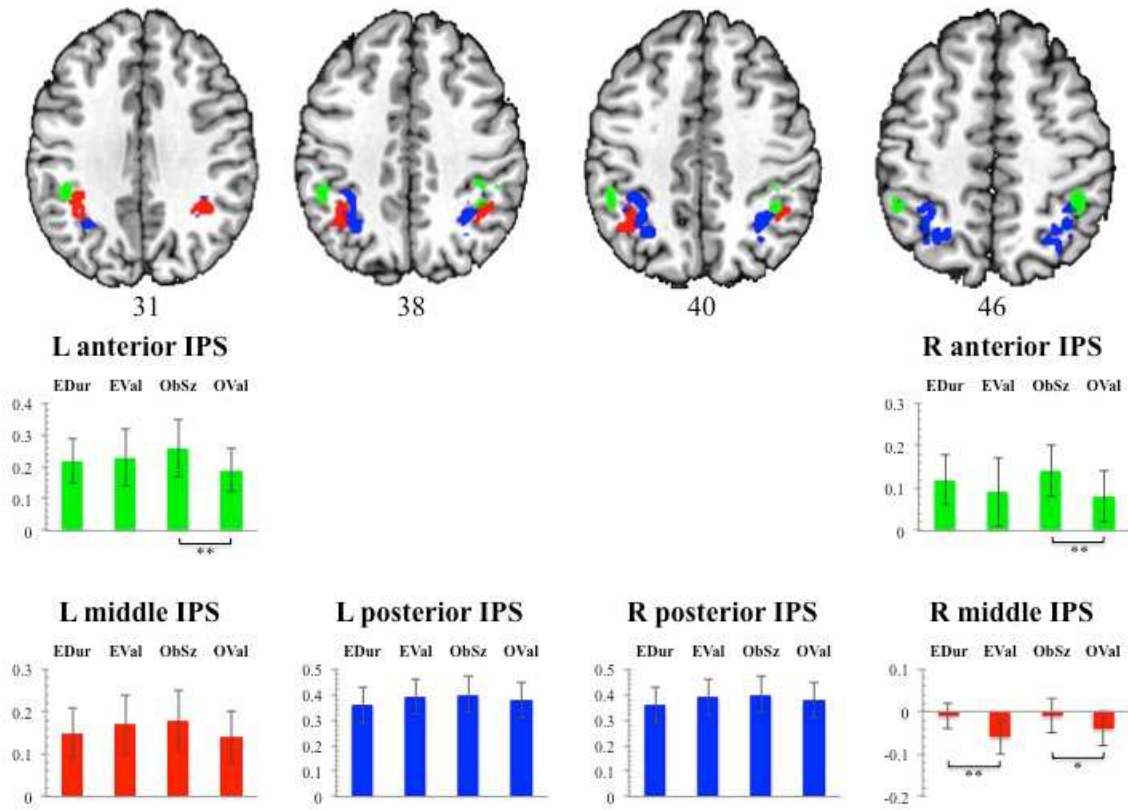
Figure 3.11 Intraparietal Sulcus ROI Analysis. Activation in bilateral areas of the IPS ROIs. Axial brain slices, numbers below slices indicate LPI coordinates from left to right: z = 31, 38, 40, 46. Green is anterior, red = middle, blue = posterior. Y axis symbolizes the average percent signal change within the ROI. The error bars are the standard error of the mean for each of the four conditions (EDur, EVal, ObSz and OVal). * < 0.05, ** < 0.01, *** < 0.001.

main effect of magnitude, where magnitude tasks activated the PPA to a greater extent

$[t(19) = 4.06, p = 0.005$, Cohen's $d = 0.92]$. Furthermore, there was not an interaction

$[t(19) = 0.24, p = 1.00$, Cohen's $d = 0.06]$ (figure 3.10).
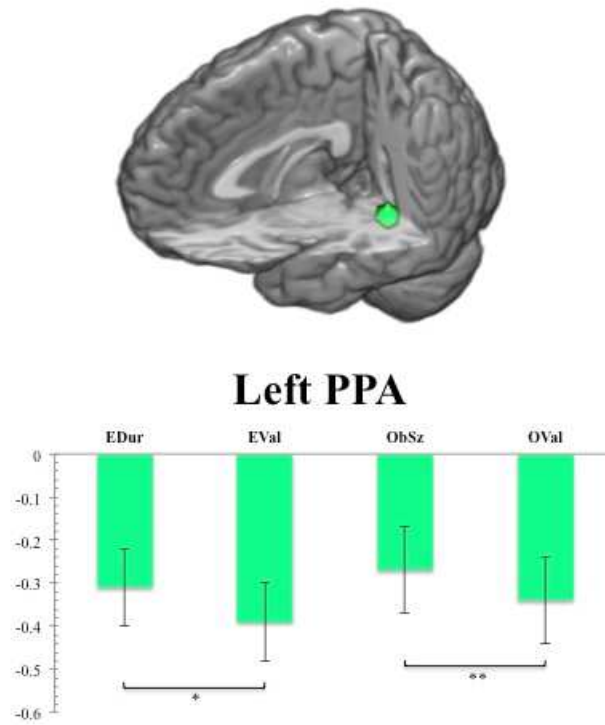
Figure 3.12 Parahippocampal Place Area ROI Analysis. Activation in left Parahippocampal Place Area (PPA) ROI. Y axis symbolizes the average percent signal change in the ROI. The error bars are the standard error of the mean for each of the four conditions (EDur, EVal, ObSz and OVal). * < 0.05, ** < 0.01, *** < 0.001.

