

PREFERENTIAL ACCESS TO OBJECT SEMANTICS VIA LEXICAL PROCESSING IN
THE VENTRAL STREAM OF THE BRAIN

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ABSTRACT

Converging evidence supports a distributed-plus-hub view of semantic processing in the brain, in which there are distributed modular semantic sub-systems (e.g., for shape, colour, and action) connected to an amodal semantic hub. Furthermore, object semantic processing of colour and shape, and lexical reading and identification, are processed mainly along the ventral stream, while action semantic processing occurs mainly along the dorsal stream. In Experiment 1, participants read a prime word that required imagining either the object or action referent, and then named a lexical word target. In Experiments 2 and 3, participants performed a lexical decision task (LDT) with the same targets as in Experiment 1, in the presence of foils that were legal nonwords (NWs; Experiment 2; allows orthography, phonology, and semantics to contribute to responding) or pseudohomophones (PHs; Experiment 3; allows only orthography to contribute to responding). Semantic priming was similar in effect size regardless of prime type for naming and the LDT with NW foils, but was greater for object primes than action primes for the LDT with PH foils, suggesting a shared-stream advantage when the task demands focus on orthographic lexical processing. Experiment 4 used functional magnetic resonance imaging (fMRI) and identified the potential loci of shared-stream processing to regions in the ventral stream anterior to colour sensitive visual area V4 cortex and anterior to lexical and shape sensitive regions in the left fusiform gyrus, as well as in cerebellar lobule VI. Action priming showed more activation than object priming in dorsal stream motion related regions of the right parietal occipital junction, right superior occipital gyrus, and bilateral visual area V3. Experiment 5 identified structural connectivity using diffusion tensor imaging (DTI), and implicated connections from the cerebellar lobule VI to the anterior temporal lobe (ATL) semantic hub via the thalamus, supporting that this cerebellar region may act as a visual object semantic sub-system of the semantic network. The behavioural experiments demonstrate that object semantic and lexical processing are temporally shared, and the fMRI activation supports the theory that spatially shared-stream activation occurs in the ventral stream during object (but not action) priming of lexical processing. The DTI connectivity analysis supports the theory that lobule VI may act as an additional object semantic sub-system. This research suggests that shared-stream processing occurs between lexical identification and object semantic processing in the ventral stream, providing preferential access to object semantics via lexical processing. This shared-stream processing has implications for models of reading and the semantic system, which

currently do not delineate between different modalities of semantic processing. The shared-stream regions identified may prove useful for pre-surgical localization of important intersections between the reading and semantic networks. These results also provide predictions that pure alexia and surface dyslexia patients with comorbid semantic deficits may be disproportionately affected by object semantic deficits compared to action semantic deficits.

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LIST OF ABBREVIATIONS

ATL	Anterior Temporal Lobe
BOI	Body Object Interaction
CBOW	Continuous Bag Of Words
CDP++	Connectionist Dual Process
DRC	Dual Route Cascaded
DTI	Diffusion Tensor Imaging
EPI	Echo-Planar Imaging
ER	Error Rate
fMRI	Functional Magnetic Resonance Imaging
FuG	Fusiform Gyrus
FWHM	Full Width Half Maximum
GLMM	General Linear Mixed Model
GPC	Grapheme-to-Phoneme Conversion
ISI	InterStimulus Interval
LDT	Lexical Decision Task
LMM	Linear Mixed Model
LRT	Likelihood Ratio Test
MPRAGE	Magnetization Prepared Rapid Acquisition Gradient Echo
MRI	Magnetic Resonance Imaging
NW	Nonword
PDP	Parallel Distributed Processing
PET	Positron Emission Tomography
PH	Pseudohomophone
POJ	Right Parietal Occipital Junction
RT	Reaction Time
SOA	Stimulus Onset Asynchrony
SOG	Right Superior Occipital Gyrus
SR	Serial Response
TFCE	Threshold Free Cluster Enhancement
UKWAC	UK Web Archiving Consortium
VWFA	Visual Word Form Area

CHAPTER 1: Introduction

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and

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(Chapters 1 and 3-4, particularly Experiments 4-5).

Our interpretation of the meanings of words shape the way we perceive and interpret our subjective experience of reality. Associated meanings for a referent object's colour, shape, and actions are stored in semantic memory, and are intricately connected to the words we use to label and describe them. Endel Tulving was among early researchers to define separate categories of long-term memory, including episodic memories for events and semantic memories for associated meanings (Tulving, 1984). Early theories about how the brain stores and processes semantic information include Fodor's (1983) theory that semantic memory relied on a general, abstract semantic system utilizing high connectivity in the brain. A commonly used behavioural paradigm for examining semantic processing is the semantic priming paradigm, which demonstrates that the reading of a prime word facilitates the reading of a related target word, supporting the theory that word representations connected via semantic memory spread activation to one another (e.g., Collins & Loftus, 1975; see McNamara, 2005 for a review). Although important research has worked to simulate, predict, and understand semantic processes (e.g., picture naming, Rogers et al., 2004; words, Armstrong & Plaut, 2016) and reading processes (e.g., the Dual Route Cascaded (DRC) model, Coltheart, Rastle, Perry, & Langdon, 2001; the Parallel Distributed Processing (PDP) model, Plaut, McClelland, Seidenberg, &

Patterson, 1996; the Connectionist Dual Process (CDP++) model, Perry, Ziegler, & Zorzi, 2010; see also Wingerak, Neudorf, Ekstrand, & Borowsky, 2017 for a direct comparison of some of these models), the overlapping brain networks utilized by these processes can and should lead to novel, testable hypotheses. The current research, motivated by evidence from clinical and neuroimaging research in the fields of semantic processing and reading suggesting that visual semantics and lexical reading may utilize shared-stream regions of the ventral visual processing stream, investigates whether there is a *temporal* (i.e., behavioural reaction time, RT) priming advantage for visual object word primes (“imagine this object”) over action word primes (“imagine this action”) in semantic priming word naming and lexical decision paradigms. An object priming advantage for lexical processing in these paradigms would support the theory that cognitive processing for object semantics and lexical word representations are temporally shared. Furthermore, a functional magnetic resonance imaging (fMRI) investigation of this semantic priming paradigm will explore this theory by testing whether there is *spatial* evidence for shared-stream ventral activation between lexical and semantic processing using the semantic priming lexical decision paradigm.

1.1 Models of Semantic Processing

The distributed-only model of semantic processing posits that there are distributed sets of connected, modality specific sub-systems for processing colour, shape, and action, which are integrated into a semantic network (e.g., Shallice, 1988, 1993). Alternatively, the distributed-plus-hub model of semantic processing describes an additional amodal semantic hub located in the anterior temporal lobe (ATL) connected to all the sub-systems of semantic processing and supporting integration of semantic representations, and is supported by converging evidence from neuroimaging, computational modeling, and neuropathology cases (e.g., Binney, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Visser, Jefferies, & Ralph, 2010; see Patterson, Nestor, & Rogers, 2007 for a review; see Figure 1.1). Patterson et al. (2007) reviewed the literature around the debate for amodal ATL semantic processing versus distributed modal semantic processing and pointed to evidence from fMRI, neuropathology cases, and computational modeling (e.g., Rogers & McClelland, 2003), demonstrating that global deficits were associated with localized ATL damage while specific modal deficits were related to damage in one or more of the modal regions outside of the ATL. Both the distributed-only and the distributed-plus-hub models of semantic processing hold that there are distributed sub-

systems of semantic processing, and have been supported by evidence that lesions can cause selective dysfunction of certain types of semantic memory (e.g., Goodale & Milner, 1992). Neuroimaging and neuropathology evidence suggests that the semantic sub-systems responsible for processing action are located mainly within the dorsal visual processing stream, proximal to the motor and sensory cortical regions involved (e.g., hand-related vs. foot-related objects, Esopenko et al., 2012), while visual sub-systems for colour and shape are processed mainly within the ventral visual processing stream just anterior to the modalities involved (e.g., colour and shape; Patterson et al., 2007; see Figure 1.1; see also Chao & Martin, 1999, Thompson-Schill, Kan, & Oliver, 2006, Martin, 2007, Martin, Douglas, Borghesani et al., 2016, and Newsome, Man & Barense, 2018).

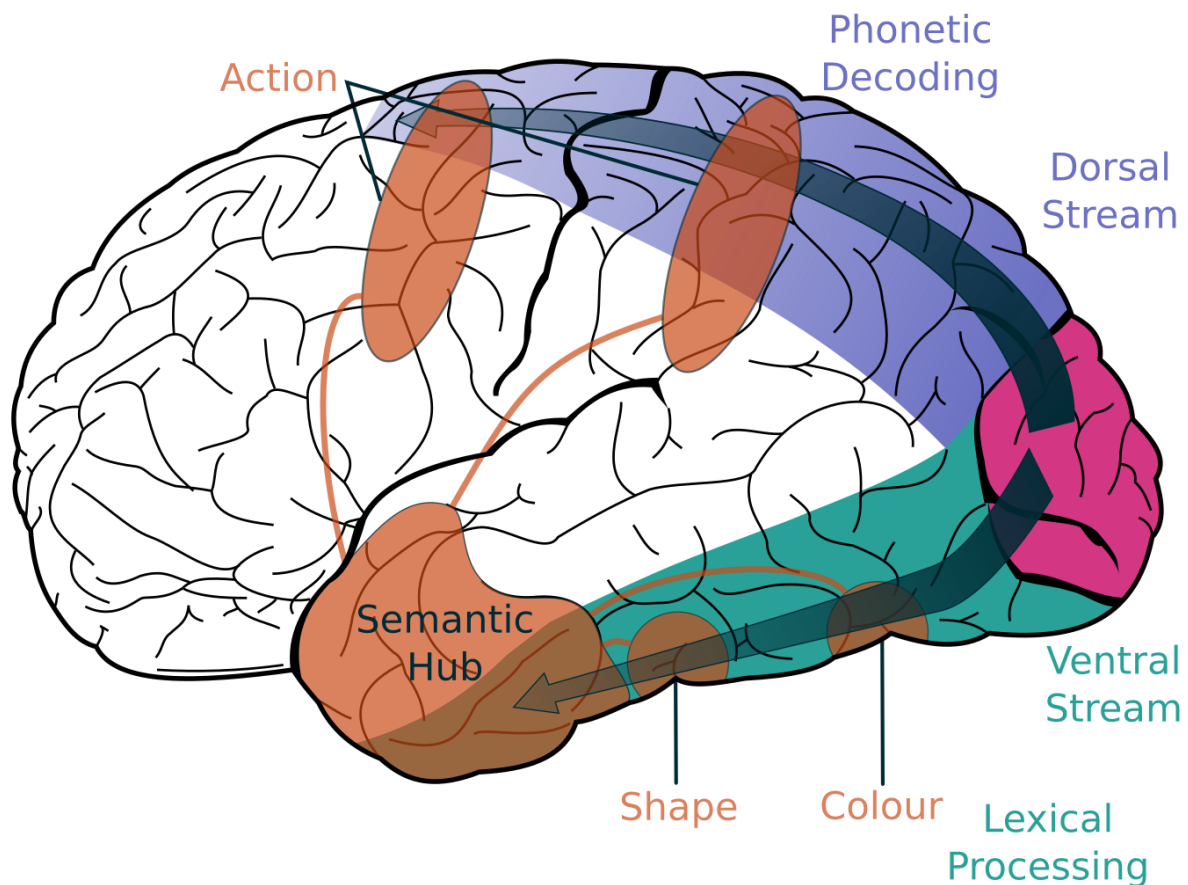


Figure 1.1. Sublexical phonetic decoding and lexical processing superimposed on the distributed-plus-hub architecture of semantic processing, showing the potential for shared processing between the action semantic and phonetic decoding processing, and between object semantic (shape and colour) and lexical processing, adapted from Borowsky et al. (2006) and Patterson et al. (2007). Background brain adapted from Gray (1918) illustration.

Thompson-Schill et al. (2006) proposed that semantics are processed in brain regions that are anterior to brain regions involved in perception (i.e., semantics are processed downstream from earlier perceptual processes). For example, colour semantic processing has been shown to occur just anterior to the colour perception area (V4) that has been well documented (e.g., Chao & Martin, 1999). Similarly, object shape semantic processing not related to action occurs in a region of the left fusiform gyrus (FuG) that has been shown to be activated by semantic tasks involving reading of food words (inanimate), but not tool and animal words (interactive/animate; Carota, Moseley, & Pulvermüller, 2012). This region has also been suggested to be an interface between orthographic and semantic processing through studies of lesion deficits, owing to its position just anterior to the visual word form area (Purcell, Shea, & Rapp, 2014). Processing in the ventral stream has been described as developing in a gradient from basic perceptual sensitivity to generic semantic sensitivity from posterior to anterior regions, respectively. This has been supported by research in word reading (Borghesani et al., 2016), semantic question tasks (Martin, Douglas, Newsome, Man, & Barense, 2018), and semantic ‘how’ tasks (“How do you interact with the object?”; Borowsky et al., 2005; Esopenko et al., 2012).

1.2 Two-stream Model of Visual Processing

Seminal primate lesion research by Ungerleider and Mishkin (1982) demonstrated that impaired object discrimination performance, which they labeled ‘what’ identification, was observed following inferior temporal cortex lesions, while impaired landmark discrimination performance, which they labeled ‘where’ identification, followed parietal cortex lesions. Goodale and Milner (1992) later proposed that the two visual processing streams should be described as the ‘what’ versus ‘how’ streams, with the ‘what’ stream processed ventrally (occipital-temporal-frontal) and the ‘how’ stream processed dorsally (occipital-parietal-frontal; Goodale & Milner, 1992). The ventral ‘what’ stream was described as being involved in object identification, while the dorsal ‘how’ stream was involved in object interaction. Goodale and Milner’s (1992) patient DF suffered lesions to the lateral occipital cortex, a part of the ventral processing stream, and consequently developed visual form agnosia. DF had impaired ventral ‘what’ identification processing, as illustrated by her acquired inability to process colour and visual information about an object, but she had intact dorsal ‘how’ interaction processing, and thus was able to interact with a presented object as the task required (e.g., correctly putting a card through a slot despite not being able to identify the orientation). The comorbidity of processing

impairments for various types of visual information in this ventral region indicates there may be collocation of processing for visual identity characteristics.

Neuroimaging evidence has also found support for a distinction between the ventral-what stream and the dorsal-how stream for word reading. It has been shown using positron emission tomography (PET) that words with more action-related semantic meaning (e.g., tools) are processed more in the dorsal stream than words with shape-related semantic meaning (e.g., animals; see Damasio et al., 1996; Damasio, Tranel, Grabowski, Adolphs, & Damasio, 2004). Using fMRI, Borowsky et al. (2005) presented participants with either words or pictures in one of eight locations around a central fixation point and asked them to report in terms of ‘what’ (name the stimulus; e.g., ‘jeans’), ‘where’ (cardinal location on screen; e.g., ‘northwest’), or ‘how’ (how to interact with the stimulus; e.g., ‘wear them’). The results revealed both shared and unique patterns of activation, with the ‘what’ task activating more of the ventral stream and the ‘where’ and ‘how’ tasks activating more of the dorsal stream, with ‘where’ processing occurring more in the posterior parietal areas and ‘how’ processing leading into the anterior frontal regions proximal to the motor cortex (Borowsky et al., 2005). This evidence from object ‘what’ and ‘where’/‘how’ tasks supported the dissociated ventral visual processing of object identification and dorsal visual processing for object location and interaction, while also showing similarly dissociated streams of activation for lexical and sublexical reading (described below, see Borowsky, Esopenko, Cummine, & Sarty, 2007). Esopenko et al. (2012) used the ‘how’ task in an fMRI study to provide evidence for embodiment of semantic processes utilizing the motor and sensory processes of the dorsal stream, whereby hand and foot objects produced activation near respective hand and foot motor and sensory regions. Ekstrand et al. (2017) showed converging behavioural evidence for this semantic processing near sensory cortex (most earlier studies focused on just motor cortex) in the dorsal stream, in a behavioural paradigm of vibratory sensory priming of the ‘how’ task.

