Neural Correlates of Repetition Priming: Changes in fMRI Activation and Synchrony

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ABSTRACT

The neural mechanisms of behavioural priming remain unclear. Recent studies have suggested that category-preferential regions in ventral occipitotemporal cortex (VOTC) play an important role; some have reported increased neural synchrony between prefrontal cortex and temporal cortex associated with stimulus repetition. Based on these results, I hypothesized that increased neural synchrony, as measured by functional connectivity analysis using functional MRI, between category-preferential regions in VOTC and broader category-related networks would underlie behavioural priming. To test this hypothesis, I localized several category-preferential regions in VOTC using an independent functional localizer. Then, Seed Partial Least Squares was used to assess task-related functional connectivity of these regions across repetition of stimuli from multiple categories during an independent semantic classification task. While the results did not show the hypothesized differences in functional connectivity across stimulus repetition, evidence of category-specificity of neural priming and novel insights about the nature of category-related organization of VOTC were revealed.

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Introduction

One of the most studied phenomena in psychology is behavioural priming (Schacter and Bucker, 1998). A common form of behavioural priming, repetition priming, occurs when repeated interaction with a stimulus leads to improvement in identification, classification, or production of that stimulus (Tulving and Schacter, 1990). Priming is considered an implicit memory process, as it does not involve the conscious recollection of a stimulus, but still has an effect on behaviour. Amnesic patients have maintained a priming effect, presenting evidence that there is at least some dissociation from explicit memory (Milner, Corkin, and Teuber, 1968). However, the neural correlates of priming are still not fully understood. Neural changes associated with repetition of a stimulus are known as neural priming. Neural priming is most often observed as a decrease in neural activity to repeated stimuli (repetition suppression), but enhanced neural activity has also been observed (repetition enhancement or neural enhancement) (Stevens, Wig, Schacter, 2008). The prevailing view within the field is that repetition suppression is more closely associated with behavioural priming than repetition enhancement (Wiggs and Martin, 1998). While neural and behavioral priming are related, they are not perfectly correlated, suggesting that a more complex neural mechanism is at work. Several models have been proposed, but no consensus has yet been reached (Gotts and Martin, 2012). A hypothesis with burgeoning support is a neural synchrony model, postulating that strengthened coupling between neurons associated with repetition underlies the behavioral improvements of priming.

Behavioural Priming

There are two forms of behavioural priming: perceptual priming and conceptual priming.

Perceptual Priming

Perceptual priming does not require any semantic encoding and is modality specific (Schacter and Buckner, 1998). Changing the modality of a primed stimulus will eliminate the effect (Schacter and Buckner, 1998). Perceptual priming is enduring in both healthy and amnesic populations, but it wanes over time (Schacter and Buckner,1998; Milner et al., 1968). A classic paradigm for producing perceptual priming is the word-stem task (Schacter and Buckner, 1998), wherein participants study a list of words, then in a later test phase, they are asked to complete word stems. Priming occurs when words which had been studied previously are used to complete the stem.

Conceptual Priming

Conceptual priming, in contrast to perceptual, is more complex; the meaning or significance of a stimulus is encoded. Conceptual priming is most apparent in the category instance production task, where participants are asked to generate examples of a category. Participants tend to use previously studied exemplars in the test phase of the task (Schacter and Buckner, 1998). One of the challenges of studying conceptual priming is avoiding contamination from explicit memory. Dissociating the two mechanisms has proven difficult and explicit memory may be involved in conceptual priming tasks (Schacter and Buckner, 1998; Viadya, Gabrieli, Demb, Keane, and Wetzel, 1996).