CHAPTER 4

DISCUSSION AND CONCLUSION

This study examined the representation of duration using event nouns. We found

event concepts to generally activate spatial perception regions. Although, when temporal

information such as a duration judgment is required, semantic processing utilized

temporal perception areas as well. We found that duration judgments of event nouns

activate areas around the perisylvian cortex, such as the IPL, including the right SMG and

AG in the ROI analysis. The whole-brain analysis corroborated these findings. The

whole-brain analysis examining duration minus valence, revealed a predominately right

hemispheric network including the right middle frontal/superior frontal sulcus, the IPL

including the AG, a separate cluster in the SMG, right precuneus/ middle cingulate cortex

and the posterior ventral cingulate gyrus/lingual gyrus. Only three clusters in the left

hemisphere were activated for the duration minus valence contrast, including the AG,

middle MTG/ITG and parahippocampal gyrus.

4.1 SMG

Temporal ROIs suggested a dissociation between hemisphere and role of the

SMG. We found the right SMG to display greater activation for magnitude versus

valence tasks. Although, this effect was driven by duration, as activation for duration

was greater in both contrasts of event duration minus event valence and event duration

minus object size. Conversely, the temporal ROI located in the left SMG revealed a main

effect of noun, indicating that event nouns produced more activation than object nouns.

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Contrasts examining pairwise conditions suggested significantly greater activation for both tasks involving event nouns; event duration minus object size and for event valence minus object valence. The whole-brain analysis confirmed the ROI analysis results, for the right SMG's involvement in temporal tasks. There was a main effect of task favoring magnitude in the right SMG. Contrasts of conditions revealed that duration minus valence produced a peak cluster of significant activation in the right SMG. Additionally, object size minus object valence also produced a peak cluster in the right inferior SMG/IPS. The left SMG displayed greater activation for the main effect of noun type, favoring event nouns, although the peak activation for this cluster was located in the AG. Specific contrasts of event duration minus object size and event valence minus object valence suggested that the left SMG was part of a significant cluster with the peak value in the left AG.

The bilateral coordinates of our SMG ROIs were based on the findings of temporal perception in a meta-analysis (Weiner et al., 2010a). While the main effect of noun type indicated that events compared to objects significantly activated the SMG bilaterally, only the right SMG was found in the ROI and whole-brain analysis to be related to processing duration. A number of other reviews of temporal perception have found the right SMG to be involved in time perception (Harrington & Haaland, 1999; Lewis & Miall, 2003a ; Macar et al., 2002) A more recent study by Weiner et al. (2010b) administered rTMS to the left SMG, right SMG or vertex while participants performed a temporal discrimination task. The authors found that rTMS to the right but not the left SMG significantly lengthened the participants' perception of time. Based on these results it was concluded that the right SMG was an important component of encoding durations

and modulating attention to temporal tasks. Weiner et al. (2012) replicated this result by administering rTMS to the right SMG and subsequently performing simultaneous electroencephalography (EEG) while participants encoded stimulus durations. Similar to the 2010 study, rTMS to the right SMG increased the length of participants' perception of duration.

In addition to disruption of temporal processes during rTMS, Hayashi et al. (2015) found decreased activity in the right SMG following repeated stimuli of the same duration. Hayashi et al. (2015) asked participants to encode the duration of various sub-second visual stimuli during fMRI. Percentage signal change from the peak clusters in the right SMG were significantly less following repeated exposure to the same duration. Interestingly the beta-coefficients for most of the tests of duration were negative. This finding was similar to our ROI analyses where the activation for areas were reflected by the degree of reduction in Blood Oxygenation Level Dependent (BOLD) signal. Hayashi et al. (2015) suggested that the negative regression coefficients might be a combination of the task and specific duration-selective neurons within a relatively small area. We suggest an alternative explanation, as positive and negative beta coefficients are in respect to resting state. The negative beta coefficients that were found in ROIs of the SMG, AG and pSTS as well as in similar regions of the whole-brain analysis are likely a consequence of these structures being involved in the brain's resting state or default network (Gusnard & Raichle, 2001; Buckner, Andrews-Hanna & Schacter, 2008). Participants' free thoughts during a rest period likely involve numerous aspects of semantics including events and time estimations. Therefore, thought that occurs in between trials chiefly activates a number of regions associated with the default network,

including these three coordinates along the perisylvian fissure and other regions within the default network. Since our contrasts involved comparing one task to another, not to rest, the reductions in BOLD signal should not reduce the impact of our results.

While we found that the right SMG was involved in temporal tasks others have suggested activation in the left IPL including the SMG (Coull, 2004; Livesey, Wall & Smith, 2007) or bilateral SMG activation occurs during temporal tasks (Weiner et al., 2010a). We found that events activated the left SMG significantly more than objects in ROI and whole-brain analyses. Since the contrast of event duration > event valence was not significant it seems that the left SMG is involved in processing events but not the information related to the duration of the events. It is possible that the event noun activation is the result of the left SMG's role in processing action information. Binder et al.'s (2009) review of the semantic system suggested that the representation of some action knowledge might be located in the left SMG, based on a number of neuropsychological studies. Others have suggested that the left SMG is involved in processing spatial relations. One patient study examining spatial and temporal processing by using prepositions found that all three patients with damage to the left SMG displayed impaired knowledge of spatial meanings (Kemmerer, 2005). A review of spatial semantics by Kemmerer (2006) also indicated the left IPL including the SMG was involved in categorical spatial relations. Indeed event knowledge includes actions of what occurs during an event as well as the rough spatial setting in which an event occurs. Both actions within events or the spatial setting could be adding to the activation for events in the left SMG. Based on our results it is possible that the left SMG has a greater role in spatial processing, while the right SMG is involved in temporal processing.