1.3 Dual-route Reading Models and the Two-stream Model of Visual Processing

Dual-route models of reading (e.g., Coltheart, Rastle, Perry, & Langdon, 2001; Perry, Ziegler, & Zorzi, 2010) also describe two distinct pathways: the orthographic lexical pathway accesses the word meaning from the whole word visually, which then activates the appropriate phonology, while the phonetic decoding pathway converts letters to sounds (i.e., grapheme-to-phoneme conversion (GPC)) in order to pronounce the word and then access meaning (see also

Poeppel & Monahan, 2008 for a model of speech perception that is consistent with this dual-route model). Neuroimaging research has also shown preferential activation of the ventral-lexical stream during lexical processing of language through reading of exception words (words that cannot be sounded out to be read correctly; e.g., ‘yacht’; Borowsky et al., 2006; Borowsky et al., 2007; Cummine et al., 2013; Gould, Mickleborough, Ekstrand, Lorentz, & Borowsky, 2017), and of the dorsal-sublexical stream during phonological processing when reading pseudohomophones (PHs; non-words that must be sounded out in order to be read correctly; e.g., ‘yawt’). Highly familiar regular words (e.g., ‘boat’) have also been shown to activate predominantly the ventral-lexical stream, similar to exception word activation, because although regular words can be read both lexically and sublexically, highly familiar regular words tend to be automatically processed orthographically because of how frequently they are encountered in text (Cummine et al., 2013).

Current computational models of reading (e.g., Coltheart et al., 2001; Perry et al., 2007; Plaut, McClelland, Seidenberg, & Patterson, 1996) typically describe a semantic system connected to orthographic and phonological systems (the “orthographic lexical system” and “phonological lexical system” for dual-route models; see Figure 1.2). In these computational models, it is assumed that the type of semantic information does not influence the efficiency with which the information is sent and received from the semantic system for orthographic or phonological processing. Currently, these models assume that the orthographic and phonological lexicons should have fixed excitatory parameters for connections to the semantic system. However, neurological and clinical evidence suggest that there is a semantic hub integrating information from distributed sub-systems for processing different types of semantic information (Patterson et al., 2007). It may be that access to the semantic system is facilitated when a semantic sub-system is processed within the visual stream of reading being used (i.e., object and ventral-lexical; see Figure 1.1).

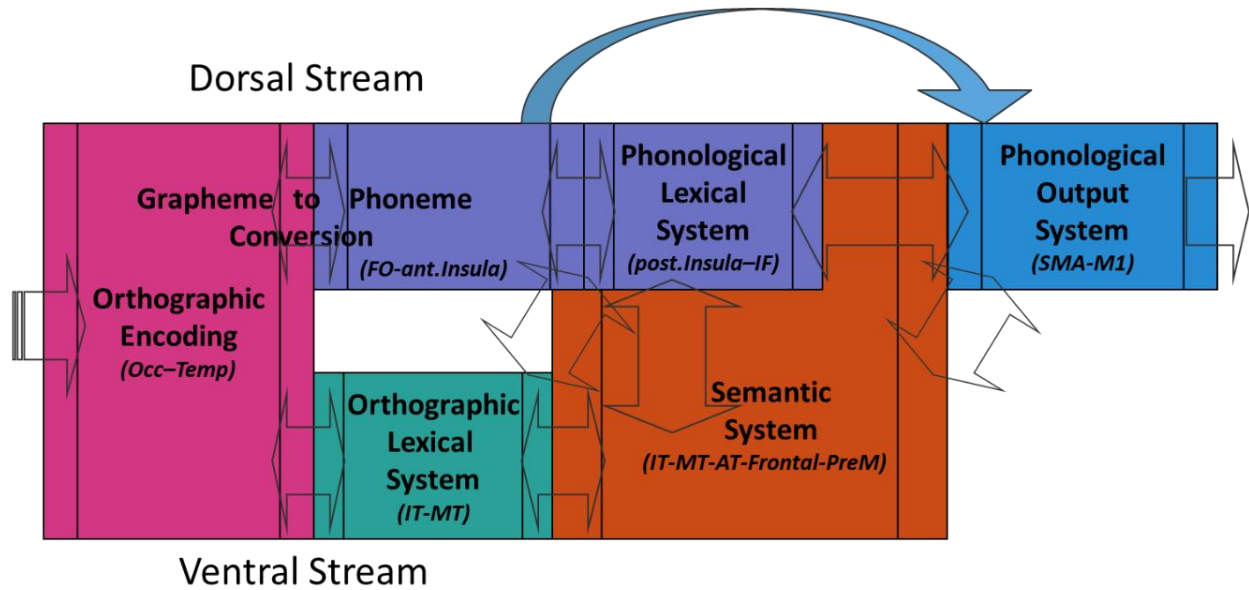


Figure 1.2. A dual-route model of reading, with the ‘Dorsal Stream’ route corresponding to sublexical phonetic decoding and the ‘Ventral Stream’ route corresponding to orthographic lexical processing (adapted from Borowsky et al., 2013; abbreviations: Occ-Temp: Occipito-Temporal; FO-ant. Insula: Fronto-Occipital, anterior Insula; IT-MT: Inferior-Temporal, Middle Temporal; post. Insula-IF: Posterior Insula, Inferior-Frontal; IT-MT-AT-Frontal-PreM: Inferior-Temporal, Middle Temporal, Anterior-Temporal, Frontal, Premotor area; SMA-M1: Supplementary Motor Area, Primary Motor Cortex). Colours are coded to correspond with those in Figure 1.1.

1.4 The Current Research

The current experiments seek to elucidate the behavioural relationship between reading and semantic processing using semantic priming of naming (Experiment 1) and lexical decision task (LDT) paradigms (Experiments 2 and 3). Specifically, reliance on lexical processing was assessed by using familiar words as targets. Prime words with either object related meanings (object primes; e.g., ‘canoe’) or action related meanings (action primes; e.g., ‘paddled’) were used to prime differential semantic sub-systems by instructing participants to imagine the objects for the former and the actions for the latter. Object primes were chosen to encourage reliance on the ventral stream, as their corresponding semantic sub-systems have been shown to be located more ventrally, and thus may result in shared-stream activation with the ventral-lexical stream of reading. Conversely, action primes were chosen to encourage reliance on the dorsal stream, as their corresponding semantic sub-systems have been shown to be located more dorsally. To further restrict processing to the ventral lexical stream, a second experiment had participants perform a lexical decision task with familiar words as targets and legal nonwords (NW) as foils

(Experiment 2). A third experiment restricted processing to the ventral lexical stream even further by using PH foils in an LDT, whereby the PH foils would cause participants to inhibit phonological and semantic processing in order to correctly respond to the word targets (Experiment 3; e.g., see Cummine, Aalto, Ostevik, Cheema, & Hodgetts, 2018 for a discussion of phonological inhibition in LDT with PH foils). Specifically, the LDT provides a way to more closely monitor orthographic lexical processing, particularly when the foils serve to eliminate reliance on other systems (i.e., PH foils preclude semantic or phonological reliance in the LDT, and sharpen the focus even more on what is happening within the orthographic lexical system).

Although various metrics have been used to measure semantic variables (e.g., associative strength, Canas, 1990; semantic density, Shaoul & Westbury, 2010; semantic distance, Mandera et al., 2016), separable dimensions of object versus action semantics have not been studied in this way before. Similar past research includes research on priming of noun and verb *targets*. For example, Kersten and Earles (2004) found that verb targets benefit more from semantic priming than noun targets. However, the current research focused on different types of *primes*, setting it apart from previous research focusing on types of *targets* (e.g., Kersten & Earles, 2004; Moss, Ostrin, Tyler, & Marslen-Wilson, 1995). Additionally, although all object primes were nouns and all action primes were verbs, the related primes were not just required to be associatively related, but also were required to be related in terms of being able to interact with the target using the action described, or for the object prime to be visually similar to the target. These requirements for the prime words, while maintaining a within-target design, set this research apart from previous studies and was developed to serve as a manipulation of the visual processing stream and the semantic relationship between the semantic prime and the target.

Using the same semantic priming lexical decision behavioural task described above (Experiment 3), Experiment 4 used fMRI to examine the hypothesis that the shared-stream priming effect could be localized to spatially-shared regions of the ventral-lexical visual processing stream. Experiment 5 used diffusion tensor imaging (DTI) to investigate whether the cerebellum may act as an additional object semantic subsystem in the semantic network based on fMRI results from Experiment 4.

1.4.1 Hypotheses

The neurobiologically-inspired distributed-plus-hub model leads to the following behavioural hypotheses regarding the underlying cognitive architecture. To the extent that word

target priming relies on modal object semantic processing that is shared with lexical reading, a two-way interaction was expected, whereby the size of priming effects would be commensurate (i.e., largest for shared prime-target streams). Considering that the semantic sub-systems for objects are thought to be located more ventrally, to the extent that they are shared with lexical word target processing, word target RTs may exhibit a larger priming effect with object primes than with action primes, particularly when task demands focus on orthographic lexical processing (i.e., LDT with PH foils). Conversely, to the extent that priming relied on the amodal semantic hub, the size of priming effects should be similar regardless of shared prime-target stream processing. For the neuroimaging analysis, we hypothesized that there should be regions in the ventral stream associated with colour semantics (just anterior to V4 in FuG) and shape semantics (anterior FuG) that would produce greater activation in contrasts between lexical word targets and the sublexical PH foils for object priming than action priming, owing to the ventral shared-stream processing for lexical and object semantic processing. Based on observed contrasts in the cerebellum we hypothesized that the structural connectivity DTI analysis would show robust structural connectivity between the cerebellum and semantic regions of the temporal lobe including the ATL semantic hub as a demonstration of the potential for the cerebellum to be integrated in the semantic network as an object semantic sub-system.

CHAPTER 2: Behavioural Semantic Priming of Reading and Lexical Decision

2.1 Experiment 1

2.1.1 Method

2.1.1.1 Participants

Twenty-four English first-language participants were recruited from the undergraduate psychology participant pool at the University of Saskatchewan. Of the 24 participants analyzed, 12 were female and 12 were male, with a mean age of 21.960 ($SEM = 1.587$, range 18 to 48). The participants' consent was obtained, and the experiment was performed in compliance with the relevant laws and institutional guidelines and was approved by the University of Saskatchewan Research Ethics Board (see Appendix A).

2.1.1.2 Apparatus and stimuli

Stimuli were presented using Eprime 2.0 (Psychology Software Tools, Pittsburgh, PA) on a 13-inch Compaq 7500 CRT monitor. White characters in 12-point Courier New font were presented against a black background, subtending a vertical visual angle of 1.0° , a minimum horizontal visual angle of 1.9° , and a maximum horizontal visual angle of 5.7° . Vocal RT was recorded using a microphone interfaced with the serial-response (SR) box. The participant began each prime-target trial by pressing the rightmost button on the SR box with their right hand index finger.

The stimuli were selected from datasets with ratings of imageability (the word's capacity to arouse a sensory experience such as a mental picture or sound, on a scale from 1-7; Cortese & Fugett, 2004), and body object interaction (BOI; the ease with which one can physically interact with a word's referent, on a scale from 1-7; Tillotson, Siakaluk, & Pexman, 2008). From these merged datasets of words, 60 stimuli rated highly on imageability and BOI were chosen that could be matched with believable object *and* action primes. Primes were selected from words with the closest possible semantic distance in the Snaut distributional semantics model, a computational prediction method applying the Continuous Bag of Words (CBOW) model to corpora of 385 million words from Open Subtitles (<http://opensubtitles.org>) and the UK Web Archiving Consortium (UKWAC; Ferraresi, Zanchetta, Baroni, & Bernardini, 2008), consisting

of 2 billion words (Mandera, Keuleers, & Brysbaert, 2016). See Appendix A for the list of target words with their associated object and action primes. The 58 stimuli included in the analysis were subjected to a paired-samples t-test to compare the semantic distance between the Object and Action prime groups, which did not produce a significant difference, $t(57) = -1.32, p = 0.19$.

2.1.1.3 Design

A 2 (Priming; Related vs. Unrelated) within-subject x 2 (Prime Type; Object vs. Action) within-subject experimental design was used. Participants completed 4 blocks of 60 prime-target reading trials, followed by a relatedness judgement of each of the prime-target related pairs on a 5-point scale. For the first 2 participants, the first 2 blocks were action primes and the last 2 blocks were object primes, and for the next 2 participants the first 2 blocks were object primes and the last 2 blocks were action primes. Each target was presented once in each block, and was presented with a related prime in one block of each prime type and an unrelated prime in the other block of each prime type. The order of related vs. unrelated primes was counterbalanced, with odd participants receiving one half of the targets with related primes first, and even participants receiving the other half of targets with related primes first. The relatedness proportion within each block was 50%, meaning half of all prime-target pairs in each block were related, while the other half were unrelated.

2.1.1.4 Procedure

After obtaining consent, participants were tested individually for 30 minutes in a quiet room for 1 course credit through the psychology undergraduate participant pool. For the object-priming blocks, the participants were instructed to imagine what the object prime word looked like, in terms of clearly visualizing it, and then name the target word. For the action-priming blocks, the participants were instructed to imagine performing the action depicted by the action prime word and then name the target word. On each trial, a white fixation cross (+) appeared at the center of the screen. When the participant pressed the rightmost button on the SR box the prime appeared for 300 ms, followed by an interstimulus interval (ISI) of 700 ms, and then an auditory beep was presented and the target appeared, resulting in a 1000 ms stimulus onset asynchrony (SOA). The 50% relatedness proportion combined with the relatively long SOA of 1000 ms were chosen so as to allow every opportunity for both automatic and controlled expectancy priming to operate. The target disappeared when the voice-key was triggered by the participant's response, at which point the experimenter entered whether the response was correct,

incorrect, or spoiled (if the voice-key was not triggered by the onset of speech; see Figure 2.1).

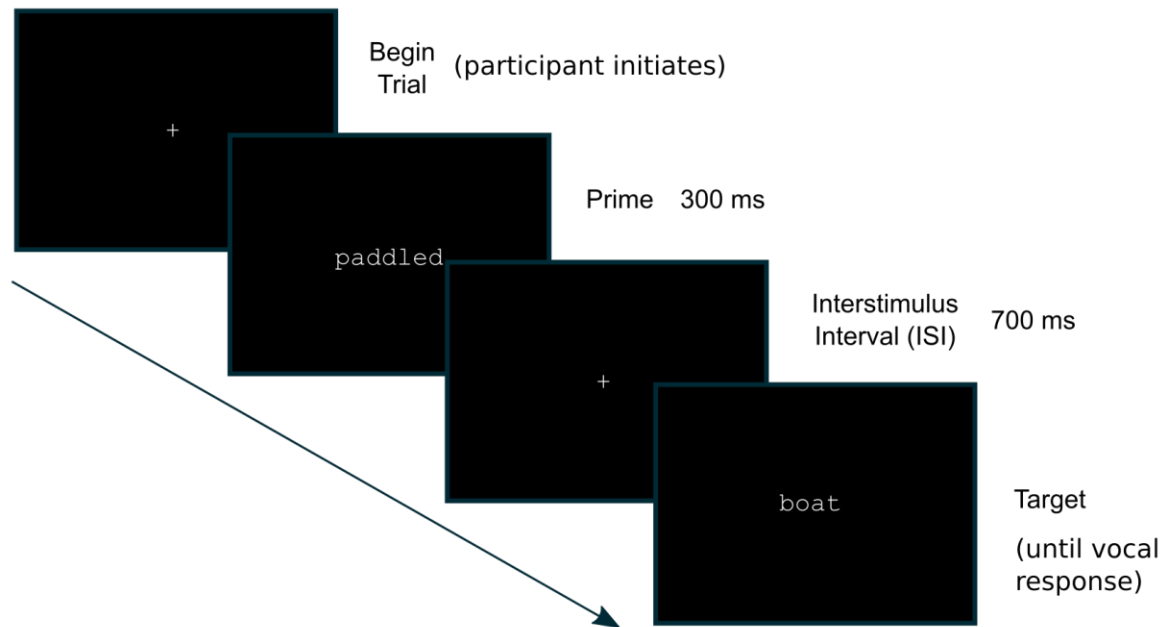


Figure 2.1. Example progression of an object prime, word target trial.