Neural Priming

The neural underpinnings of priming are still not fully understood, however, changes in neural activity have been observed in priming tasks. This phenomenon is known as neural priming and is also referred to as repetition suppression, repetition enhancement, adaption, and mnemonic filtering (Stevens et al., 2008). Reduced neural activity with repeated stimuli has been suggested to underlie behavioural priming (Schacter, Wig, Stevens, 2007). Several important characteristics of neural priming have been documented using functional magnetic resonance imaging (fMRI), single cell recording, magnetoencephalography (MEG), and electroencephalography (EEG). The most commonly observed form of neural priming is repetition suppression, (Stevens et al., 2008). Single cell recording and fMRI experiments have shown that decreases in neural activity occur monotonically with increased repetitions (Grill-Spector, Henson, Martin, 2006). Neurons that show the highest initial activation also show the greatest repetition suppression (Li, Miller, Desimone, 1993). Interleaving stimuli between repetitions diminishes neural priming (Sayres and Grill-Spector, 2003), but it is possible that the repetition effects can last days after the initial presentation of the stimuli (van Turennout, Bielamowicz, Martin, 2003). Neural priming tends to plateau between 6 to 8 repetitions for visual stimuli (Sayres and Grill-Spector, 2003), but this depends on many factors, such as the type of stimulus and task (Stevens et al., 2008). Single cell recording in macaques reveals that repetition effects occur quickly; in the perirhinal cortex, neural priming can be seen on average within 70-80 ms after the stimulus onset (Xiang and Brown, 1998). Similarly, in the inferior temporal cortex of macaques, repetition effects occur approximately 150 ms after repetition (Ringo, 1996). Using EEG in humans, Henson *et al.* (2004) found that repetition effects occurred within 160-190 ms (N170) after stimulus onset when the stimulus was repeated in close succession; with intermixed stimuli, repetition effects did not occur until at least 200 ms after stimulus onset (Henson et al., 2004). The speed at which neural priming is apparent suggests that it is a mostly a bottom-up process (Xiang and Brown, 1998).

Specificity of Behavioural and Neural Priming

According to Schacter *et al.* (2004), specificity of priming can be broken down into three categories: stimulus specificity, associative specificity, and response specificity. Stimulus specificity refers to sensitivity to changes in the perceptual features of the stimulus. Associative specificity is sensitivity to the relationship between target items. Finally, response specificity is sensitivity to the consistency of a response to a particular stimulus (Schacter, Dobbins, Schnyer, 2004).

Stimulus Specificity

Amnesic patient K.C. has provided insight into the specificity of behavioural priming (Kohler et al., 1997). K.C. was asked to study words in the auditory and visual modalities and was then tested in the visual modality by completing word fragments. In the within modality condition, K.C. had a significantly higher success rate in completing primed words than novel words. The priming effect was eliminated in the cross modality condition (Kohler et al., 1997).

Neural priming also shows a similar effect when changing modality between study and test. Using Positron Emission Tomography (PET) Schacter *et al*. (1999) observed repetition suppression in right extrastriate regions in a within-modality condition, which was consistent with previous work (Squire et al., 1992). A cross-modality condition did not show repetition suppression in the same regions (Schacter, Badgaiyan, Alpert, 1999).

Evidence suggests that priming may be feature dependent. Changing the font of words between the study phase and the test phase can reduce behavioural priming (Roediger and Blaxton, 1987). A similar effect occurs when changing the speaker's voice during auditory priming tasks (Schacter and Church, 1992). Neural priming in the posterior lateral occipital complex shows feature specificity for changes in viewpoint, illumination, size and position (Grill-Spector et al., 1999); the anterior regions of the lateral occipital complex are relatively invariant to a change in size or position compared to illumination and viewpoint (Grill-Spector et al., 1999). Similar results have been found for orientation related neural priming. Vuilleumier et al. (2005) displayed overlapping objects to participants in a study phase; participants were asked to attend to only one of the objects. In the test phase, participants viewed single objects that were studied or novel objects and were asked to judge them as real or nonsense objects. Studied objects were presented in both the original viewpoint as well as a mirrored viewpoint. For both attended and unattended objects, neural priming in the extrastriate cortex was viewpoint specific. (Vuilleumier et al., 2005). In the ventral occipital temporal cortex (VOTC), Bunzeck *et al*. (2005) observed priming within two category-preferential regions, the fusiform face area (FFA; preferential for faces) and the parahippocampal place area (PPA; preferential for scenes). Priming was category specific in these regions.

Evidence suggests that neural priming in the later ventral visual stream is more lateralized than in the early visual regions. Initial work exploring hemispheric differences used divided-visual-field techniques and found that neural priming was greater when stimuli were presented in the left visual field (mostly processed by the right hemisphere) than in the right visual field (mostly processed by the left hemisphere) (Maroslek et al., 1992). Koutstaal et al. (2001) asked participants to judge if a series of objects were larger than a 13-inch box during the study phase. In the test phase they were shown the studied object, a different exemplar of the studied object, or a novel object. Behavioural priming was shown for the studied objects and exemplars. Neural priming differences between the studied objects and exemplars were found in the bilateral middle occipital lobe, parahippocampal gyri, and fusiform gyri. Neural priming showed a laterality effect, such that the right hemisphere showed an overall greater repetition suppression effect than the left hemisphere for studied objects compared to exemplars (Koutstaal et al., 2001). Further studies have found that the left fusiform gyrus and PPA show greater neural priming for exemplars whereas the right fusiform gyrus and PPA show greater neural priming for studied stimuli (Simons et al., 2003; Stevens, Kahn, Wig, and Schacter, 2012). The neural priming results observed in these studies demonstrate that the right hemisphere is more sensitive to from-specific features of a stimulus; in contrast the left hemisphere is more sensitive to generalized/abstract features of a stimulus (Koutstaal et al., 2001; Simons et al., 2003; Stevens et al., 2012)