4.2 Angular Gyrus

A previous meta-analysis of 120 fMRI studies found the AG and specifically the left to be consistently activated in semantic processing (Binder et al., 2009). It was hypothesized that the AG is involved in integrating complex information and retrieving knowledge. Our results reflect the importance of the AG in semantic processing of temporal information. ROI of the right AG revealed an interaction for noun category and judgment type. This effect was facilitated by duration in that only the contrasts of duration > valence and duration > size revealed greater activation in the right AG. Moreover the PGa and PGp were activated for duration compared to event valence or object size. Only the PGp of the IPL was activated for the contrast of event duration > event valence. Activation of the right AG during temporal processing has been demonstrated in reviews (Harrington & Haaland, 1999; Lewis & Miall, 2003a). Additionally, rTMS to the right but not the left AG disturbed temporal perception (Bueti et al., 2008). Our ROI analysis of the left AG suggested a main effect of noun category favoring events located anteriorly. Further investigations revealed that duration > size and event valence > object valence significantly activated the left AG for events. Whole-brain analyses corroborated the interaction of the right AG. Additionally, bilateral clusters with peaks of activations in the AG were found in a number of contrasts including: events > objects; magnitude > valence; duration > valence; duration > size. Moreover a cluster of significant activation in the size > valence task was found in the left AG.

Based on our results it seems that the AG is important for processing event information. A possible preference was found for duration in the right hemisphere whereas residual event information might be processed in the left hemisphere. Indeed a

review of semantic memory examined the data pertaining to the AG and concluded that the level of activation in the AG might be positively correlated with the amount of semantic information that can be gleamed from a particular concept (Binder & Desai, 2011). The authors expanded upon that conclusion with a suggestion that the AG might be involved in the representation of events and possibility the processing of temporal and spatial information from the events. Additionally, a review of spatial semantics concluded that the left AG was involved in categorical spatial information (Kemmerer, 2006). Our results support these notions. We found that contrasts involving more semantic information (events compared to objects or event duration compared to object size) activated bilateral angular gyri in whole-brain analysis. Along the same lines, semantic concepts with slightly less information (size of an object compared to valence of an object) significantly activated only the left AG. Indeed, comparing the size of an object inherently activates spatial information while valence judgments may also involve spatial aspects. Interestingly though, is that the contrast of event duration > event valence which involved the same event nouns displayed a bilateral activation of the AG in whole-brain analysis. Additionally, ROI analyses revealed events compared to objects produced greater activation in bilateral angular gyri, but the contrast of event duration > event valence displayed significantly greater activation in the right AG and PGa and PGp. Duration tasks might also activate the left AG although it seems to be limited to the PGp. One might argue that the task of judging duration involved more semantic information than judging pleasantness of an event. While this might be true, it is curious that the ROI analysis suggested the AG in the right hemisphere was activated to a greater extent during duration tasks compared to other tasks. This preference of semantic duration

information preferring the right hemisphere matched our results from the SMG ROI and whole-brain analysis.

A recent neuroimaging study by Boylan et al. (2015) used two-word phrases to examine change in voxel pattern of a given noun or verb. The authors found that the left AG represented information specific to verbs, event structure or thematic relations facilitated by verbs. The authors combined verbs with nouns that were mostly non-events, although a few event nouns were also used such as "the opera" or "the traffic." We found that event nouns also produced greater activation in the left AG compared to object nouns. Moreover the task affected activation of the left AG for event nouns in our study as duration judgments activated the PGp to a greater extent than valence. Contrastingly, event valence activated the left PGa more than event duration, but this difference was not statistically significant. Others, Bedny et al. (2014) found verbs to activate the left AG marginally more than event nouns (whole-brain analysis suggested a difference only at a corrected $p < 0.1$). Therefore, it seems that the left AG is involved in processing events regardless of the grammatical classification.

4.3 Main Effect of Events

Not surprisingly we found a larger network to be activated for event nouns compared to object nouns. The whole-brain analysis, events > objects revealed peak activation clusters in bilateral angular gyri, STS, superior frontal gyri, middle frontal gyri and left and medial precuneus, temporal pole and middle MTG. ROI analyses of temporal coordinates suggested that the left SMG and right pSTS were involved in event semantics. Additionally, ROI of the angular gyri confirmed the whole-brain analysis where events displayed greater activation than objects. ROI of areas within the IPL

revealed that the left PFm was significantly activated for events. Moreover the IPL ROI analysis revealed that the PGa and PGp for events compared to objects whereas activation in the right AG (PGa and PGp) was produced mostly by event duration.

Bedny et al., (2014) performed a neuroimaging study that examined the location of events using event nouns. Participants in this study were engaged in an auditory task where they rated how similar two nouns were while undergoing fMRI. An *a priori* ROI analysis revealed that the left pMTG was activated to a greater extent for event nouns compared with object nouns. Additionally, in their event noun > object noun comparison, part of the AG was also activated, consistent with the present study. One of the possible explanations for activation in the left pMTG for events was that the left pMTG stores sequential temporal information as well as information concerning interactions between objects and agents within an event. Additionally, it was suggested that if this event hypothesis was correct, then it is possible that the left pMTG stores temporal information. However, their event nouns had much lower imageability than object nouns, which may have confounded the comparisons, given that the AG also responds to higher imageability and concreteness (Binder, Westbury, McKiernan, Possing, & Medler, 2005; Wang, Conder, Blitzer & Shinkareva, 2010). This confound could have affected the pMTG activation as well.

Previously, the role of the left pMTG in processing event information was demonstrated by two research studies using action events (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002). These studies suggested that action/motion features of events are represented in the left pMTG. We found confirming evidence for the role of the left pMTG in storing

information related to events compared to objects in the whole-brain analysis. Both whole-brain contrasts of event valence minus object valence as well as event duration minus object size revealed a similar area in the left pMTG activated for events. Interestingly the contrast of event duration minus event valence also reported activation in the left MTG, but it was more in the middle of the structure and combined with the ITG. This suggests that the left pMTG is not likely involved in processing temporal information but rather processing general event information.