Participants named the word after reading a prime that required imagining either visualizing an object (to prime the ventral stream) or performing an action (to prime the dorsal stream). A blocked presentation of object and action primes was used in order to optimize consistent reliance on the particular visual stream. The prime was presented before each target and naming RT was recorded using a voice key trigger. Sixty target words were presented for each of the 4 blocks, matched with either one related or one unrelated action prime for each of the 2 action blocks, as well as one related or one unrelated object prime for each of the 2 object blocks. Following the 4 prime-target blocks, participants rated the related 60 action prime-target pairs and 60 object prime-target pairs on relatedness from 1 (very unrelated) to 5 (very related). The participants then received the debriefing form and an explanation of the experiment.

2.1.2 Results

The trial-level naming RT was analysed in a linear mixed model (LMM) and the trial-level errors were analysed in a general linear mixed model (GLMM) with a binomial distribution and logit link function. The LMM and GLMM analyses were performed using the *lmer* and the *glmer* functions respectively in the *lme4* package version 1.1.13 (Bates, Mächler, Bolker, &

Walker, 2015) in R version 3.4.2 (R Core Team, 2017). Priming (Related vs. Unrelated; within-subject) and Prime Type (Object vs. Action; within-subject) were modeled as fixed effects, plus the 2-way interaction, along with the counterbalancing order (Object prime blocks first vs Action prime blocks first; between-subject) and the corresponding relevant interactions with Prime Type and with Priming x Prime Type. For the initial model, random intercepts for items and subjects were included, and fixed effects factors of Prime Type and Priming plus the two-way interaction were included as random slopes for items and subjects (when the factor was a within-subjects manipulation). The likelihood-ratio test (LRT) criterion was then used with $\alpha = .20$ in a backward-selection heuristic to obtain a parsimonious model for the RT analyses as recommended by Matuschek, Kliegl, Vasishth, Baayen, and Bates (2017). After removing random slopes with the least variance until the model converged, either this converging model was selected or a more parsimonious model passing the LRT criterion was selected. Linear mixed models do not produce precise degrees of freedom, so a t ratio of 2 was used as the criterion for significance (see Baayen, Davidson, & Bates, 2008). Reaction time was the primary dependent variable of interest, while error rate (ER) was included as an additional analysis to determine whether any significant speed-accuracy trade-offs occurred. Trials with RTs greater than 3 standard deviations from the mean of the Stimulus Type were discarded from analysis in order to deal with the positively skewed distribution of the RT data (1.3% of trials). The items ‘boot’ and ‘teeth’ were removed from the analysis due to a high occurrence of errors for the PH pronunciation of ‘bute’ across many participants, and a high proportion of spoils where the microphone did not detect the onset of speech for ‘teeth’. The figure means presented are partial means, with the effects of Counterbalance and its interactions partialled out, using the *remef* function provided in the R *remef* package (Hohenstein & Kliegl, 2015).

2.1.2.1 Reaction time

A Priming main effect was observed whereby unrelated primes produced slower target naming RTs than related primes, *Estimate* = 11.627, *SE* = 5.406, *t* = 2.151. A main effect of Prime Type was observed whereby object primes produced faster target naming than action primes, *Estimate* = -31.316, *SE* = 10.059, *t* = -3.113. A Prime Type x Counterbalance interaction was observed whereby object primes resulted in slower target naming for those participants who received the object prime blocks first, *Estimate* = 47.055, *SE* = 14.218, *t* = 3.310. All other main

effects and interactions were not significant at the $t > 2.0$ cut-off (see Table 2.1)^{1,2}. See Figure 2.2 for partial effects means produced by the *remef* package in R (Hohenstein & Kliegl, 2015) and 95% confidence intervals from the Priming x Prime Type interaction of the LMM analysis (this method of showing confidence intervals for partialled mean figures of LMM analysis is a novel approach first applied in Neudorf, Ekstrand, Kress, Neufeldt, & Borowsky, 2019). The partial effects means have been used in recent research to more clearly show the statistical effects, which can make interpretation more straightforward (e.g., Hohenstein, Matuschek, & Kliegl, 2017).

Table 2.1. Linear Mixed Model for Experiment 1 RTs with variances and standard deviations for random effects and estimates of coefficients, standard errors and t ratios for fixed effects.

Random effects	RT	
	Variance	SD
Items		
Intercept	347.533	18.642
Subjects		
Intercept	4970.548	70.502
Priming	179.068	13.382
Prime Type	1043.848	32.309
Prime Type x Priming	192.707	13.882
Residual	4768.801	69.057

¹ To address concerns about the inclusion of the same targets in all four blocks, an extra factor of Block (1, 2, 3, or 4) was included in an additional model. The effect of Block was not significant, *Estimate* = -3.854, *SE* = 4.530, $t = -0.851$, while Priming was significant with block included in the model, *Estimate* = 11.566, *SE* = 3.741, $t = 3.091$, demonstrating that Priming accounted for variance over and above across-block repetition priming.

² In order to verify that subject level differences in subjective ratings of relatedness between the Object and Action Prime-Target pairs were not biasing the Priming effect towards either the Object or Action primes, an additional model was run with the ratings used in place of the dichotomous Priming factor, where Unrelated was given a value of 0, and Related pairs were assigned a value from 1 to 5 based on the relatedness rating given by the participant, for a continuous measure of prime-target relatedness. With this variable in place of the dichotomous Priming factor, the same pattern of effects was observed, except that the Prime Type x Counterbalance interaction was not significant, *Estimate* = 30.229, *SE* = 18.500, $t = 1.634$.

Fixed Effects	Estimate	Std. Error	t-value
Intercept	543.903	20.671	26.312
Priming (Unrelated-Related)	11.627	5.406	*2.151
Prime Type (Object-Action)	-31.316	10.059	*-3.113
Priming x Prime Type	3.863	6.679	0.578
Counterbalance (Object 1 st -Action 1 st)	-53.150	29.025	-1.831
Prime Type x Counterbalance	47.055	14.218	*3.310
Priming x Prime Type x Counterbalance	-6.438	5.756	-1.118

*Asterisks denote significant fixed effects ($t > 2.00$).

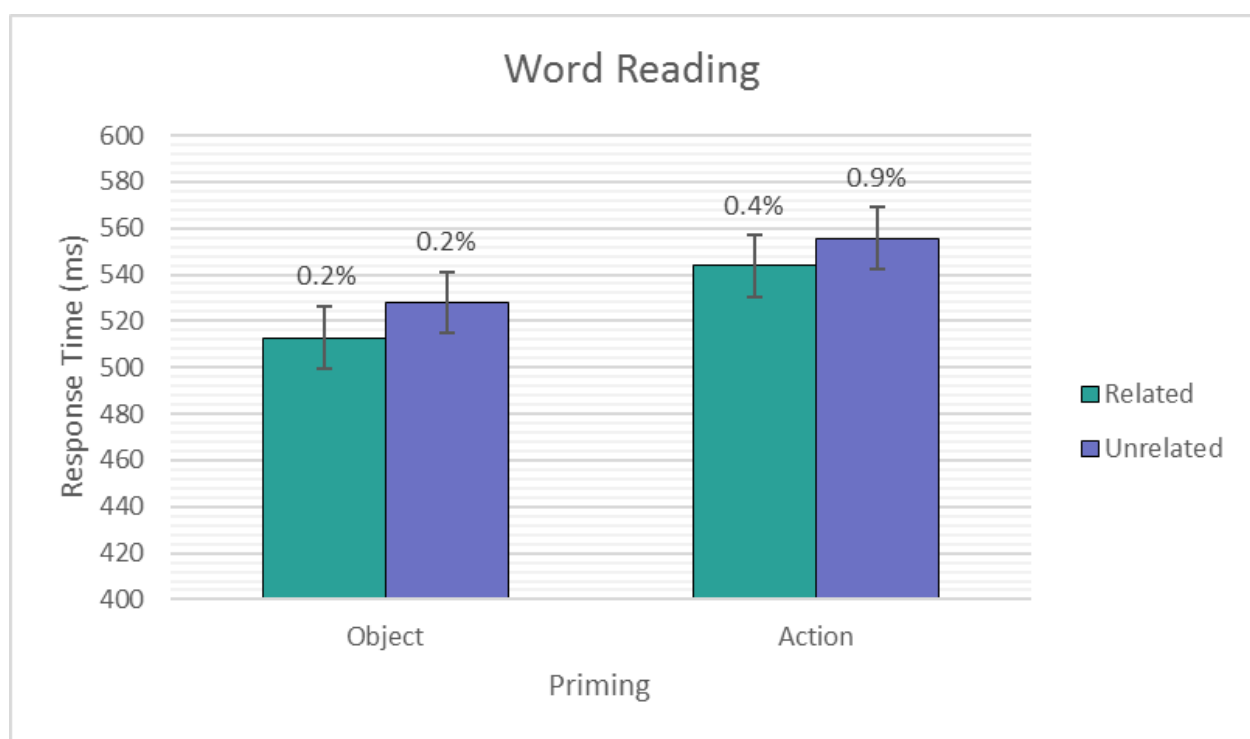


Figure 2.2. Experiment 1 partial mean target naming RTs (with partial mean ERs above each) for targets as a function of Priming and Prime Type for the LMM analysis. Error bars represent 95% confidence intervals of the repeated measures Priming x Prime Type interaction for the LMM analysis.

2.1.2.2 Error rate

Although most of the previous literature involving LMM analyses of word identification data have not included analyses of error rates, a GLMM using the binomial distribution is presented here as an appropriate method of analyses. No significant effects were observed at the $z > 2.0$ cut-off, with no evidence for speed accuracy trade-offs (see Table 2.2). See Figure 2.2 for

partial mean ERs.

Table 2.2. Experiment 1 ERs on targets analyzed in a General Linear Mixed Model using Binomial distribution and logit link with variances and standard deviations for random effects and odds ratio (OR) estimates of coefficients, standard errors of the estimates and *z* ratios for fixed effects.

Random effects	Errors		
	Variance	SD	
Items			
Intercept	1.390	1.179	
Priming	1.597	1.264	
Prime Type	0.960	0.980	
Subjects			
Intercept	2.571	1.604	
Fixed Effects	Estimate (OR)	Std. Error	<i>z</i> -value
Intercept	0.001	0.001	-6.448
Priming (Unrelated/Related)	1.866	2.224	0.523
Prime Type (Object/Action)	0.205	0.272	-1.195
Priming x Prime Type	0.608	0.901	-0.335
Counterbalance (Object 1 st /Action 1 st)	1.890	2.121	0.567
Prime Type x Counterbalance	0.722	0.946	-0.249
Priming x Prime Type x Counterbalance	4.043	5.549	1.018

*Asterisks denote significant fixed effects ($z > 2.00$).

2.1.2.3 Discussion

The semantic priming paradigm produced an RT advantage for word target naming with related primes relative to unrelated primes. A Prime Type advantage was observed in Experiment 1 for word naming RT, whereby words were named faster in the context of object prime blocks, but note that such main effects are not diagnostic of shared-stream effects in and of themselves. This object prime block advantage suggests that participants may have entered into an easier response set for visualizing prime words than for imagining action words. For example, it may be faster to imagine a canoe than it is to imagine someone paddling a canoe. There was a Prime Type x Counterbalance interaction, owing to practice effects, whereby participants who received object blocks first would be more practiced in naming the targets for the later action blocks,

leading to faster target naming for action primes when the object blocks were presented first. The expected shared-stream priming advantage (i.e., an interaction between Priming and Prime Type whereby Object primes produce a greater priming effect than Action primes) was not observed with this word naming task. The ER analysis did not indicate that there were any speed accuracy trade-offs.

2.2 Experiment 2

Experiment 1 provided a demonstration of equivalent priming effects for object and action primes with word naming targets, so a second experiment was conducted using a LDT on the word targets, with NW foils, to restrict processing more so to the ventral lexical stream. This enhanced reliance on the ventral lexical stream was expected to produce a stronger priming effect with object primes than with action primes, due to the ventrally located semantic system for visual object processing, compared to the more dorsally located semantic system for action semantic processing.

2.2.1 Method

2.2.1.1 Participants

Twenty-four English first-language participants were recruited from the undergraduate psychology participant pool at the University of Saskatchewan. Of the 24 participants analyzed, 20 were female and 4 were male, with a mean age of 19.375 ($SEM = .287$, range 17 to 22).

2.2.1.2 Apparatus, stimuli, design, and procedure

The methods for Experiment 2 were identical to that of Experiment 1, except that the task was changed from a naming task to a LDT. When the target letterstring appeared, participants were to respond by pressing the rightmost button on the SR box if the target was a word (e.g., “boat”), or by pressing the leftmost button on the SR box if the target was a NW (e.g., “boit”). Nonwords were matched to the word targets and created by changing a single letter from the real word counterpart (see Appendix A for a list of NWs used). Only RTs from the correctly answered word targets were analysed. With the addition of the NW foils, 120 trials (60 NW foils and 60 word targets) were completed in each block, but only correct responses to the 60 word targets were analysed. See Figure 2.3 for examples of the word target and NW foil trial progressions.

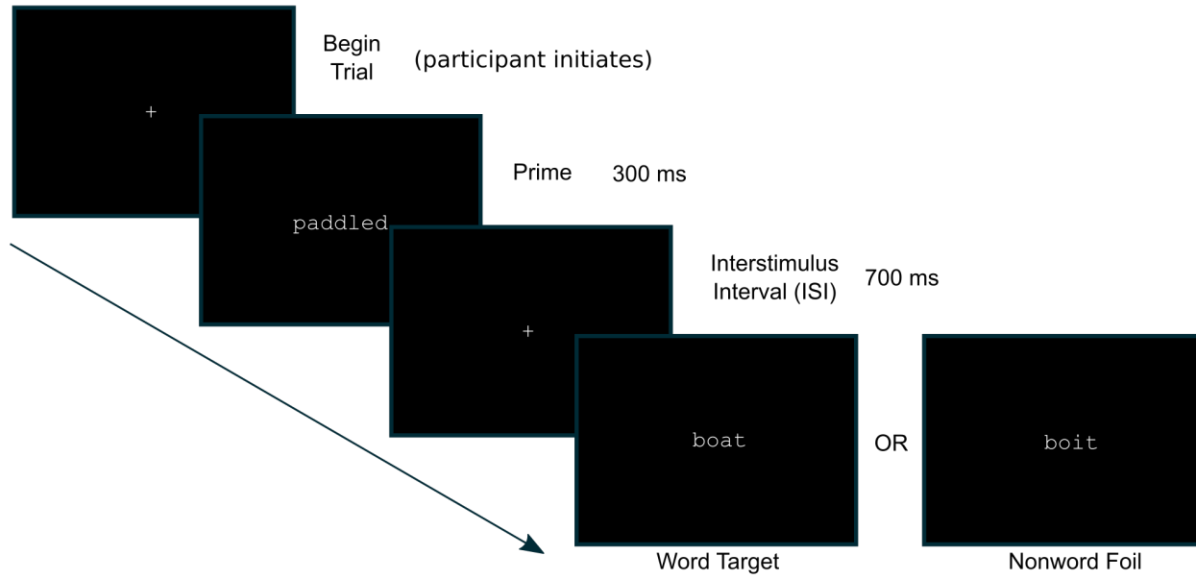


Figure 2.3. Example progression of an object prime, word target trial and an object prime, NW foil trial.

2.2.2 Results

The same procedure was used as in Experiment 1 to analyze the trial-level LDT RT data in an LMM and the trial-level errors in a GLMM with a binomial distribution and logit link function. Trials with RTs greater than 3 standard deviations from the mean of the Stimulus Type cell were discarded from analysis in order to deal with the positively skewed distribution of the RT data (1.8% of trials).

2.2.2.1 Reaction time

The only significant effect observed was that of a Prime Type x Counterbalance interaction, $Estimate = 58.870$, $SE = 21.740$, $t = 2.708$. A secondary analysis without the Priming x Prime Type x Counterbalance interaction was conducted, which produced a significant priming effect, $Estimate = 36.656$, $SE = 9.914$, $t = 3.697$, while diminishing the estimate for the Priming x Prime Type interaction, $Estimate = -1.601$, $SE = 7.353$, $t = -0.218$, down from the first model, $Estimate = 14.834$, $SE = 10.435$, $t = 1.422$. This difference between the models suggests that the Priming effect is qualified by an emerging Priming x Prime Type interaction, and that this Priming x Prime Type interaction relies on the presence of the Priming x Prime Type x Counterbalance interaction in the model. All other main effects and interactions were not significant at the $t > 2.0$ cut-off (see Table 2.3). See Figure 2.4 for partial means and confidence intervals from the LMM.