Associative Specificity

Associative specificity has been studied using a variation of the word stem-completion task. In this task, participants studied unrelated word pairs; then in the test phase, participants completed stems of target words that were paired with a studied or novel word. Controls and mild amnesic patients showed greater priming when the stems were presented with studied words (Graf and Schacter, 1985). Participants with more severe amnesia showed reduced priming or none at all (Schacter and Graf, 1986). A PET study using a similar stem-completion task found increased activation in the medial temporal lobe when participants were completing stems paired with studied words (Badgaiyan, Schacter and Alpert, 2003). This provides some evidence that associative priming may be dependent on explicit memory.

Response Specificity

Dobbins *et al.* (2004) have shown that changing the response to a stimulus impacts both behavioural and neural priming. In this experiment, participants were shown pictures of objects and asked if each object was larger than a shoebox during a fMRI scan. The object was presented once or three times. Both behavioural and neural priming occurred as expected during this phase. Neural priming was observed in the left hemisphere in the prefrontal cortex (PFC), fusiform gyrus, and extrastriate cortex. In the second phase, participants viewed a new set of objects, half of which were presented in the previous phase and the other being novel stimuli. In this phase, the cue was reversed and the participants had to answer whether or not the object was smaller (rather than larger) than a shoebox. The cue reversal had a significant effect on behavioural and neural priming; behavioural priming was reduced, there was no neural priming observed in the left fusiform gyrus, and a disruption of priming occurred in the left PFC. When the cue was reversed again to the original question in a third phase, the behavioural and neural priming effects recovered to a level similar to that of the first phase (Dobbins, Schnyer, Verfaellie and Schacter, 2004). These findings suggest that priming is dependent on a consistent response across repetitions, and that representations of primed objects and novel objects are equally accessible when the task requires an opposite response for primed objects. The study highlights the role of response learning in neural priming; the authors postulated that neural priming is driven by a learned association between a stimulus and a response (Dobbins et al., 2004).

Linking Behavioural and Neural Priming

Early neuroimaging experiments studying priming were limited to block designs (Squire et al., 1992). With the introduction of event-related designs, it became possible to intermix repeated and novel stimuli and delineate activity on a trial by trail basis. Research on priming has focused on frontal and perceptual brain regions.

Perceptual Regions

Current research suggests that neural priming in early perceptual areas does not underlie behavioral priming. Sayres and Grill-Spector (2003) used an fMRI-adaption method during a semantic classification task. As expected, they found neural priming in the lateral occipital cortex and posterior fusiform gyrus. However, the repetition suppression in these regions did not correlate with behavioural priming (Sayres and Grill-Spector, 2003).

Correlations between neural priming in later perceptual areas and behavioural priming have provided mixed results. Neural priming in the fusiform gyrus for images of scenes has been found to correlate with behavioural priming (Turk-Browne, Yi, Chun, 2006). However, this was only the case for repeated scenes that were later remembered, rather than those that were subsequently forgotten, further complicating the neural relationship/dissociation between implicit and explicit memory. Work within the auditory modality has found that changes in activity in the bilateral superior temporal sulci and the right superior temporal gyrus were correlated with behavioural priming (Bergerbest, Ghahremani, and Gabrieli, 2004). Despite these results, the vast majority of studies have found no direct correlation between neural priming in later perceptual regions and behavioural priming (Dobbins et al., 2004, Maccota and Buckner, 2004, Bunzeck et al., 2005)

Frontal Regions

Research has shown a correlation between behavioural priming and neural priming in frontal regions. The previously mentioned Dobbins et al. (2004) study found that behavioural priming was positively correlated with repetition suppression in the left PFC for repeated stimuli. Several studies have examined this relationship using a living/non-living classification task. The results showed that behavioural priming was related to the magnitude of neural priming in the left inferior frontal gyrus and pre supplementary motor areas (Maccota and Buckner, 2004; Lustig and Buckner, 2004). In addition, some frontal regions have also shown category specific priming (Bunzeck et al. 2005).