Another region related to motion processing that was indicated in the whole-brain analysis of events > objects was the bilateral STS. The posterior STS has been found to be involved in perception of visual biological motion (Grossman & Blake, 2001; Grossman & Blake, 2002). A meta-analysis of the left STS proposed a functional division of the structure based on neuroimaging studies (Liebenthal, Desai, Humphries, Sabri, & Desai, 2014). We found bilateral activation of the STS for events compared to objects and pSTS activation in the ROI analysis. In our whole-brain analysis, the left STS was activated from anterior to posterior regions while the right STS activation was located in the middle of the structure. Activation of the middle STS especially on the left is likely related to language processing (Liebenthal et al., 2014). The pSTS has also been found to be involved when reading temporal metaphors (Lai & Desai, 2016). Although we found STS activation for events compared to objects our data did not suggest that the STS was involved in processing duration information. The direct contrast of duration > valence did not indicate involvement of the STS.

Prefrontal activation for events compared to objects activated dorsomedial locales including bilateral superior frontal sulci and middle frontal gyri. Semantic activation of

prefrontal cortices has not been well studied. Based on limited information, it has been proposed that the dorsomedial activation is related to coordinating a plan for knowledge retrieval (Binder & Desai, 2011). This is a possible interpretation of our results since the majority of contrasts displayed some type of activation in the dorsomedial prefrontal cortex (PFC). Alternatively, the structural temporal representation binding (STRing) theory by Krueger, Barbey, & Grafman (2009a) proposed a connection from the dorsomedial PFC to the posterior cortex and limbic system. STRing suggested that event simulators called elators were located in the dorsomedial PFC. Social event knowledge was proposed to arise from elators in the dorsomedial PFC via links to the posterior cerebral cortex and limbic system.

Krueger et al. (2009b) found support of STRing with a study that found a left-hemispheric network including a cluster in the dorsomedial PFC as well as in the posterior parietal lobule to be activated when participants read about events. Similar results have been found when participants were required to think about prior or imagine future events (Demblon, Bahri, & D'Argembeau, 2016). Others have suggested that the inferior PFC and precuneus are implicated in episodic memory retrieval (Lundstrom, Ingvar, & Petersson, 2005). Although our results did not suggest a role of the inferior PFC in event nouns compared to object nouns, a large cluster stemming from the left precuneus was found in the whole-brain analysis for the event > object contrast. This cluster extended from the anterior to posterior regions. A review of the function of the precuneus suggested a functional subdivision of the structure, where anterior locations were involved in mental imagery strategies while posterior regions were recruited for episodic memory retrieval (Cavanna & Trimble, 2006). Conversely, others found the

right precuneus to be activated when participants encoded durations (Harrington et al., 2004). We found bilateral precuneus in the event > object contrast, with peak activation in the left hemisphere. Additionally, the right precuneus displayed peak activation for a cluster revealed by the duration > valence contrast. These results add to the possible hemispheric preference for duration tasks.

4.4 Right Hemispheric Preference for Duration?

We have reported a preferential right hemispheric network involved in semantic representation of duration. Whole-brain analyses supported this notion and ROI contrasts examining duration and valence suggested that duration activated only the right hemispheres of the IPL including the AG and SMG. A right-hemispheric network involved in temporal perception has been previously suggested (Harrington & Haaland, 1999; Lewis & Miall, 2006; Koch, Oliveri & Caltagirone, 2009). Despite this, there has been much debate about regions important for temporal processing. Reasons for the discrepancy in temporal perception have been proposed to involve the time interval used; sub-second versus supra-second, (Lewis & Miall, 2003b), the type of resources activated; automatic or cognitively controlled (Lewis & Miall, 2003a; Lewis & Miall, 2006), or the task of predicting time or estimating durations (Coull, Davranche, Nazarian & Vidal, 2013).

Coull et al. (2013) examined the differences in networks activated during a temporal prediction compared to a duration estimation task using the same experimental paradigm. The authors found that when participants were asked to estimate an interval of duration, the SMA, basal ganglia and right frontal/parietal cortices were activated. In contrast, when participants used the same visual-spatial paradigm to predict the onset of a

given sensory event, the left IPL, left premotor cortex and cerebellum were recruited.

Similar results have been found when participants encoded a specific duration. Rao,

Mayer and Harringtion (2001) found that early activation occurred when participants

encoded duration as measured by fMRI. The activation was localized in the basal

ganglia, right IPL and bilateral premotor cortex. Later activation was found in the right

dorsolateral PFC as a result of comparison of the time intervals. A later study by some of

the same investigators suggested that encoding of durations involved right hemisphere

regions including the caudate and IPL as well as the left cerebellum (Harrington et al.,

2004). Furthermore, the same study found that making decisions about comparing the

durations involved activation in the left parietal cortex. Hayashi et al. (2015) also found

the right IPL to be involved in encoding judgments about the duration of stimuli. In

addition to neuroimaging studies, a right hemispheric preference for duration processing

has been found in patient populations and healthy participants with use of rTMS and

transcranial Random Noise Stimulation (tRNS; Dormal, Javadi, Pesenti, Walsh, &

Cappelletti, 2016)

The right hemisphere has been indicated in temporal processing from

neuropsychological and brain stimulation studies. Harrington et al. (1998) found that

patients with right hemispheric damage made significantly more errors when comparing

durations of auditory stimuli than patients with left hemispheric damage. Danckert et al.