Table 2.3. Linear Mixed Model for Experiment 2 RTs with variances and standard deviations for random effects and estimates of coefficients, standard errors and *t* ratios for fixed effects.

Random effects	RT		
	Variance	SD	
Items			
Intercept	737.170	27.151	
Subjects			
Intercept	3685.587	60.709	
Priming	1654.027	40.670	
Prime Type	2200.917	46.914	
Residual	17410.551	131.949	
Fixed Effects	Estimate	Std. Error	t-value
Intercept	544.689	18.605	29.277
Priming (Unrelated-Related)	20.768	13.830	1.502
Prime Type (Object-Action)	-27.282	15.371	-1.775
Priming x Prime Type	14.834	10.435	1.422
Counterbalance (Object 1 st -Action 1 st)	-49.304	25.822	-1.909
Prime Type x Counterbalance	58.870	21.740	*2.708
Priming x Prime Type x Counterbalance	-0.877	19.627	-0.045

*Asterisks denote significant fixed effects ($t > 2.00$).

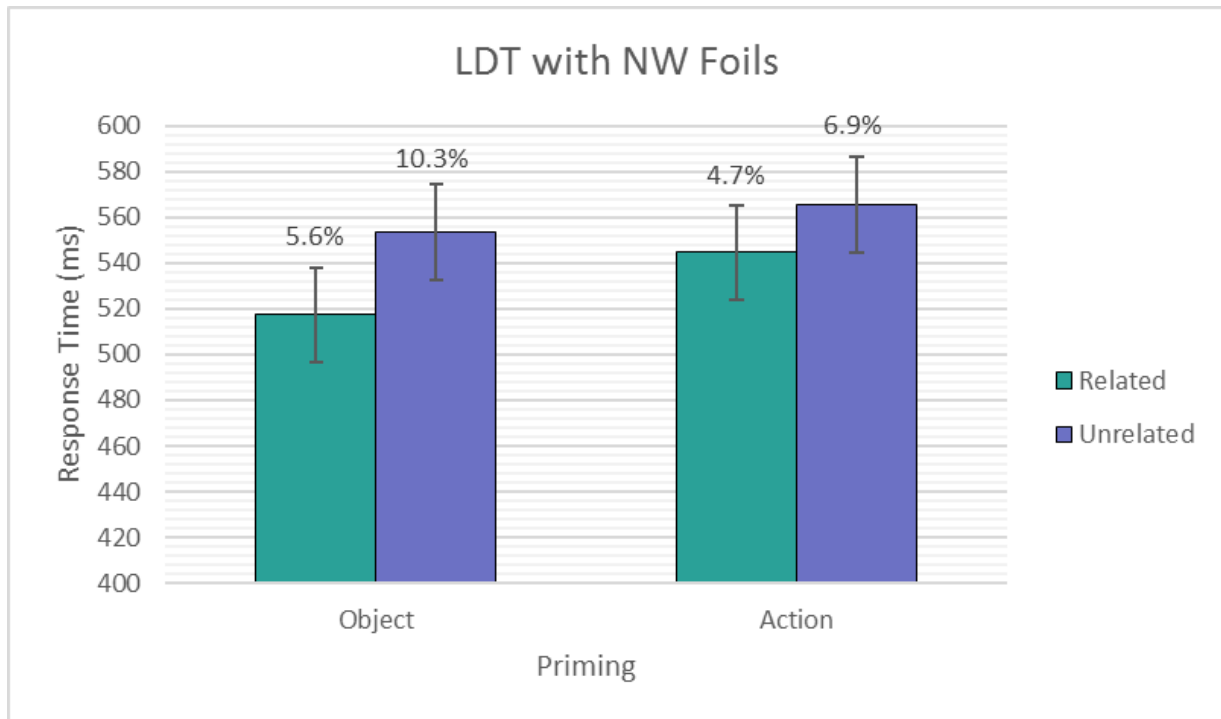


Figure 2.4. Experiment 2 partial mean word target LDT RTs (with partial mean ERs above each) as a function of Prime Type and Priming for the LMM analysis. Error bars represent 95% confidence intervals of the repeated measures Priming x Prime Type interactions for LMM analysis.

2.2.2.2 Error rate

See Figure 2.4 for partial mean ER. A Priming x Prime Type x Counterbalance interaction was observed whereby unrelated object primes produced more errors for those participants who received the object prime blocks first, $OR\ Estimate = 0.615$, $SE = 0.215$, $z = -2.254$. All other interactions and main effects were not significant at the $z > 2.0$ cut-off, with no evidence for speed accuracy trade-offs (see Table 2.4).

Table 2.4. Experiment 2 ERs on word targets analyzed in a General Linear Mixed Model using Binomial distribution and logit link with variances and standard deviations for random effects and odds ratio (OR) estimates of coefficients, standard errors of the estimates and z ratios for fixed effects.

Random effects	Errors		
	Variance		SD
Items			
Intercept	0.190		0.436
Subjects			
Intercept	1.051		1.025
Fixed Effects	Estimate (OR)	Std. Error	z-value
Intercept	0.032	0.331	-10.355
Priming (Unrelated/Related)	1.350	0.169	1.782
Prime Type (Object/Action)	1.166	0.173	0.888
Priming x Prime Type	1.325	0.227	1.242
Counterbalance (Object 1 st /Action 1 st)	1.161	0.458	0.326
Prime Type x Counterbalance	0.978	0.235	-0.096
Priming x Prime Type x Counterbalance	0.615	0.215	*-2.254

*Asterisks denote significant fixed effects ($z > 2.00$).

2.2.3 Discussion

Responses to the LDT with NW foils in Experiment 2 did not demonstrate the Prime Type advantage for object primes seen for naming, nor a clear priming effect. The lack of a Priming effect is likely qualified by the emerging Priming x Prime Type interaction, and will be explored in a further analysis combining Experiments 2 and 3. Effects related to the Counterbalance were the same as seen in Experiment 1, with Prime Type interacting with Counterbalance order. The ER analysis did not provide evidence for any speed accuracy trade-offs. In order to clarify the results seen for LDT with NW foils, and further constrain the task demands to focus on orthographic lexical processing, a second LDT experiment with PH foils was conducted, and then a combined analysis of Experiments 2 and 3 presented.

2.3 Experiment 3

In order to see if a differential priming effect between object and action primes, as expected by the shared-stream priming hypothesis, could be demonstrated as a statistical two-way interaction of Priming x Prime Type, a third experiment was conducted identical to Experiment 2 except that the foils used were PHs (e.g., “bote” matched to “boat”) rather than NWs (see Appendix A for a list of PHs used).

2.3.1 Method

2.3.1.1 Participants

Twenty-four English first-language participants were recruited from the undergraduate psychology participant pool at the University of Saskatchewan. Of the 24 participants analyzed, 21 were female and 3 were male, with a mean age of 23.167 ($SEM = .758$, range 18 to 30).

2.3.1.2 Apparatus, stimuli, design, and procedure

As in Experiment 2, only correct responses to word targets were analysed. PH foils were used in order to constrain the LDT task demands to focus on orthographic lexical processing, as the matched PHs would activate the same phonological and, through the phonological lexical system, semantic representations of the target words. Successful responses to foils and targets would require inhibition of phonology and semantics, therefore isolating processing even more so to the ventral orthographic lexical stream. See Figure 2.5 for examples of the word target and PH foil trial progressions.

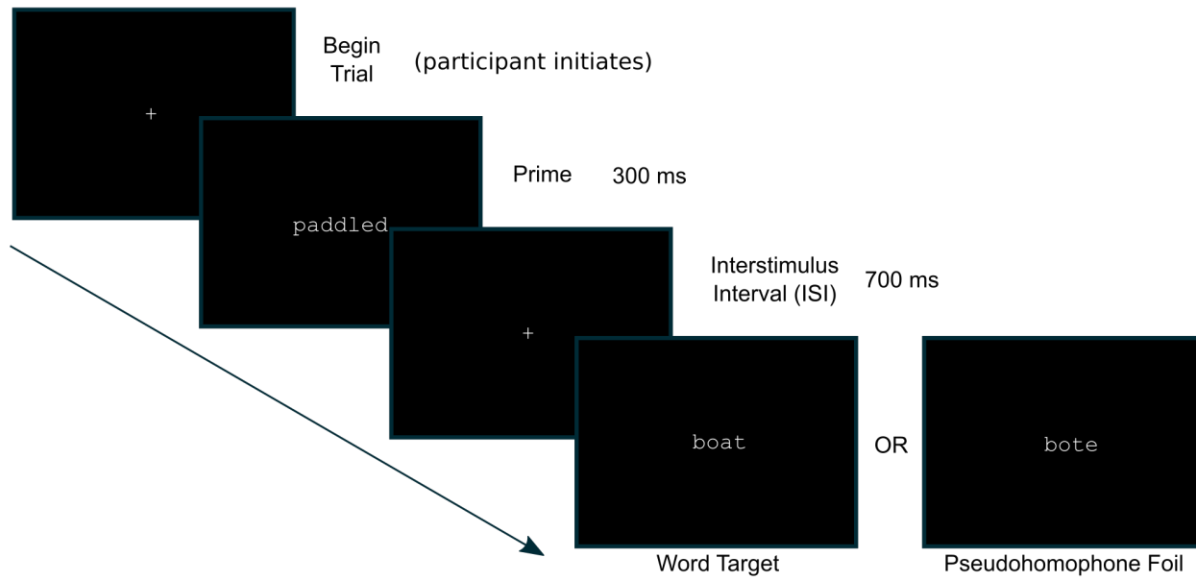


Figure 2.5. Example progression of an object prime, word target trial and an object prime, PH foil trial.

2.3.2 Results

2.3.2.1 Reaction time

A main effect of Prime Type was observed whereby object primes produced faster target naming than action primes, $Estimate = -41.021$, $SE = 11.238$, $t = -3.650$. A Priming x Prime Type interaction was observed whereby object primes produced more of a Priming effect than action primes, $Estimate = 22.598$, $SE = 10.520$, $t = 2.148$. A Prime Type x Counterbalance interaction was observed whereby object primes resulted in slower target responses for those participants who received the object prime blocks first, $Estimate = 69.227$, $SE = 15.921$, $t = 4.348$. All other main effects and interactions were not significant at the $t > 2.0$ cut-off (see Table 2.5)^{3,4}. See Figure 2.6 for partial means and confidence intervals from the LMM.

³ To address a reviewer's concern about the inclusion of the same targets in all four blocks, an extra factor of Block (1, 2, 3, or 4) was included in an additional model. The effect of Block was significant, $Estimate = -14.951$, $SE = 3.715$, $t = -4.024$, and the Priming x Prime Type interaction was also significant with block included in the model, $Estimate = 22.960$, $SE = 10.878$, $t = 2.111$, demonstrating that the Priming x Prime Type interaction accounted for variance over and above across-block repetition priming.

⁴ In order to verify that subject level differences in subjective ratings of relatedness between the Object and Action Prime-Target pairs were not biasing the Priming effect towards either the Object or Action primes, an additional model was run with the ratings used in place of the dichotomous Priming factor, where Unrelated was given a value of 0, and Related pairs were assigned a value from 1 to 5 based on the relatedness rating given by the participant, for a continuous measure of prime-target relatedness. With this variable in place of the dichotomous Priming factor, the same pattern of effects was observed, except that the Prime Type effect was not significant, $Estimate = -19.182$, $SE = 11.036$, $t = -1.738$.

Table 2.5. Linear Mixed Model for Experiment 3 RTs with variances and standard deviations for random effects and estimates of coefficients, standard errors and *t* ratios for fixed effects.

Random effects	RT		
	Variance		SD
Items			
Intercept	272.135		16.497
Subjects			
Intercept	3599.366		59.995
Prime Type	848.315		29.126
Residual			
	17904.441		133.807
Fixed Effects	Estimate	Std. Error	t-value
Intercept	508.904	18.230	27.916
Priming (Unrelated-Related)	0.103	7.416	0.014
Prime Type (Object-Action)	-41.021	11.238	*-3.650
Priming x Prime Type	22.598	10.520	*2.148
Counterbalance (Object 1 st -Action 1 st)	-20.919	25.604	-0.817
Prime Type x Counterbalance	69.227	15.921	*4.348
Priming x Prime Type x Counterbalance	-16.047	10.582	-1.516

*Asterisks denote significant fixed effects ($t > 2.00$).

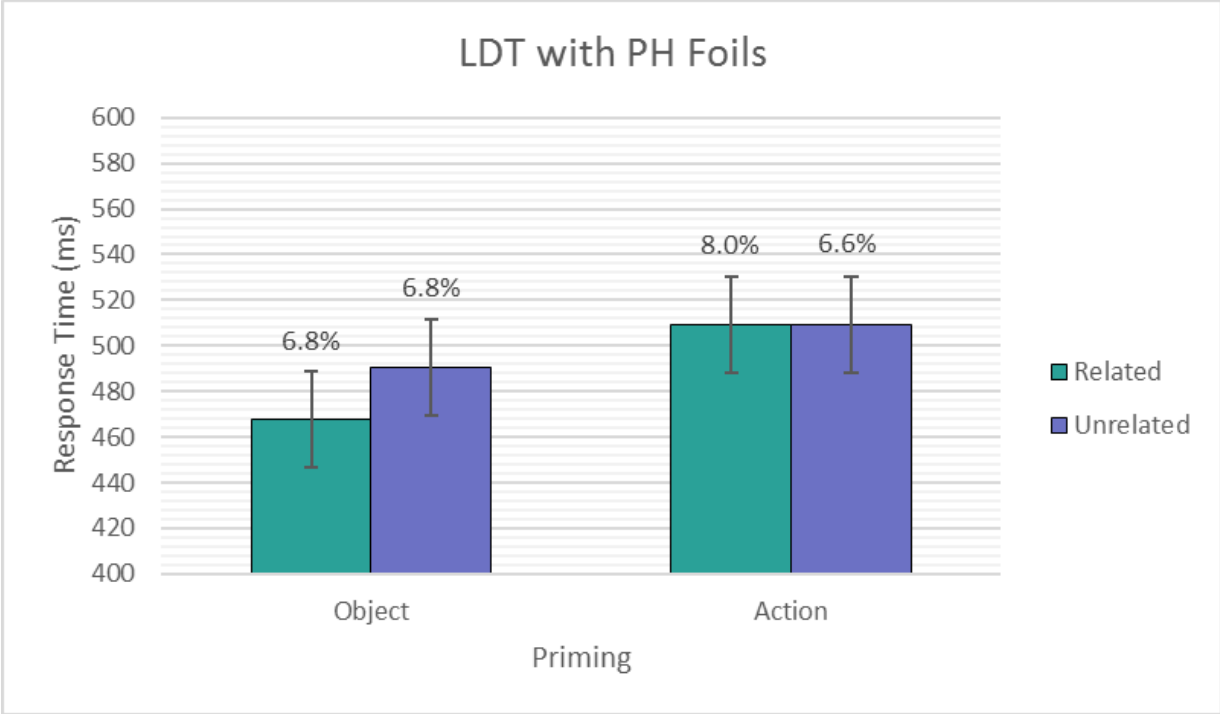


Figure 2.6. Experiment 3 partial mean word target LDT RTs (with partial mean ERs above each) for word targets as a function of Prime Type and Priming for the LMM analysis. Error bars represent 95% confidence intervals of the repeated measures Priming x Prime Type interactions for LMM analysis.

2.3.2.2 Error rate.

All main effects and interactions were not significant at the $z > 2.0$ cut-off, with no evidence for speed accuracy trade-offs (see Table 2.6). See the data labels in Figure 2.6 for partial mean ERs.

Table 2.6. Experiment 3 ERs on word targets analyzed in a General Linear Mixed Model using Binomial distribution and logit link with variances and standard deviations for random effects and odds ratio (OR) estimates of coefficients, standard errors of the estimates and z ratios for fixed effects.