(2007) used neglect and lesioned control patients to examine the location of brain damage

in estimating durations up to 60 seconds. This study found that patients with right brain

damage consistently displayed difficulties in estimating durations. It was concluded that

a right frontal-parietal network was involved in accurate perception of supra-second

durations. A review of time perception in neurologic and brain injury patients also found support for duration estimations of at least a second to recruit a network involving the right prefrontal and parietal lobes as well as bilateral temporal lobes (Piras et al., 2014). rTMS studies specifically requiring participants to determine which visual stimuli was presented for a greater duration also suggested the role of the right hemisphere in duration judgments (Bueti et al., 2008; Weiner et al., 2010). Similarly, tRNS stimulation to the right IPL (which the authors indicate is the over IPS) but not SMA enhanced duration processing (Dormal et al., 2016). Although a number of studies, including this study, have found support for duration processing to be located in the right hemisphere, the activation on neuroimaging studies might be related to general magnitude processing.

A magnitude system with the parietal lobule and PFC as key structures was proposed by the ATOM theory (Bueti & Walsh, 2009; Walsh, 2003). The generalized magnitude theory proposed the right IPL was chiefly activated for magnitude estimations in dimensions such as time, space and number. In contrast, the left IPL is preferentially recruited for exact calculations (Walsh, 2003). Overall, we did not find support for a generalized magnitude system in the processing of duration and size from nouns. Peak activations for the whole-brain analysis of magnitude minus valence revealed activation in the right IPL (AG and SMG) and left IPL (AG). Notwithstanding, the activation for magnitude in the right IPL was driven by the event duration task. The specific contrast of event duration minus object size revealed that the right IPL is most sensitive to events. This was also confirmed by the ROI analyses. ROI analysis of the right SMG and AG revealed that event duration tasks activated these right IPL structures to a greater extent than the object size task.

4.5 Event Concepts Grounded in Space?

We previously discussed that event duration judgments are grounded in temporal areas of the right IPL (SMG and AG) but it seems that event concepts in general are grounded in areas that process spatial information. Whole-brain analysis of the main effect of noun type and ROI analyses supported this notion. The event minus object nouns whole-brain analysis identified a large cluster in the left AG and SMG that was activated for events compared to objects. Similarly, ROI of the left SMG, AG, PGa and PGp revealed significantly greater activation for events compared to objects, with large effect sizes (Cohen's *d* 1.99; 1.68; 1.66; 1.10, respectively). Both left SMG and AG have been implicated in spatial processing and specifically for categorical spatial relations in both patient and healthy participant studies (for reviews see Jager and Postma, 2003; Kemmerer, 2006). Therefore it seems that similar areas are utilized to process event information. Activation of areas proposed to process categorical spatial relations in processing events would be logical, as there are numerous objects comprising events and if one described the spatial location/ relationship of objects, prepositions such as 'to the left of' or 'to the right of' would inevitably be used.

The IPS which divides inferior and superior parietal lobules has been suggested to be involved in a number of important tasks such as processing spatial attention (Husain & Nachev, 2007), number processing and size processing (Harvey, Fracasso, Petridou, & Dumoulin, 2015). Here we found the left IPS to be activated for event valence compared to event duration in the whole-brain analysis. Our whole-brain analyses also revealed that the right IPS was activated in the main effect of nouns favoring object nouns and an area of the right SMG/IPS was activated for the main effect of task favoring magnitude as

well as object size compared to object valence. When specifically examining different regions of IPS in *a priori* ROI analyses, bilateral anterior IPS was found to be activated during object size judgments. Interestingly, the right middle IPS was activated for event duration compared to event valence and object size compared to object valence. This suggests that duration may be processed in spatial terms. A previous study found that duration judgments were not affected by rTMS to the left or right IPS (Dormal, Andres & Pesenti, 2008). Dormal et al. (2008) applied rTMS to the left and right IPS as well as the vertex and found that duration judgments of flashed dots were not affected by rTMS to either hemispheric IPS. A more recent study by the same first author found that the tRNS stimulation to the right IPS actually enhanced duration processing (Dormal et al., 2016). Based on our results, only a small portion of the IPS may respond to event duration processing and thus this could be the reason for previous conflicting findings.

Another structure that is commonly associated with processing spatial information and that was activated in contrasts favoring magnitude, duration and size was the left hippocampal gyrus. Left parahippocampal gyrus activation is likely related to processing spatial layout of events and objects (Epstein & Kanwisher, 1998). To further examine the activation within the left parahippocampal gyrus we performed an *a posteriori* ROI analysis focused around the coordinates found to represent the PPA (Epstein & Kanwisher, 1998). ROI of the left PPA suggested a main effect of magnitude compared to valence. Separate contrasts revealed greater activation for event duration minus event valence and object size minus object valence. This ROI analysis provided evidence that processing event concepts is grounded in space and that spatial grounding of event concepts may occur even during a task that specifically asked for temporal processing

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(i.e., duration). The fact that event duration minus event valence and object size minus object valence were the only contrasts that significantly activated two areas thought to be involved in spatial processing suggests that duration may be processed in terms of space as well as time. Indeed a "longer" duration of time may actually activate some areas associated with processing size in space.

4.6 Other Regions

Although a there are a number of studies that have examined the location of temporal processing, there is still much debate as to which areas are most important for timing. Indeed, we failed to find a number of areas that have been suggested to be crucial to temporal processing, such as the SMA (Macar, Coull, & Vidal, 2006) and insula (Wittmann, Simmons, Aron, & Paulus, 2010). Our lack of findings in some regions might be explained by prior reviews. A review of the perception and estimation of time by Merchant and Harrington (2013) suggested that SMA activity was lost when more difficult control tasks were implemented. Our behavioral results of reaction times suggested that the tasks involved in our study were of similar difficulty. Moreover, accuracy results of our study suggested that valence judgments were actually more difficult than duration and size judgments. Cognitive difficulty of tasks has also been associated with similar areas that are involved in temporal processing (Radua, del Pozo, Gómez, Guillen-Grima, & Ortuño, 2014). Insula and left putamen have been previously associated with time perception and were found to be activated with increasing difficulty of tasks. We also failed to find significant activation in either the insula or left putamen. Although, this does not necessarily mean that these areas are not involved in temporal

processing. Based on our results it seems they are not involved in duration judgments of event nouns.

Prefrontal cortex activation in studies of duration perception is consistently located in the dorsolateral PFC (Lewis & Miall, 2006), in contrast, we found activation for duration in the dorsomedial PFC. Semantic studies concerning the dorsomedial PFC are sparse (Binder & Desai, 2011). One study, though, found that judgments of two words describing people compared to objects activated social cognition networks including the dorsomedial PFC (Mitchell, Heatherton & Macrae, 2002). In comparison, pairs of words describing objects compared to people activated IFG. Additionally, the dorsolateral PFC has been involved in emotional processing. Herrington et al. (2005) performed an fMRI study to examine the processing of pleasant and unpleasant words and they found that pleasant words produced greater activation in the left compared to the right dorsolateral PFC. Although our nouns were matched for valence ratings, it is possible that the instructions to select the more pleasant word during the valence tasks influenced areas related to processing positive valence. Alternatively, it is possible that the semantic PFC networks involved in duration processing differed from temporal perception networks. For example Rao et al. (2001) found right dorsolateral PFC activation when participants compared time intervals. It is possible that comparison of durations stemming from language rather than visual or auditory stimuli are processed in slightly different areas. Additionally some of the differences we found in processing of semantic duration representation might be related to processing large temporal durations. None of the duration studies of temporal perception examined durations greater than 60

seconds whereas the majority of our event nouns were greater than 60 seconds in duration.

4.7 Conclusion

We are the first, to our knowledge, to present evidence for grounding of event concepts. Our data suggested that event concepts are generally grounded in spatial areas, unless the task specifically required a temporal process such as a duration task. When a duration task is required, a right hemispheric network is preferred, involving partial grounding in temporal perception areas. Temporal perception studies have revealed a number of areas and regions associated with timing. When we compare our results to timing studies that specifically examined duration we find similar results. Therefore, we provided support for a partial grounding of duration in temporal perception areas. Although, we must be careful with this conclusion, as there is much variability in the literature concerning the location of temporal and spatial perception. Nonetheless we found that similar areas thought to be involved in spatial perception were also associated with the representation of event concepts, whereas duration information derived from event concepts activated areas thought to be involved in temporal perception.

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APPENDIX A – STIMULI USED IN THIS EXPERIMENT

EDur1 = Event Duration in Experiment 1; EVal1 = Event Valence in Experiment 1; ObSz1 = Object Size in Experiment 1; OVal1 = Object Valence in Experiment 1; EDur2 = Event Duration in Experiment 2; EVal2 = Event Valence in Experiment 2; ObSz2 = Object Size in Experiment 2; OVal2 = Object Valence in Experiment 2; L = Noun on the left was judged to be greater than the right; S = Nouns were judged to be similar; R = Noun on the right was judged to be greater than the left.

A.1 Experiment Version 1

EDur1	1	L	the avalanche	the exam
EDur1	2	L	the ballet	the sip
EDur1	3	L	the birth	the chore
EDur1	4	L	the blizzard	the alarm
EDur1	5	S	the breakfast	the lunch
EDur1	6	R	the chant	the rain
EDur1	7	R	the dusk	the nap
EDur1	8	S	the film	the parade
EDur1	9	L	the fire	the thunderstorm
EDur1	10	L	the flight	the meal
EDur1	11	S	the gala	the banquet
EDur1	12	L	the game	the quiz

EDur1	13	R	the growl	the test
EDur1	14	R	the heartbeat	the picnic
EDur1	15	R	the hike	the cruise
EDur1	16	L	the hunt	the stunt
EDur1	17	L	the hymn	the punt
EDur1	18	R	the kiss	the party
EDur1	19	R	the leap	the interview
EDur1	20	S	the lecture	the class
EDur1	21	R	the manicure	the concert
EDur1	22	R	the massage	the drought
EDur1	23	R	the murder	the exercise
EDur1	24	L	the night	the riot
EDur1	25	R	the prom	the honeymoon
EDur1	26	R	the punch	the battle
EDur1	27	L	the ride	the sob
EDur1	28	S	the shock	the hug
EDur1	29	S	the shoeshine	the rosary
EDur1	30	L	the skit	the cough
EDur1	31	R	the spasm	the hurricane
EDur1	32	R	the splash	the report
EDur1	33	S	the sprint	the song
EDur1	34	R	the stomachache	the famine
EDur1	35	R	the stroll	the movie
EDur1	36	S	the sunset	the sunrise
EDur1	37	L	the tornado	the sneer

EDur1	38	L	the trip	the recital
EDur1	39	L	the twilight	the blast
EDur1	40	L	the typhoon	the bullfight
EVal1	1	L	the adventure	the rodeo
EVal1	2	L	the afternoon	the polka
EVal1	3	S	the autopsy	the hangover
EVal1	4	S	the barbecue	the symphony
EVal1	5	R	the brawl	the duel
EVal1	6	L	the cookout	the pedicure
EVal1	7	R	the crime	the seizure
EVal1	8	R	the cyclone	the dinner
EVal1	9	S	the fever	the flood
EVal1	10	S	the fiesta	the brunch
EVal1	11	L	the flare	the coma
EVal1	12	R	the flu	the task
EVal1	13	R	the gunfire	the reflex
EVal1	14	S	the heartburn	the earthquake
EVal1	15	L	the landslide	the shot
EVal1	16	R	the matinee	the autumn
EVal1	17	L	the melody	the jamboree
EVal1	18	R	the migraine	the tournament
EVal1	19	L	the newscast	the pageant
EVal1	20	R	the newsreel	the slumber
EVal1	21	S	the opera	the concerto
EVal1	22	R	the playoff	the recess