Random effects	Errors	
	Variance	SD
Items		
Intercept	0.255	0.505
Subjects		
Intercept	0.559	0.748

Fixed Effects	Estimate (OR)	Std. Error	z-value
Intercept	0.067	0.248	-10.916
Priming (Unrelated/Related)	0.824	0.146	-1.323
Prime Type (Object/Action)	0.764	0.149	-1.816
Priming x Prime Type	1.305	0.212	1.255
Counterbalance (Object 1 st /Action 1 st)	1.287	0.335	0.752
Prime Type x Counterbalance	1.169	0.195	0.802
Priming x Prime Type x Counterbalance	0.914	0.201	-0.448

*Asterisks denote significant fixed effects ($z > 2.00$).

2.3.3 Discussion

Responses to the LDT with PH foils in Experiment 3 demonstrated the Prime Type advantage for object primes seen for naming, as well as a differential priming effect, with a larger Priming effect for object primes, consistent with the hypothesis based on shared-stream processing. Effects related to the Counterbalance were the same as seen in Experiment 1, whereby Prime Type interacted with Counterbalance order. The ER analysis provided no evidence for any speed accuracy trade-offs.

2.4 Experiments 2 & 3 – LDT Analysis

A combined analysis was performed with RT data from Experiments 2 and 3, with factors of Priming, Prime Type, and Foil Type (NW vs. PH), plus Counterbalance and its interactions with effects and interactions including Prime Type. This analysis produced no significant main effects or interactions including the factor of Foil Type, so a LRT was used with $\alpha = .20$ between this model and the same model with Foil Type and its interactions removed, which provided no justification for leaving Foil Type in the model, $\chi^2(12) = 12.271, p = .424$.

2.4.1 Results

2.4.1.1 Reaction time

A main effect of Prime Type was observed whereby object primes produced faster target naming than action primes, *Estimate* = -34.494, *SE* = 9.515, *t* = -3.625. A Priming x Prime Type interaction was observed whereby object primes produced more of a Priming effect than action primes, *Estimate* = 19.861, *SE* = 7.630, *t* = 2.603. A Prime Type x Counterbalance interaction was observed whereby object primes resulted in slower target responses for those participants

who received the object prime blocks first, $Estimate = 65.232$, $SE = 13.458$, $t = 4.847$. All other main effects and interactions were not significant at the $t > 2.0$ cut-off (see Table 2.7)^{5,6}.

Table 2.7. Linear Mixed Model for Experiment 2 and 3 RTs with variances and standard deviations for random effects and estimates of coefficients, standard errors and t ratios for fixed effects.

Random effects	RT		
	Variance		SD
Items			
Intercept	456.272		21.361
Subjects			
Intercept	3933.739		62.720
Priming	992.963		31.511
Prime Type	1485.514		38.542
Residual	17865.944		133.664
Fixed Effects	Estimate	Std. Error	t-value
Intercept	526.776	13.617	38.685
Priming (Unrelated-Related)	10.311	8.295	1.243
Prime Type (Object-Action)	-34.494	9.515	*-3.625
Priming x Prime Type	19.861	7.630	*2.603
Counterbalance (Object 1 st -Action 1 st)	-35.805	18.873	-1.897
Prime Type x Counterbalance	65.232	13.458	*4.847
Priming x Prime Type x Counterbalance	-9.175	11.894	-0.771

*Asterisks denote significant fixed effects ($t > 2.00$).

⁵ To address concerns about the inclusion of the same targets in all four blocks, an extra factor of Block (1, 2, 3, or 4) was included in an additional model. The effect of Block was significant, $Estimate = -15.771$, $SE = 3.598$, $t = -4.383$, and the Priming x Prime Type interaction was also significant with block included in the model, $Estimate = 19.414$, $SE = 7.582$, $t = 2.561$, demonstrating that the Priming x Prime Type interaction accounted for variance over and above across-block repetition priming.

⁶ In order to verify that subject level differences in subjective ratings of relatedness between the Object and Action Prime-Target pairs were not biasing the Priming effect towards either the Object or Action primes, an additional model was run with the ratings used in place of the dichotomous Priming factor, where Unrelated was given a value of 0, and Related pairs were assigned a value from 1 to 5 based on the relatedness rating given by the participant, for a continuous measure of prime-target relatedness. With this variable in place of the dichotomous Priming factor, the same pattern of effects was observed, except that the Prime Type effect was not significant, $Estimate = -15.563$, $SE = 9.536$, $t = -1.632$.

2.4.2 Discussion

Analyses of RTs from the LDT Experiments in Experiments 2 and 3 demonstrated the Prime Type advantage for object primes seen for naming, as well as a differential priming effect, with a larger Priming effect for object primes, consistent with the hypothesis based on shared-stream processing. Foil Type did not account for a significant amount of additional variance in the model, suggesting that the Priming x Prime Type interaction was significant when averaging over the Foil Type used. Effects related to the Counterbalance were the same as seen in Experiment 1, whereby Prime Type interacted with Counterbalance order.

2.5 Discussion

These experiments explored the degree of shared-stream Priming advantages in reading and lexical decision, such that word targets would exhibit more of a priming effect when primed by imagined objects than when primed by imagined actions. Words showed an object priming advantage in Experiment 3 for the LDT in the presence of PH foils, and in a combined analysis of Experiments 2 and 3 for the LDT of both foil types, whereby the LDT produced more of a priming effect with object primes than action primes, supporting the theory that there are semantic sub-systems of visual object form shared with the ventral-lexical processing stream. In Experiment 1, word reading showed faster RTs in the object prime blocks, but there were similar sized Priming effects for both object and action priming, supporting the notion that there is no shared-stream priming advantage in the naming task. The combined analysis of Experiments 2 and 3 suggests that the LDT experiments demonstrated greater shared-stream priming effects than simply reading words aloud (Experiment 1), but based on the findings from Experiment 2 and Experiment 3 separately, PH foils do a better job of constraining access to the ventral lexical stream than NW foils, given that the two-way interaction was observed for Experiment 3 but not for Experiment 2. The systematic manipulation of experiments demonstrated no significant difference in priming effects between object and action primes for word naming (Experiment 1) and lexical decision in the presence of NW foils (Experiment 2). Only for lexical decision in the presence of PH foils (Experiment 3) did we observe the pattern of object priming with no observable action priming. This systematic experimentation demonstrates that in general the object primes and action primes do equally well at priming the targets, but only in the case of highly constrained lexical activation for lexical decision of words in the presence PH foils (Experiment 3) did we observe the hypothesized interaction, whereby priming was observed for

object primes but not for action primes. This interaction represents clear support of the hypothesis based on shared streams of activation for object semantic priming and lexical processing in the ventral-lexical stream.

2.5.1 Distributed-Plus-Hub Model of the Semantic System

The comparable size of the Priming effect observed for object and action primes for word naming is consistent with the distributed-plus-hub model of the semantic system, which proposes that the distributed modality-specific sub-systems are integrated into an amodal hub in the ATL in order to process semantic information (Patterson et al., 2007). In this case, in the absence of sufficient shared-stream activation between a specific sub-system of the semantic system (e.g., object or action) and processing used for reading words aloud would not have any additional benefit over the base Priming effect produced by the ATL semantic hub. The distributed modules aspect of the distributed-plus-hub model of semantic processing (Patterson et al., 2007) is supported by the shared-stream Priming advantage for object primes in the LDT with PH foils and the combined LDT analyses. It is important to note that this shared-stream advantage manifests as a significant interaction (i.e., significant Priming for objects but not actions), and that any main effect advantage for object primes could simply reflect that objects are easier to process (i.e., imagine) than actions. However, any such overall benefit in processing objects can not account for the observed interaction in the LDT with PH foils but not with NW foils, nor in reading words aloud.

2.5.2 Conclusion

These results represent behavioural support for the theory that object semantic priming and word identification share processing in the ventral stream. Additionally, equivalent priming effects across prime types for reading words aloud supports the notion that there is also a generic, integrative, semantic hub. Together, these additive and interactive joint effects support and extend the distributed-plus-hub model of the semantic system. Furthermore, demonstrating these joint effects of reading and semantic processing provided a novel paradigm for further research. These findings will provide important insights to computational models of reading, which will need to accommodate the object semantic prime type advantage for lexical processing. Finally, this augmented understanding of how the semantic system and reading interact temporally in the underlying cognitive architecture has implications for the neuroimaging research conducted in Chapter 3 on determining where they interact spatially in

the brain. Specifically, the priming advantage for object priming and word identification suggests they may have a significant volume of conjunction in the ventral visual processing stream. These behavioural experiments tested hypotheses based on a neurobiological model, and have in turn led to new hypotheses about the neurobiological model.

CHAPTER 3: Neuroimaging of Ventral Shared-Stream Lexical Identification and Object Semantics

3.1 Experiment 4 - fMRI

Using the same semantic priming lexical decision task as Experiment 3, which demonstrated that object processing and word identification are temporally-shared in the form of a priming effect for imagined object primes that is greater than imagined action primes, the current experiment used fMRI to examine the hypothesis that this effect could be localized to spatially-shared regions of the ventral-lexical visual processing stream. Specifically, we hypothesized that there should be regions in the ventral stream associated with colour semantics (just anterior to V4 in FuG) and shape semantics (anterior FuG) that would produce greater activation in contrasts between lexical word targets and the sublexical PH foils for object priming than action priming, owing to the ventral shared-stream processing for lexical and object semantic processing.

3.1.1 Methods

3.1.1.2 Participants

Twenty-five healthy participants with normal or corrected-to-normal vision and fluent English participated in the experiment. The sample of participants consisted of 15 females and 10 males, with a median age of 25 years. The participants' consent was obtained according to the Declaration of Helsinki (2013), and the experiment was performed in compliance with the relevant laws and institutional guidelines and was approved by the University of Saskatchewan Research Ethics Board.

3.1.1.3 Stimuli

Stimuli were 15 prime-target pairs chosen from the stimuli used in Chapter 2. The stimuli with the highest previously measured priming effect size and ratings of prime-target relatedness from these experiments were chosen. Targets were equivalent between the object and action priming conditions, with only the prime word varying across conditions. The LDT from Experiment 3 was used with PH foils to optimize reliance on orthographic lexical processing.

3.1.1.4 Imaging Protocol

All imaging was conducted using a 3 Tesla Siemens Skyra scanner. Whole-brain anatomical scans were acquired using high resolution axial magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence, consisting of 192 T1-weighted images of 1 mm thickness (no gap) with an in-plane resolution of 1 x 1 mm (field of view = 256; TR = 1900 ms; TE = 2.1 ms). For the functional scans, T2*-weighted single-shot gradient-echo echo-planar imaging (EPI) scans were acquired using an interleaved ascending EPI sequence, consisting of 149 volumes of 25 axial slices of 4 mm thickness (1 mm gap) with an in-plane resolution of 2.7 x 2.7 mm (field of view = 250), using a flip angle of 90°, a TR of 1650 ms, and a TE of 30 ms. The top 2 coil sets (16 channels) of a 20-channel Siemens head-coil were used, with the bottom set for neck imaging (4 channels) turned off. Additional foam padding was used to reduce head motion.

3.1.1.5 Procedure and Apparatus

Stimuli were presented to participants in the center of a screen using a PC running EPrime software (Psychology Software Tools, Inc., <http://www.pstnet.com>) through MRI compatible goggles (Cinemavision Inc., <http://www.cinemavision.biz>). Participants completed 2 blocks of 15 prime-target pairs and 15 prime-foil pairs in both a related and an unrelated condition, one for each prime type (object and action; 60 trials in each block). The order of these blocks was counterbalanced across participants. Presentation of the prime-target pairs was randomized in each block. The presentation start time of the prime word was jittered by a random amount chosen from 100, 200, 300, 400, or 500 ms in order to reduce activation related to expectation resulting from stimuli appearing predictably at the beginning of each acquisition, and to allow for sampling at a range of time points after the onset of acquisition, which reduces correlation with successive evoked activations and increases detection efficiency (see Dale, 1999). The prime appeared for 300 ms, followed by an interstimulus interval of 700 ms and then the target or foil appeared until the participant responded with a left mouse button click for a ‘word’ response or a right mouse button click for a ‘nonword’ response (lexical decision task, LDT, see Figure 3.1), using a magnetic resonance imaging (MRI) compatible fiber optic mouse (Nata Technologies Inc., <http://www.natatech.com/>). The leading edge (10 μ s) of the fibre-optic signal that is emitted by the MRI at the beginning of each acquisition volume was detected by a Siemens fMRI trigger converter and passed to the Eprime PC via the serial port. In this way,

perfect continuous synchronization between the MRI and the experimental paradigm computer was obtained at each volume.

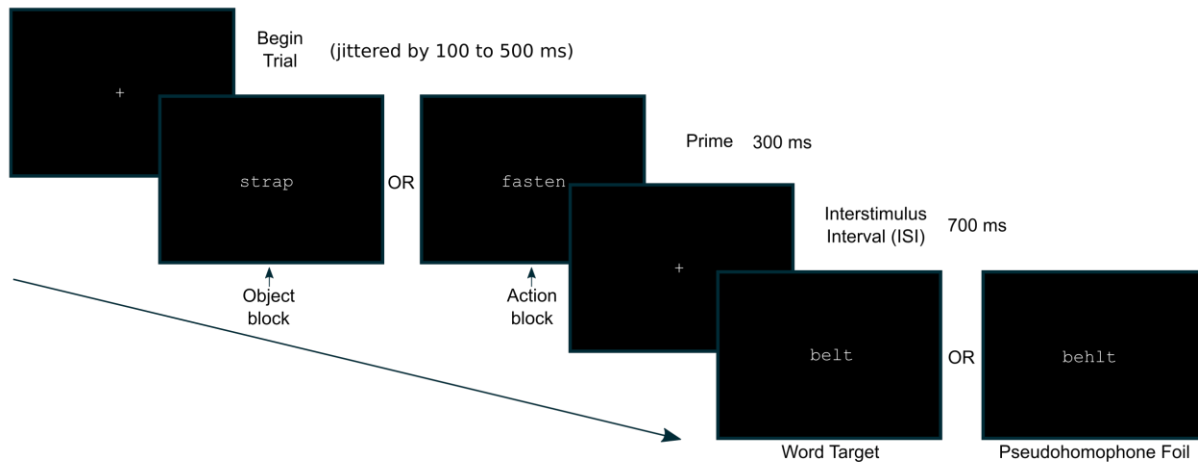


Figure 3.1. Example progression of a related prime, then word target trial or PH foil trial.

3.1.1.5 FMRI Analysis

All preprocessing and statistical analyses for functional images were performed using FMRIB Software Library (FSL; Jenkinson et al., 2012). Functional images were preprocessed including slice scan time acquisition correction, 3D motion correction, spatial smoothing with a 5mm Full Width Half Maximum (FWHM) gaussian filter, and temporal filtering with a high-pass filter to filter frequencies lower than one complete block/rest cycle (12 TRs; period of 20 seconds). Functional volumes were then registered to anatomical brain images using FSL *flirt* with 7 degrees of freedom before being registered to standard MNI space (Mazziotta, Toga, Evans, Fox, & Lancaster, 1995) with 12 degrees of freedom. Motion parameters were regressed as variables in the model to eliminate any artifacts from motion. Event related effects were modeled including the time from the start of the prime to the time of mouse button response to the word target or PH foil. Two models were considered in this analysis: first an analysis of Word Type (Word and PH) was conducted and contrasted across Object and Action prime blocks; and second an analysis of Word Type (Word and PH) and Priming (Related and Unrelated) was conducted and contrasted across Object and Action prime blocks. Statistics were calculated using FSL *randomize* with 5000 permutations and Threshold Free Cluster Enhancement (TFCE) at $p < .05$.

3.1.2 Results

3.1.2.1 Reaction Times

A within-items factorial analysis of variance of the reaction time data from responses during the fMRI experiment with factors of Priming (Related vs. Unrelated) and Prime Type (Object vs. Action) verified that the stimuli produced reliable priming effects for the correct responses to target words whereby Related prime-target pairs ($M = 732.6$ ms) were faster than Unrelated prime-target pairs ($M = 767.1$ ms; $F(1,56) = 9.994$, $p = .002$).

3.1.2.2 Lexical Processing with Object Priming Greater Than Action Priming

The contrast of Prime plus Target > Prime plus PH Foil was greater for Object priming than for Action priming in a region of the left FuG (see Figure 3.2). This region has been associated with mental rotation of tools (Seurinck, Vingerhoets, Vandemaele, Deblaere, & Achten, 2005), sensory effect of colour (Schoenfeld et al., 2003), representation of colour information (e.g., McKeefry & Zeki, 1997; Hadjikhani et al., 1998), attention to colour (e.g., Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Clark et al., 1997), and object-based adaptation in a naming paradigm with no grasp-based adaptation in this region (Shmuelof & Zohary, 2005). This region has also been associated with certain language related tasks, such as picture naming in multilinguals (Vingerhoets et al., 2003), and naming embossed (raised) letters and words in acquired blind participants (Burton, McLaren, & Sinclair, 2006). See Table 3.1 for fMRI contrast coordinates.

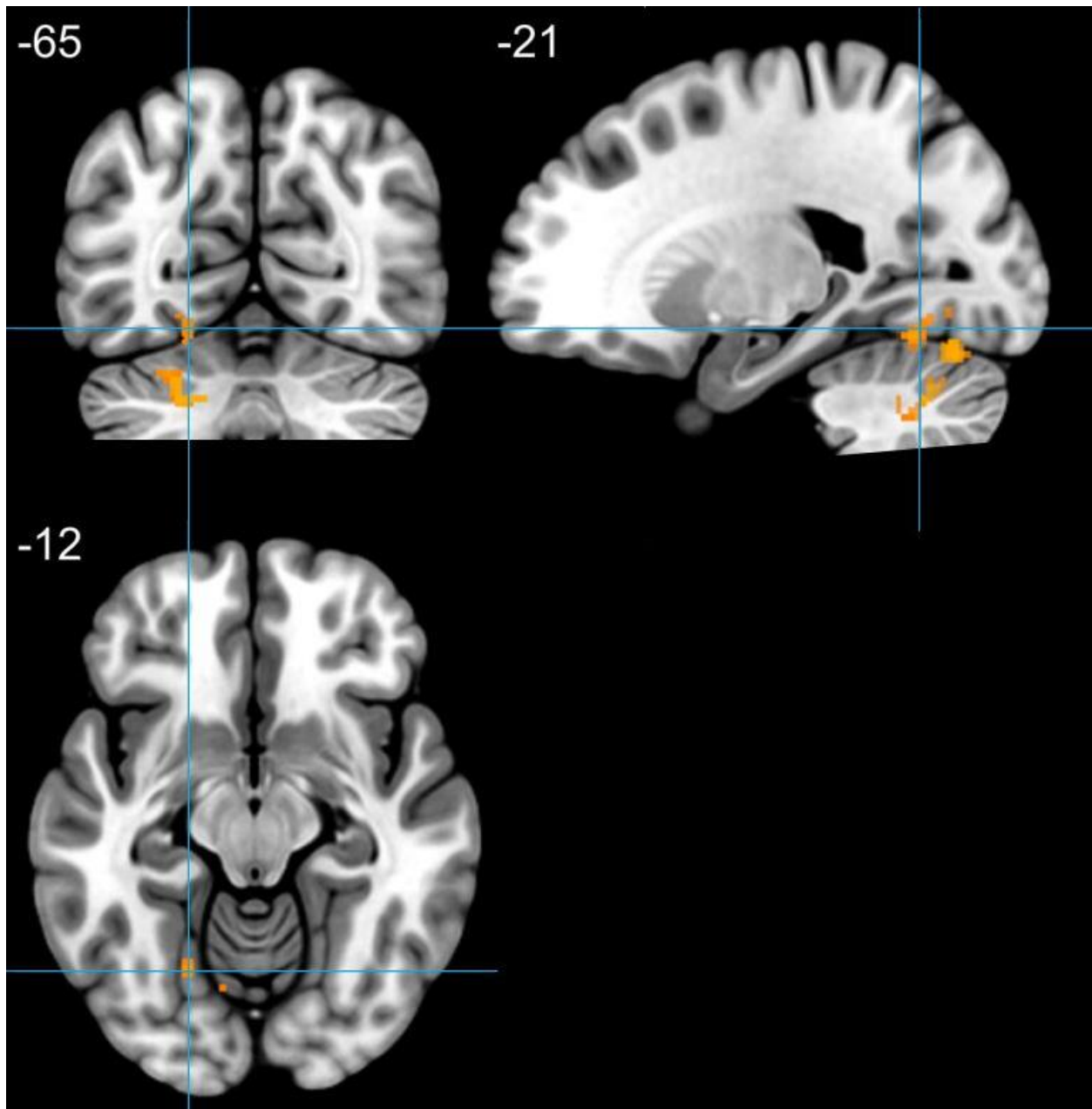


Figure 3.2. Significant region for Object > Action priming of the Prime plus Target > Prime plus PH Foil contrast, located in the left FuG.

The contrast of Prime plus Target > Prime plus PH Foil was greater for Object priming than for Action priming in a more anterior region of the left FuG (see Figure 3.3). This region has been shown to be activated by semantic tasks involving reading of food words but not tool and animal words (Carota, Moseley, & Pulvermüller, 2012). The sensitivity to food words over tool and animal words suggests that this region is sensitive to shape characteristics more so than action (tool) and animal (animate) characteristics. This region is also sensitive to word frequency during reading of visual-related words but not during reading of action-related words (Hauk, Davis, Kherif, & Pulvermüller, 2008). Given that this region is anterior to the more posterior “visual word form area” (VWFA) it may be that the visual semantic processing occurring in the anterior FuG is sensitive to lexical word frequency effects owing to the upstream sensitivity of the VWFA to word frequency (e.g., Kronbichler et al., 2004; Cummine, Sarty, Borowsky, 2010). See Table 3.1 for fMRI contrast coordinates.

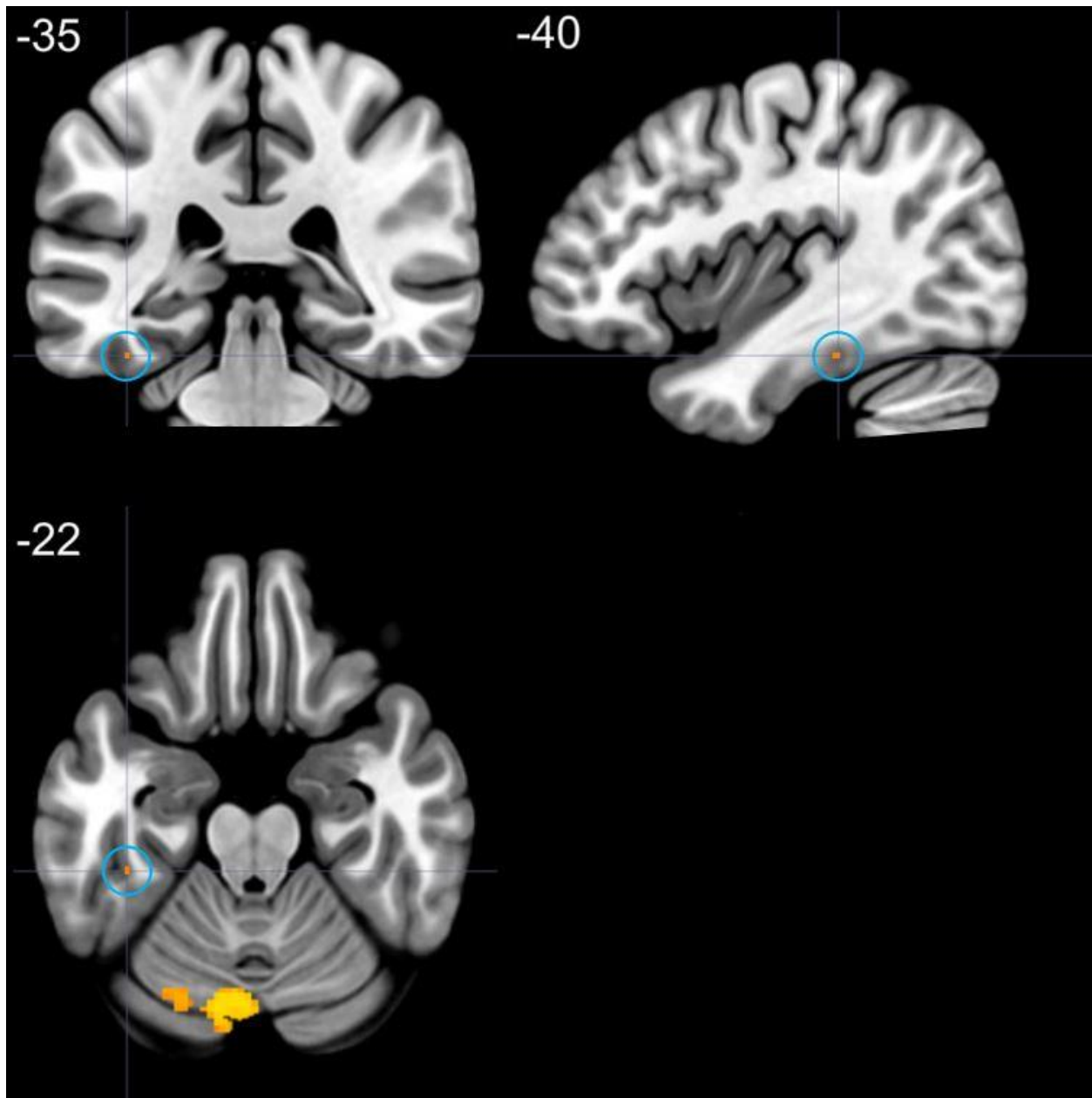


Figure 3.3. Significant region for Object > Action priming of the Prime plus Target > Prime plus PH Foil contrast, located in the left FuG anterior to VWFA. This voxelwise activation represents FSL *randomize* analysis using threshold free cluster enhancement, whereby single voxel activation maps represent a consensus of clustered activation around that voxel.

The contrast of Prime plus Target > Prime plus PH Foil was greater for Object priming than for Action priming in regions of the cerebellum including the left cerebellar lobule VI (see Figure 3.4). This region has been shown to be activated during picture naming following a 4-week lexical training of those items (Raboyeau et al., 2004). This region is also important for semantic categorization as opposed to specific item identification (Braunlich, Gomez-Lavin, & Seger, 2015). Mental imagery paradigms involving imagining grasping objects or grasping next to an object have identified the left cerebellar lobule VI as well as the left FuG (also identified by this contrast; see Figure 3.2) as having greater activation when imagining grasping next to an object than when imagining grasping the object directly (Schulz, Ischebeck, Wriessnegger, Steyrl, & Müller-Putz, 2018). This contrast suggests that regions of the cerebellum such as lobule VI may process visual object semantic information in the context of lexical processing and visual imagery. The potential for the cerebellar lobule VI to play a role as an additional subsystem in the semantic network will be explored further in the DTI analysis of Experiment 5. See Table 3.1 for fMRI contrast coordinates.

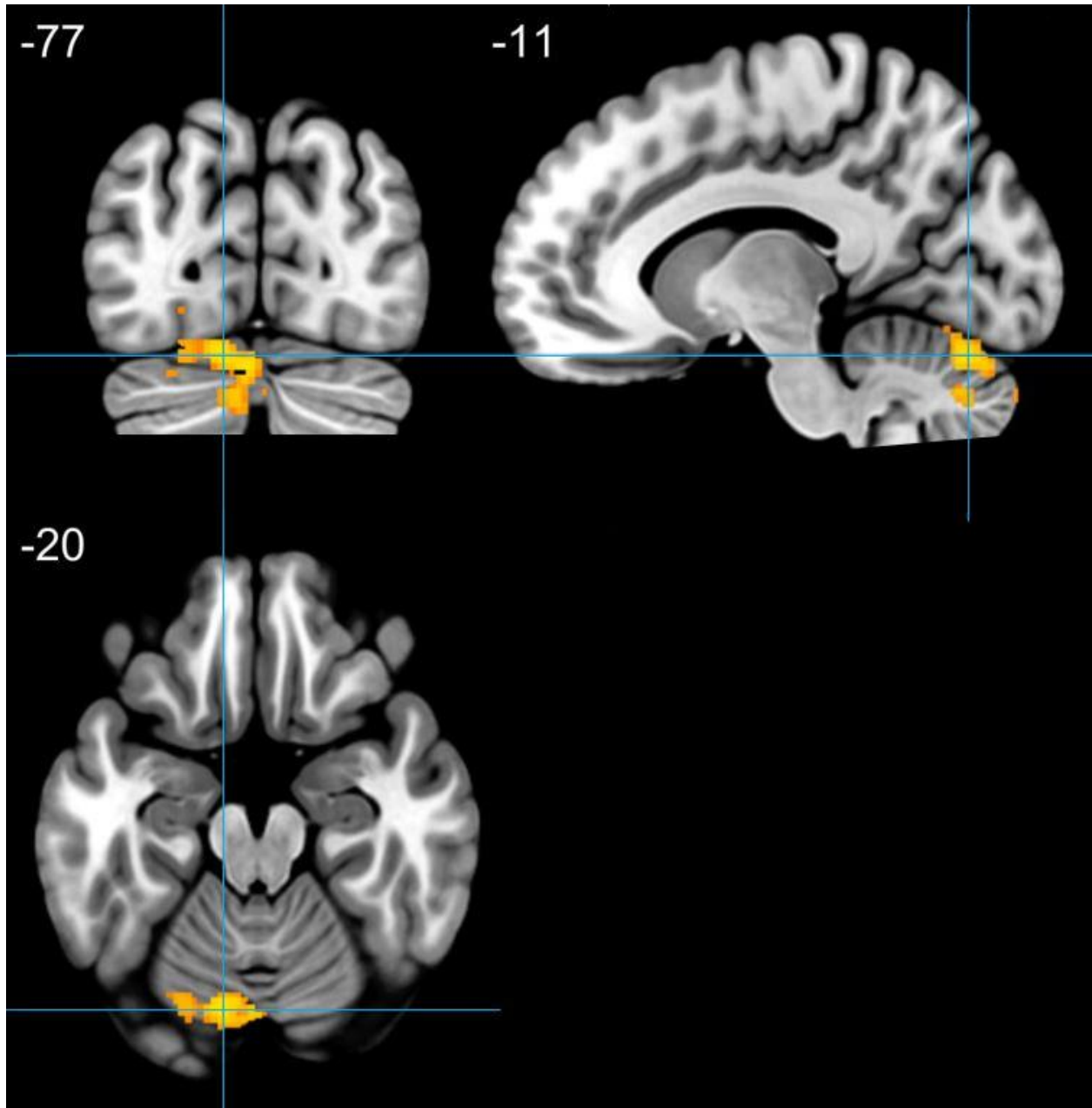


Figure 3.4. Significant region for Object > Action priming of the Prime plus Target > Prime plus PH Foil contrast, located in the left cerebellum including lobule VI.

3.1.2.3 Priming by Action Greater Than Object

The contrast of the Related > Unrelated prime-target/foil pairs was greater for Action priming than for Object priming in regions of the right parietal occipital junction (POJ) and the right superior occipital gyrus (SOG; see Figure 3.5). It has been demonstrated that the POJ and SOG are activated more strongly in response to motion of objects than static objects, and that coherent motion produces more activation than incoherent random motion (Paradis et al., 2000). Given that object-oriented action involves tracking where an object is in space and how to interact with it given its current orientation, these motion sensitive areas may play an important role in action-related semantics. See Table 3.1 for fMRI contrast coordinates.