EVal1	23	L	the playtime	the marathon
EVal1	24	L	the pregnancy	the traffic
EVal1	25	R	the safari	the lullaby
EVal1	26	R	the sandstorm	the buzzer
EVal1	27	L	the season	the episode
EVal1	28	S	the sermon	the errand
EVal1	29	R	the siren	the stampede
EVal1	30	R	the snack	the vacation
EVal1	31	R	the snort	the spark
EVal1	32	L	the somersault	the conference
EVal1	33	L	the storm	the chemotherapy
EVal1	34	L	the story	the employment
EVal1	35	L	the supper	the waltz
EVal1	36	S	the tantrum	the surgery
EVal1	37	L	the tour	the decathlon
EVal1	38	L	the twister	the monsoon
EVal1	39	R	the video	the weekend
EVal1	40	R	the voyage	the breeze
ObSz1	1	R	the atom	the chunk
ObSz1	2	R	the braid	the ranch
ObSz1	3	R	the capital	the state
ObSz1	4	L	the cheetah	the revolver
ObSz1	5	R	the circuit	the club
ObSz1	6	S	the clutch	the cap
ObSz1	7	L	the continent	the registrar

ObSz1	8	L	the country	the contact
ObSz1	9	S	the dispenser	the baritone
ObSz1	10	R	the dormitory	the slum
ObSz1	11	L	the eel	the moth
ObSz1	12	S	the embassy	the hostel
ObSz1	13	S	the emporium	the inn
ObSz1	14	S	the facility	the spa
ObSz1	15	R	the fang	the dragon
ObSz1	16	L	the fawn	the pest
ObSz1	17	R	the fireplace	the loft
ObSz1	18	L	the fleet	the sample
ObSz1	19	R	the generator	the track
ObSz1	20	L	the heart	the nut
ObSz1	21	R	the herd	the wilderness
ObSz1	22	L	the hospital	the shop
ObSz1	23	L	the lark	the shunt
ObSz1	24	L	the library	the transformer
ObSz1	25	R	the limb	the pew
ObSz1	26	L	the lodge	the clump
ObSz1	27	L	the lounge	the flounder
ObSz1	28	R	the match	the vacuum
ObSz1	29	R	the mint	the paw
ObSz1	30	R	the molecule	the willow
ObSz1	31	L	the monument	the drill
ObSz1	32	S	the mutt	the hound

ObSz1	33	L	the nation	the hulk
ObSz1	34	S	the peach	the carnation
ObSz1	35	L	the ram	the mole
ObSz1	36	S	the root	the herb
ObSz1	37	L	the tunic	the wad
ObSz1	38	R	the urchin	the cockpit
ObSz1	39	R	the wand	the sleigh
ObSz1	40	R	the world	the galaxy
OVal1	1	L	the amphibian	the broach
OVal1	2	R	the apothecary	the heirloom
OVal1	3	R	the atmosphere	the photon
OVal1	4	S	the bear	the chart
OVal1	5	L	the bonsai	the incline
OVal1	6	L	the burrow	the catalogue
OVal1	7	R	the caper	the kernel
OVal1	8	L	the cash	the southwest
OVal1	9	R	the cluster	the primate
OVal1	10	R	the conservatory	the solarium
OVal1	11	R	the dab	the bazaar
OVal1	12	L	the dipstick	the crutch
OVal1	13	R	the drug	the reptile
OVal1	14	S	the dungeon	the probe
OVal1	15	R	the dust	the quarry
OVal1	16	R	the farm	the award
OVal1	17	L	the flan	the clog

OVal1	18	L	the kingdom	the particle
OVal1	19	R	the machine	the citrus
OVal1	20	R	the monitor	the landscape
OVal1	21	R	the novel	the suite
OVal1	22	S	the perch	the hamper
OVal1	23	L	the picture	the fairway
OVal1	24	R	the precinct	the exhibit
OVal1	25	R	the predator	the treasury
OVal1	26	S	the present	the sanctuary
OVal1	27	L	the region	the façade
OVal1	28	L	the scroll	the harness
OVal1	29	L	the shortcake	the gizzard
OVal1	30	S	the slice	the institute
OVal1	31	S	the sliver	the beam
OVal1	32	R	the souvenir	the prize
OVal1	33	L	the starch	the bacterium
OVal1	34	L	the strand	the trace
OVal1	35	L	the sweatshop	the penitentiary
OVal1	36	S	the terminal	the rig
OVal1	37	R	the territory	the treasure
OVal1	38	L	the train	the frame
OVal1	39	S	the venue	the stack
OVal1	40	L	the watch	the hurdle

A.2 Experiment Version 2

EDur2	1	L	the adventure	the rodeo
EDur2	2	L	the afternoon	the polka
EDur2	3	S	the autopsy	the hangover
EDur2	4	S	the barbecue	the symphony
EDur2	5	S	the brawl	the duel
EDur2	6	L	the cookout	the pedicure
EDur2	7	L	the crime	the seizure
EDur2	8	L	the cyclone	the dinner
EDur2	9	R	the fever	the flood
EDur2	10	L	the fiesta	the brunch
EDur2	11	R	the flare	the coma
EDur2	12	L	the flu	the task
EDur2	13	L	the gunfire	the reflex
EDur2	14	S	the heartburn	the earthquake
EDur2	15	L	the landslide	the shot
EDur2	16	R	the matinee	the autumn
EDur2	17	R	the melody	the jamboree
EDur2	18	R	the migraine	the tournament
EDur2	19	R	the newscast	the pageant
EDur2	20	R	the newsreel	the slumber
EDur2	21	S	the opera	the concerto

EDur2	22	L	the playoff	the recess
EDur2	23	R	the playtime	the marathon
EDur2	24	L	the pregnancy	the traffic
EDur2	25	L	the safari	the lullaby
EDur2	26	L	the sandstorm	the buzzer
EDur2	27	L	the season	the episode
EDur2	28	S	the sermon	the errand
EDur2	29	S	the siren	the stampede
EDur2	30	R	the snack	the vacation
EDur2	31	S	the snort	the spark
EDur2	32	R	the somersault	the conference
EDur2	33	R	the storm	the chemotherapy
EDur2	34	R	the story	the employment
EDur2	35	L	the supper	the waltz
EDur2	36	R	the tantrum	the surgery
EDur2	37	R	the tour	the decathlon
EDur2	38	R	the twister	the monsoon
EDur2	39	R	the video	the weekend
EDur2	40	L	the voyage	the breeze
EVal2	1	R	the avalanche	the exam
EVal2	2	L	the ballet	the sip
EVal2	3	L	the birth	the chore
EVal2	4	L	the blizzard	the alarm
EVal2	5	L	the breakfast	the lunch
EVal2	6	R	the chant	the rain

EVal2	7	R	the dusk	the nap
EVal2	8	S	the film	the parade
EVal2	9	R	the fire	the thunderstorm
EVal2	10	R	the flight	the meal
EVal2	11	S	the gala	the banquet
EVal2	12	L	the game	the quiz
EVal2	13	S	the growl	the test
EVal2	14	R	the heartbeat	the picnic
EVal2	15	S	the hike	the cruise
EVal2	16	R	the hunt	the stunt
EVal2	17	L	the hymn	the punt
EVal2	18	L	the kiss	the party
EVal2	19	S	the leap	the interview
EVal2	20	R	the lecture	the class
EVal2	21	R	the manicure	the concert
EVal2	22	L	the massage	the drought
EVal2	23	R	the murder	the exercise
EVal2	24	L	the night	the riot
EVal2	25	R	the prom	the honeymoon
EVal2	26	S	the punch	the battle
EVal2	27	L	the ride	the sob
EVal2	28	R	the shock	the hug
EVal2	29	L	the shoeshine	the rosary
EVal2	30	L	the skit	the cough
EVal2	31	S	the spasm	the hurricane

EVal2	32	L	the splash	the report
EVal2	33	R	the sprint	the song
EVal2	34	R	the stomachache	the famine
EVal2	35	R	the stroll	the movie
EVal2	36	S	the sunset	the sunrise
EVal2	37	L	the tornado	the sneer
EVal2	38	L	the trip	the recital
EVal2	39	L	the twilight	the blast
EVal2	40	R	the typhoon	the bullfight
ObSz2	1	S	the amphibian	the broach
ObSz2	2	L	the apothecary	the heirloom
ObSz2	3	L	the atmosphere	the photon
ObSz2	4	L	the bear	the chart
ObSz2	5	R	the bonsai	the incline
ObSz2	6	L	the burrow	the catalogue
ObSz2	7	S	the caper	the kernel
ObSz2	8	R	the cash	the southwest
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ObSz2	10	S	the conservatory	the solarium
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ObSz2	17	S	the flan	the clog
ObSz2	18	L	the kingdom	the particle
ObSz2	19	L	the machine	the citrus
ObSz2	20	R	the monitor	the landscape
ObSz2	21	R	the novel	the suite
ObSz2	22	R	the perch	the hamper
ObSz2	23	R	the picture	the fairway
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ObSz2	32	S	the souvenir	the prize
ObSz2	33	L	the starch	the bacterium
ObSz2	34	S	the strand	the trace
ObSz2	35	S	the sweatshop	the penitentiary
ObSz2	36	L	the terminal	the rig
ObSz2	37	L	the territory	the treasure
ObSz2	38	L	the train	the frame
ObSz2	39	L	the venue	the stack
ObSz2	40	R	the watch	the hurdle
OVal2	1	L	the atom	the chunk

OVal2	2	S	the braid	the ranch
OVal2	3	R	the capital	the state
OVal2	4	L	the cheetah	the revolver
OVal2	5	R	the circuit	the club
OVal2	6	S	the clutch	the cap
OVal2	7	L	the continent	the registrar
OVal2	8	S	the country	the contact
OVal2	9	R	the dispenser	the baritone
OVal2	10	L	the dormitory	the slum
OVal2	11	R	the eel	the moth
OVal2	12	L	the embassy	the hostel
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OVal2	15	R	the fang	the dragon
OVal2	16	L	the fawn	the pest
OVal2	17	S	the fireplace	the loft
OVal2	18	R	the fleet	the sample
OVal2	19	S	the generator	the track
OVal2	20	L	the heart	the nut
OVal2	21	R	the herd	the wilderness
OVal2	22	R	the hospital	the shop
OVal2	23	L	the lark	the shunt
OVal2	24	S	the library	the transformer
OVal2	25	R	the limb	the pew
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OVal2	27	L	the lounge	the flounder
OVal2	28	S	the match	the vacuum
OVal2	29	L	the mint	the paw
OVal2	30	R	the molecule	the willow
OVal2	31	L	the monument	the drill
OVal2	32	R	the mutt	the hound
OVal2	33	L	the nation	the hulk
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OVal2	38	R	the urchin	the cockpit
OVal2	39	R	the wand	the sleigh
OVal2	40	L	the world	the galaxy