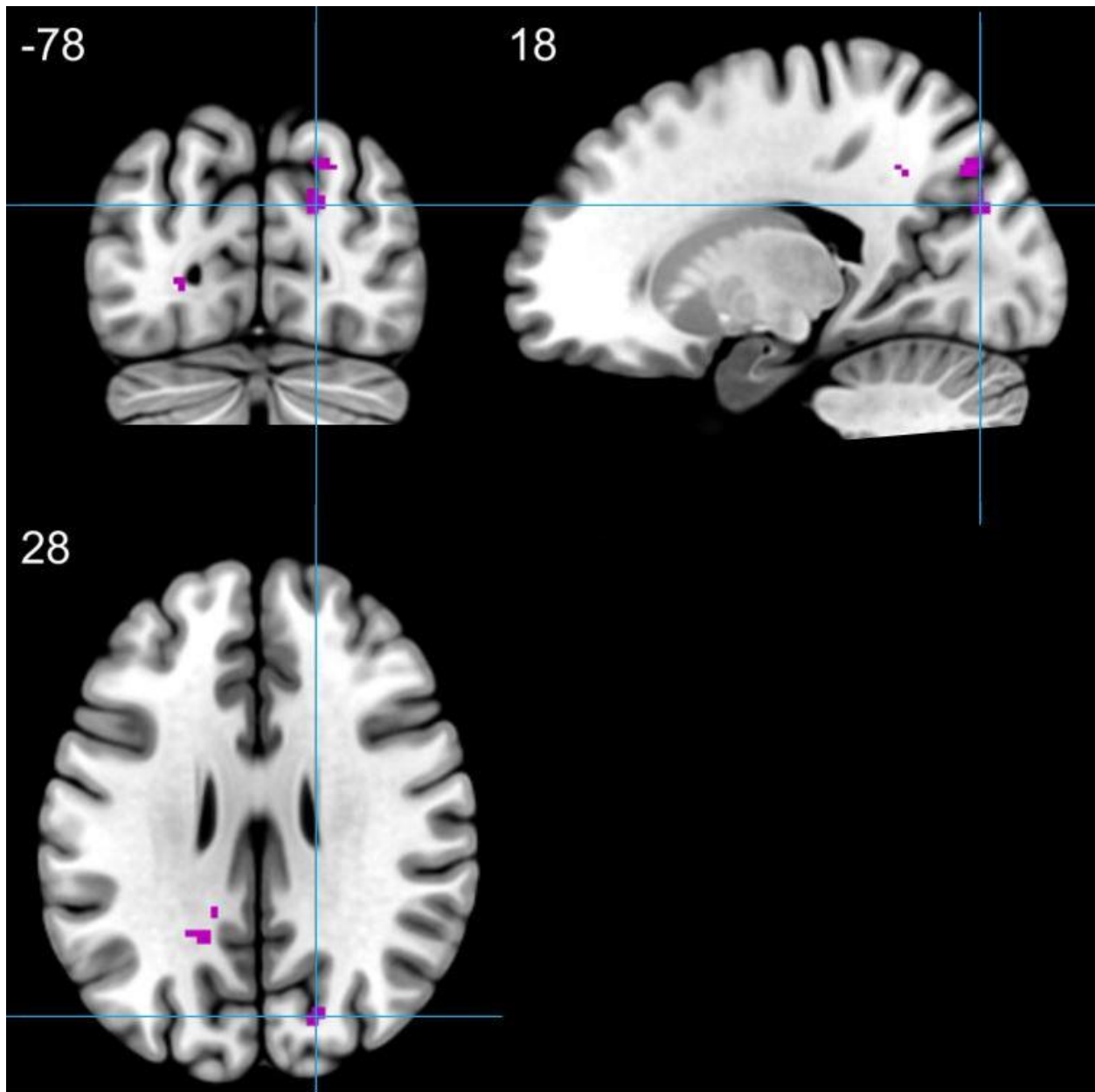


Figure 3.5. Significant region for Action > Object priming of the Related > Unrelated prime-target/foil pairs contrast, located in the right POJ and SOG.

The bilateral V3 ‘motion’ area in the cuneus was identified as having a Related > Unrelated prime-target/foil contrast that was greater for Action priming than for Object priming (see Figure 3.6). The region V3 has been well documented and is associated with visual motion (e.g., see Tootell et al., 1997 for an atlas of V3). More recent research has also associated this region with movement of a virtual ‘avatar’ (mental imagery) via grip force (Floegel & Kell, 2017). As with the POJ and SOG regions also activated by this contrast, the motion sensitive V3 region may play an important role in action semantics, suggesting that action semantics involves a mental simulation of perceived moving objects associated with the actions related to that object. See Table 3.1 for fMRI contrast coordinates.

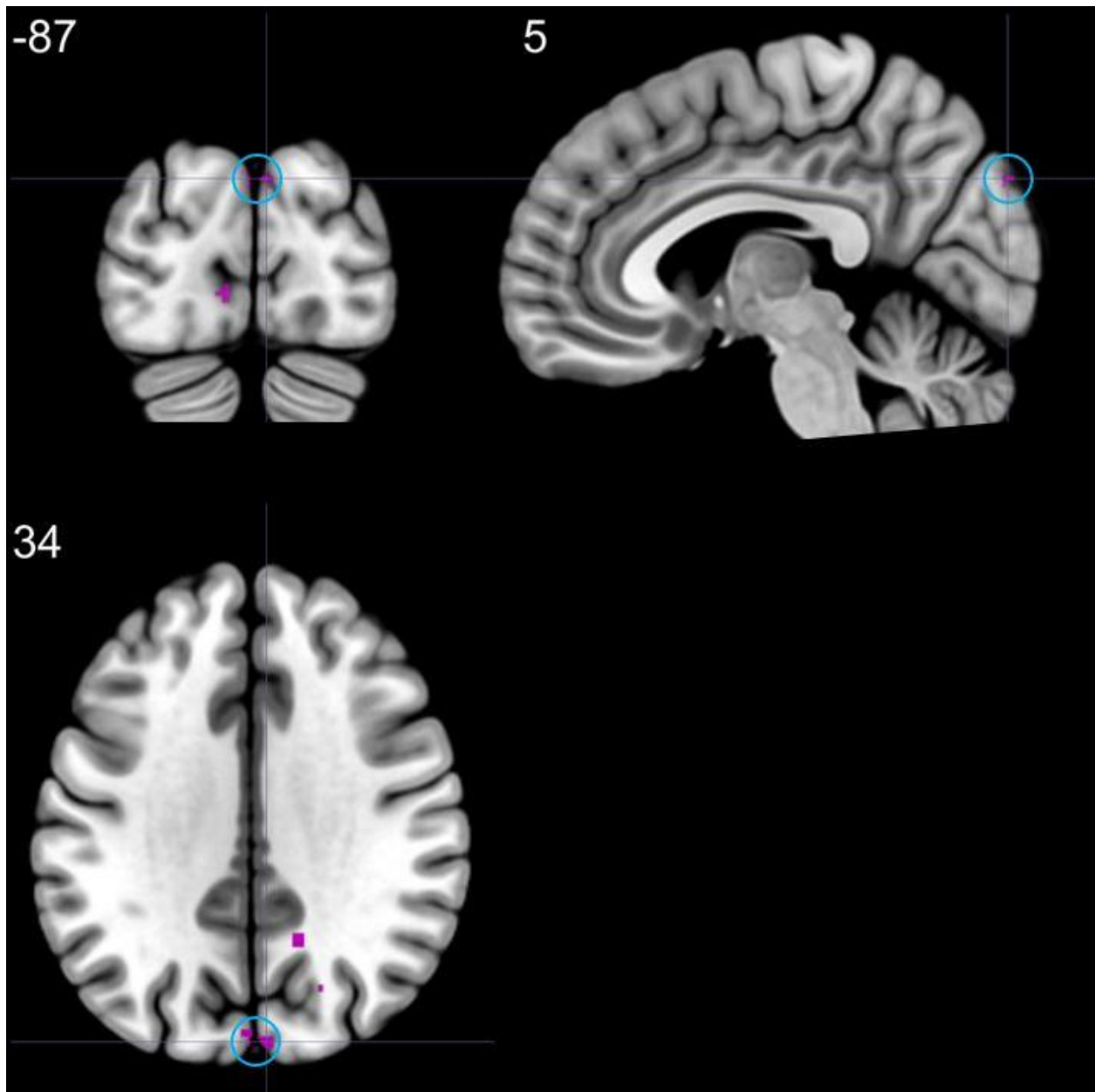


Figure 3.6. Significant region for Action > Object priming of the Related > Unrelated prime-target/foil pairs contrast, located in the right and left cuneus (V3).

Table 3.1. fMRI activation coordinates for significant contrasts.

Prime Type	Contrast	Region	Hemi-sphere	x	y	z	Voxels
Object > Action	Target > Foil	Cerebellar Lobule VI, Crus I, Crus II, Vermis VI, Vermis Crus II	L	-4	-74	-24	572
		Cerebellum I-IV	L	-6	-50	-4	5
		Cerebellar Crus I	R	36	-62	-34	4
		Fusiform Gyrus	L	-20	-62	-14	34
		Fusiform Gyrus	L	-24	-74	-6	9
		Fusiform Gyrus	L	-40	-34	-22	1
Action > Object	Related > Unrelated	V1	L	-8	-92	-2	46
		V1/MT	L	-4	-82	-2	5
		V1	L	-4	-98	2	1
		Parietal Occipital Junction	R	20	-74	40	42
		Superior Occipital Gyrus	R	18	-78	28	18
		Superior Occipital Gyrus/WM	L	-26	-70	22	20
		Cuneus (V3)	LR	0	-86	34	17
		Precuneus	R	14	-54	36	15
		Posterior Thalamic Radiation	R	32	-60	14	65
		Corpus Collosum Splenium/Tapetum	L	-24	-50	16	14
		Corpus Collosum Splenium	L	-14	-46	26	8
		Forceps Major	L	-24	-76	4	13
		Posterior Corona Radiata	L	-18	-52	28	13

3.1.3 Discussion

These neuroimaging analyses examined regions where lexical identification and object semantic processing exhibit ventral shared-stream processing. The contrast showing where responses to lexical targets produced greater activation than foils allowed for a focused

investigation of lexical processing, and this contrast was shown to be greater for object primes than for action primes in the left FuG (anterior to the V4 colour sensitive region) and in a region of the left FuG sensitive to shape semantics anterior to VWFA, as well as in cerebellar lobule VI. As hypothesized, the identified ventral stream regions correspond to sensory and semantic representation of colour (anterior to V4; e.g., Schoenfeld et al., 2003; McKeefry & Zeki, 1997; Hadjikhani et al., 1998) and shape semantics independent from interactive or animate stimuli (anterior to VWFA; Carota, Moseley, & Pulvermüller, 2012). The greater lexical contrast for object than action priming in these well-established colour and shape semantic regions supports the hypothesis that the ventral-lexical stream used for orthographic lexical identification of words engages in shared-stream processing with the ventrally located object semantic sub-systems for colour and shape. These findings also support the conclusion that shared-stream processing contributed to the behavioural temporal object prime advantage observed in Experiment 3, whereby object primes produced greater priming than action primes in the LDT.

3.2 Experiment 5 – DTI

In order to investigate the possibility that the cerebellar fMRI contrast activation observed in Experiment 4 whereby object priming produced a larger Prime plus Target > Prime plus PH foil contrast than action priming may represent an additional object semantic sub-system, DTI structural connectivity data was used to test whether there is robust white matter structural connectivity between the cerebellar lobule VI region identified and the ATL semantic hub. This connectivity would suggest it is possible for the cerebellar lobule VI to efficiently communicate with semantic regions of the temporal lobe (including the ATL semantic hub and the object semantic sub-systems identified in Experiment 4), and therefore that it may act as an additional object semantic subsystem, as suggested by the contrast from Experiment 4.

3.2.1 Methods

The publicly available Human Connectome Project 1021 participant averaged DTI structural connectivity dataset (Van Essen et al., 2013) was used in conjunction with DSI Studio (<http://dsi-studio.labsolver.org>). Cortical connectivity with the cerebellum is described in detail by Keser et al. (2015) as following a ‘loop’ of connectivity, whereby connectivity from the cerebellum to the cortex is mediated by the thalamus, while the input to the cerebellum from the cortex (including the occipital lobe) follows Cortico-Ponto-Cerebellar pathways mediated by the middle cerebellar peduncle (see also Habas & Cabanis, 2007; Koziol et al., 2014). Based on

observed activation from our fMRI analysis, the left cerebellar lobule VI (identified using a probabilistic cerebellum atlas, Diedrichsen, Balsters, Flavell, Cussans, & Ramnani, 2009) was set as a seed region with the left thalamus as a waypoint region of interest (based on the model of cerebellum to cortex structural connectivity described by Keser et al., 2015) and the left ATL as an end region (thalamus and ATL regions were set using Harvard cortical and subcortical atlases, Desikan et al., 2006; end regions including the left fusiform gyrus of the temporal lobe were also examined, with no reliable connections identified). The fiber tracking algorithm implemented in DSI Studio is a generalized version of the deterministic tracking algorithm that uses quantitative anisotropy as the termination index (Yeh, Verstynen, Wang, Fernández-Miranda, & Tseng, 2013). The angular threshold was set at 70 degrees, with trilinear direction interpolation, and an Euler streamline tracking algorithm was used and set to terminate after 1 million seeds.

3.2.2 Cerebellar Connectivity to ATL

The DTI connectivity analysis between cerebellar lobule VI and the ATL via the left thalamus identified streamlines within a tight, consistent bundle originating from a medial region of cerebellar lobule VI proximal to the region identified with fMRI where the contrast of Prime plus Target > Prime plus PH Foil was greater for object priming than for action priming. This white matter fibre bundle is consistent with an interpretation of the fMRI contrast whereby regions of the cerebellum including cerebellar lobule VI may be involved in visual object semantics and may represent an additional sub-system in the semantic network (see Figure 3.7). These are inferred to be outgoing connections from the cerebellum to the cortex as they are mediated by the thalamus, while inputs to the cerebellum from the cortex (e.g., occipital lobe) are mediated by the middle cerebellar peduncle (see Keser et al., 2015).

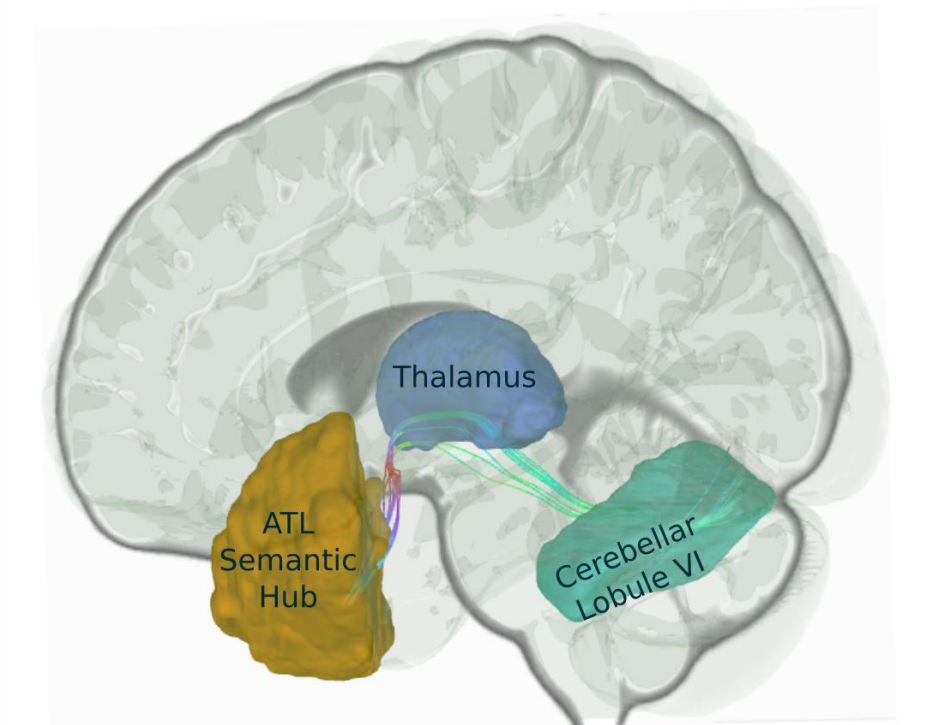


Figure 3.7. DTI tractography from left cerebellar lobule VI to the left ATL via the left thalamus.

3.3 Discussion

Results from Experiment 4 showed that the lexical processing contrast that was greater for object priming than for action priming included cerebellar activation in lobule VI, which has been implicated in picture naming (Raboyeau et al., 2004), broad category semantics (Braunlich, Gomez-Lavin, & Seger, 2015), and mental imagery not related to interaction (Schulz, Ischebeck, Wriessnegger, Steyrl, & Müller-Putz, 2018). Given that this is not a simple overlap of identified activation, but rather a higher contrast identifying lexical activation for one type of semantic processing (object) over another (action), this evidence suggests that the cerebellar lobule VI may play a role in interfacing orthographic lexical and object semantic information. Furthermore, Experiment 5 used DTI tractography to demonstrate that there is robust connectivity from the cerebellar lobule VI region identified in Experiment 4 (and that was robust for object priming) to the ATL, which supports the theory that this cerebellar region may act as an object semantic subsystem in the semantic network, given that the ATL has been described as an integral semantic hub (Patterson et al., 2007).

CHAPTER 4: General Discussion

Based on the potential for ventral shared-stream processing between lexical and object semantic processing, it was hypothesized that lexical processing would be more sensitive to the modality of object semantic priming than to action semantic priming. Word reading (Experiment 1) and lexical decision with NW foils (Experiment 2) did not produce this effect, but the anticipated result was confirmed in the case of orthographically constrained lexical decision using PH foils (Experiment 3), whereby the use of PH foils permits only orthographic lexical (but not phonological or semantic) differences between targets and foils to contribute to correct responses. fMRI investigation of this paradigm in Experiment 4 confirmed that the contrast isolating orthographic lexical processing was more sensitive to object semantic priming than action semantic priming in colour and shape related regions of the left FuG in the ventral stream, and also in cerebellar lobule VI. One of these identified regions of the left FuG has previously been associated with mental rotation of tools (Seurinck, Vingerhoets, Vandemaele, Deblaere, & Achten, 2005), sensory effect of colour (Schoenfeld et al., 2003), representation of colour information (e.g., McKeefry & Zeki, 1997; Hadjikhani et al., 1998), attention to colour (e.g., Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1991; Clark et al., 1997), and object-based adaptation in a naming paradigm with no grasp-based adaptation in this region (Shmuelof & Zohary, 2005), and has also been activated using language related tasks such as picture naming in multilinguals (Vingerhoets et al., 2003), and naming embossed letters and words in acquired blind participants (Burton, McLaren, & Sinclair, 2006). A second identified region of the left anterior FuG has been shown to be activated by semantic tasks involving reading of food words but not tool and animal words (Carota, Moseley, & Pulvermüller, 2012), and has also been shown to be sensitive to word frequency during reading of visual-related words but not during reading of action-related words (Hauk, Davis, Kherif, & Pulvermüller, 2008). Regions of cerebellar lobule VI have been implicated in picture naming (Raboyeau et al., 2004), semantic categorization as opposed to specific item identification (Braunlich, Gomez-Lavin, & Seger, 2015), and mental imagery paradigms that involve imagining grasping next to an object rather than grasping an object directly (Schulz, Ischebeck, Wriessnegger, Steyrl, & Müller-Putz, 2018).

Our DTI analysis in Experiment 5 demonstrated that this region of the cerebellum has the potential to act as an object semantic sub-system of the semantic network, in addition to the colour and shape sub-systems identified in the left FuG, given its robust connectivity to the ATL semantic hub.

4.1 Implications

While having implications for computational, cognitive, and neurobiological models of reading and semantics, this work also represents an example of the breadth of cognitive neuroscience, whereby behavioural hypotheses can be developed from a neurobiologically developed model. Studying the separable dimensions of object versus action semantics in this way represents a novel paradigm for semantic priming. Past research has examined priming of noun and verb *targets*, but not priming with noun and verb *primes* (e.g., Kersten & Earles, 2004; Moss, Ostrin, Tyler, & Marslen-Wilson, 1995). Borowsky et al. (2013) found that reading of nouns and verbs using a within-item design (i.e., noun-verb homographs presented in blocks where participants were instructed to process them as either nouns or verbs respectively) showed primarily shared activation across ventral and dorsal streams based on fMRI analyses. The current research extends this to the domain of semantic priming to demonstrate that there may be important differences in the way that object noun and action verb primes interact with the ventral-lexical stream during lexical processing.

Computational models of reading will need to account for the object prime advantage for words by implementing overlapping lexical processing with object semantic processing. The ventral stream could be activated by object semantic primes, and may give excitatory input to the orthographic lexical system. These visual streams overlapping with the dual-route model of reading could simulate the priming advantage for object primes. Current computational models of reading do not account for different types of semantic processing (e.g., Coltheart et al., 2001; Perry et al., 2007; Plaut et al., 1996), such as object and action semantics, and the current experiments suggest that sub-systems of semantic processing may play an important role in the lexical processing of words.

This research also adds to a larger collection of research examining how semantic systems interact with lexical access. For example, Broca's and Wernicke's aphasics have been examined with respect to lexical access and semantic priming (e.g., Yee, Blumstein, & Sedivy, 2008). Simulation models have also been used to demonstrate interesting dynamics of word

recognition with implications for the intersection of semantics and lexical access, in the context of aphasic brain damaged patients (e.g., Mirman, Yee, Blumstein, & Magnuson, 2011). Cases of ‘pure’ alexia with comorbid semantic deficits have been documented in patient cases, suggesting that there is an important link between semantic and lexical processing (e.g., Graham, Hodges, & Patterson, 1994; Watt, Jokel, & Behrmann, 1997). Considering the shared-stream regions observed in Experiment 4 in the left FuG associated with lexical processing and object semantic processing, it may be that ‘pure’ alexia comorbid with semantic deficits, resulting from damage in the left FuG, would disproportionately impede object semantic processing more so than action semantic processing.

The observed shared-stream object word priming of lexical identification in the ventral-lexical stream in Experiment 4 suggests that sub-systems for processing of shape and colour semantics are separate from sub-systems for action semantics, to the extent that object semantic processing gives preferential, shared access to the ventral-lexical stream. Models of semantic processing have typically described either a distributed-only (sub-systems communicating directly with one another only) or a distributed-plus-hub model (sub-systems communicating directly and with an integrative semantic hub; see Paterson et al., 2007). The shared-stream priming effects observed in Experiment 4, combined with the behavioural object prime advantage observed in Experiment 3, suggest that semantic domain-specific sub-systems may also communicate directly with the lexical processing systems before integrating semantic information from other modalities in the ATL semantic hub. This direct communication before semantic integration would lead to the greater priming effects from shared-stream prime types and target types (e.g., object primes and lexical targets) observed in Experiment 3.

The fMRI contrast observed in the cerebellum, along with past research (e.g., Raboyeau et al., 2004; Braunlich, Gomez-Lavin, & Seger, 2015; Schulz, Ischebeck, Wriessnegger, Steyrl, & Müller-Putz, 2018), suggest regions including the cerebellar lobule VI may act as part of an additional object semantic sub-system of the semantic network. This theory is supported by past functional connectivity research showing multiple areas of functional connectivity between the ATL and the cerebellum (Pascual et al., 2015), and the Experiment 5 DTI results that show structural connections between the region identified in cerebellar lobule VI and the ATL semantic hub via the thalamus (see Figure 3.7). Future research relating to object semantics and lexical processing should consider contributions beyond the ventral visual stream, and further

explore the cerebellum considering the possibility that regions of the cerebellum may act as additional object semantic sub-systems in the semantic network (e.g., see Figure 4.1).

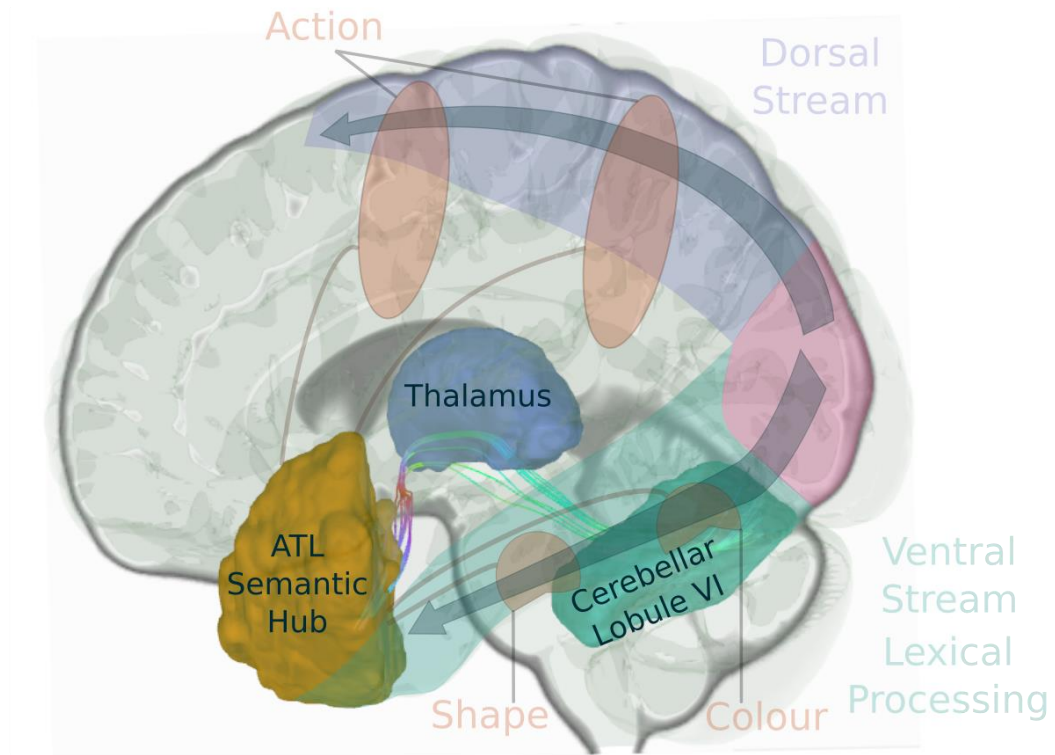


Figure 4.1. Visual streams of processing and semantic networks, with the addition of cerebellar lobule VI as a sub-system of the object semantic network.

4.2 Future Directions

In further research, the use of object-picture and action-video primes with word and PH targets could also be informative about the extent to which the effects observed here were limited to what could be evoked by word primes. To the extent to which participants were able to visualize the object primes and imagine performing the action primes, the use of picture and video primes of similar objects and actions to the primes used in these experiments would provide an interesting comparison. Faster presentation of the target word could also be examined in future studies, in order to determine whether a shorter SOA would potentially allow for automatic priming to be separately explored from automatic plus expectancy-based (long SOA) priming. Stimulus quality could also be examined in the context of the semantic priming effects observed in these experiments, to determine whether any priming effects feed back to the level of

orthographic encoding (e.g., Borowsky & Besner, 1993; 2006).

Outside of the ventral stream, the POJ, SOG, and V3 regions, which are all important for processing of motion information, were identified as being utilized to a greater extent for semantic processing (as identified by the Related > Unrelated prime contrast) involving action primes than semantic processing involving object primes. These findings suggest important regions for focus in future research investigating dorsal stream action semantic processing and potential shared-stream activation with phonological processing. For example, similar experiments could be conducted using a phonological lexical decision task (choose which letterstring *sounds* like a real word; e.g., Borowsky & Besner, 2000) to determine whether these semantic related motion processing regions may overlap and interface with the dorsal-sublexical stream when using action primes. Furthermore, given the posterior dorsal stream's involvement in 'where' processing (e.g., Borowsky et al., 2005), future research should also explore temporal and spatial overlap of 'where' processing with sublexical phonological processing.

Localization of shared-stream (versus unique region) reading and semantic processing will ultimately guide the development of comprehensive and fully implemented models of reading and semantic processing. In turn, the translation of this basic research could help identify forms of dyslexia corresponding to lexical (surface dyslexia) and sublexical (phonological dyslexia) impairments, as well as localization of function in neurosurgical cases, both of which can in turn provide unique tests of the theory. For example, surface dyslexia and 'pure' alexia patients with ventral-lexical impairments may exhibit disproportionately impaired object semantic processing more so than action semantic processing (see also Price & Devlin, 2004, Price, 2012, and Neudorf, Gould, Mickleborough, Ekstrand, & Borowsky, submitted, for discussion of co-location of object recognition and lexical processing). Neurosurgical cases could be guided by the localization of shared activation for reading and the semantic system, in order to avoid resection of eloquent cortex for semantic involvement in reading, specific to the individual patient (see Gould et al., 2015; Ekstrand et al., 2016; and Mickleborough et al., 2015 for examples of patient-specific pre-surgical localization of eloquent cortex for guiding neurosurgery).

4.3 Conclusions

The observed neurophysiological and neuroanatomical shared-stream priming for object priming of lexical identification (Neudorf, Ekstrand, Kress, & Borowsky, submitted) supports

and extends the behavioural research demonstrating a shared-stream object priming advantage (Neudorf, Ekstrand, Kress, Neufeldt, & Borowsky, 2019). Together, these findings suggest that semantic modalities may communicate directly with reading processes before semantic integration in the ATL, and this communication may be influenced by proximity to the language stream. Furthermore, the left cerebellum (including lobule VI) also demonstrated a lexical preference for object primes, suggesting that both object semantic and lexical processing networks rely on shared regions of the cerebellum, and that these regions of the cerebellum may act as part of an additional visual object semantic sub-system. DTI connectivity analysis confirmed that the cerebellar lobule VI has robust connectivity to the ATL semantic hub, supporting the theory that this region may act as an additional object semantic sub-system. This research has discovered important intersections between the lexical and semantic networks within the ventral visual processing stream and cerebellum, which provides important regions of interest for further investigation of these networks.

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Appendix A - Stimuli

<u>Word Targets</u>	<u>PH Foils</u>	<u>NW Foils</u>	<u>Action Primes</u>	<u>Object Primes</u>
arm	ahrm	ard	flex	sleeve
axe	aks	ane	chop	wood
ball	bahl	baln	bounce	round
bed	behd	bep	sleep	mattress
belt	behlt	bect	fasten	strap
bench	behnch	benck	sit	chair
bike	bycke	bime	pedal	motorcycle
boat	bote	boit	paddled	canoe
boot	bute	bool	kick	sock
box	bawks	boc	open	cardboard
broom	bruume	broim	sweep	mop
bug	buhg	bup	swat	beetle
cake	kaik	gake	bake	icing
car	kahr	gar	drive	van
cash	kahsh	casp	pay	receipts
chain	chane	shain	lock	necklace
coat	kote	loat	hang	sweater
coin	koyn	poin	flip	gold
couch	kowch	louch	lounge	cushion
cup	kuhp	nup	drink	mug
dime	dyme	sime	buy	nickel
dog	dawg	dop	pet	paw
eye	iyeye	eyk	squint	pupil
fist	phist	filt	clench	knuckle
foot	phuht	folt	walk	heel
fork	phohrk	nork	skewer	spoon
gift	gihpht	kift	unwrap	ribbon
glass	glahs	blass	shatter	window
grape	greyp	glape	pick	cranberry
hat	haat	het	wear	brimmed
jeans	jeenz	jeats	zip	denim
kite	kyte	kive	flying	parachute
knife	nyfe	knire	stab	dagger
lamp	lahmp	namp	switch	bulb
leg	lehg	heg	limp	thigh
lip	lihph	biph	kiss	cheek
nail	nale	naig	hammer	tack
neck	nehk	nuck	strain	throat
pear	payr	peab	bite	peach
pen	pehnn	pef	write	ink
phone	fohne	phote	tap	screen
pie	pye	pib	slice	crust
pool	pewl	voool	swim	water
purse	perss	lurse	carry	pouch

Word Targets

quilt
rope
sand
shirt
shoe
soap
soup
straw
sword
teeth
thumb
toe
tongue
tree
wheel
wrench

PH Foils

kwihlt
rohpe
sahnd
shert
shew
sope
sewp
strah
sord
teath
thuhm
tohw
tung
trea
wealle
rehnch

NW Foils

quiln
fope
yand
shirv
shoy
soat
voup
straj
sworg
feeth
shumb
tob
vongue
trep
wheeg
wrenth

Action Primes

knitting
untie
dig
unbutton
tie
lather
slurp
suck
unsheathe
brushing
twiddling
stubbed
lick
climb
steer
tighten

Object Primes

patch
knot
beach
plaid
sneaker
bubbles
broth
tube
blade
gums
finger
sockless
mouth
branch
tire
screwdriver