Wig et al. (2005) used a TMS-fMRI paradigm to explore how disruptions of activity in PFC influence repetition suppression in the brain. First, fMRI was used to localize regions of the left PFC that showed neural priming in a living/non-living object classification task. Participants were then asked to complete the same task with new objects while TMS was applied. TMS was applied in the localized prefrontal regions for half the objects and a control site for the other half. Participants were then scanned with fMRI while completing the same task again using the objects from the TMS session and novel objects. Objects that were shown while TMS was being applied to the prefrontal regions did not show subsequent neural priming in the stimulated prefrontal region, or in left temporal areas, and there was no behavioural priming for these objects. However neural priming was observed in the early visual areas. TMS to the control region did not disrupt behavioural or neural priming (Wig et al. 2005), demonstrating that behavioural priming required undisrupted processing in the prefrontal regions at the initial presentation of a stimulus.

Taken together, studies have shown that neural priming in the frontal and later perceptual areas in temporal cortex are associated with behavioural priming. However, research has suggested that the magnitude of neural priming in only the frontal regions is correlated with behavioural priming. The mechanisms relating behavioural priming and neural priming are still not well understood.

Neural Synchrony

Neurons communicate with each other through the release of neurotransmitters caused by an action potential. An action potential is the depolarization of a neuron triggered by synaptic input to a receptor that initiates the flow of positive ions. Depolarization, depending on the neuron, can occur at the axon, dendrites, and cell body; the point where the axon and cell body meet (axon hillock) is the most excitable. With enough depolarization, the voltage gated ion channels open, allowing for sodium and/or potassium to flow into the cell. This marks the beginning of the action potential, which is propagated along the axon away from the cell body (Kandel, Schwartz, and Jessell, 2000). Capacitance is the electrical property of a neuron that is the ability of the cell to hold an electrical charge. Neurons have a high enough capacitance that inputs that occur within a small time-window may be summed together (Kandel et al., 2000). Coordinated and synchronized inputs into a neuron are more likely to generate an action potential than random inputs (Varela, Lachaux, Rodriguez, and Martinerie, 2001; Salinas and Sejnowski, 2001). Neural synchrony is the concurrence of firing rates amongst a group of neurons.

The earliest evidence linking neural synchrony to priming comes from von Stein *et al.* (2000) who inserted micro electrodes into the brains of cats and trained them to complete a go-no go task. Recordings showed an increase in synchronization between the primary visual cortex and the visual association cortex for repeated but not novel stimuli. Similar results have been shown in single cell recording experiments with macaques (Hansen and Dragoi, 2011; Kaliukhovich and Vogels, 2012). Gotts (2003) developed a computational model based on neurobiological mechanisms to examine how repetition suppression influences neural synchrony. His simulation demonstrated that as neural firing rates decreased, the synchronization of spike times between modeled regions increased. Moreover, the model simulated reaction time results and predicted repetition priming effects with increased synchrony. MEG has been the most widely used imaging technique to study neural synchrony in humans. Ghuman et al. (2008) measured changes in neural synchrony between the PFC and temporal cortex after repeated stimuli. During a study phase, participants were shown a set of stimuli for three presentations; in the test phase, the stimuli were presented a fourth time, intermixed with novel stimuli. Reduced activity in prefrontal and temporal regions was accompanied by increased synchrony between the two regions for repeated relative to novel stimuli. This result was corroborated by Gilbert et al. (2010).

MEG studies have provided preliminary evidence of neural synchronization with the repetition of stimuli. However, changes in field activity have not been proven to be correlated with neural activity. An evenly distributed firing rate over a region of interest (ROI) may have no consequence on local field activity (Gotts and Martin, 2012). This makes linking repetition suppression to improved neural synchrony challenging.

Using fMRI to Measure Neural Synchrony

The current study will investigate the link between neural and behavioural priming, and changes in functional connectivity within category-preferential regions of the VOTC using fMRI. The overarching hypothesis of this thesis is that repetition leads to increased neural synchrony across a distributed network, which in turn leads to reduced neural activity and improved behavioural performance, i.e., neural and behavioural priming, respectively. The main advantages of fMRI are that it offers excellent spatial resolution, potentially provides a measure of neural synchronization (functional connectivity), and allows for neural activity to reliably be measured. Relative changes in the blood oxygenation level dependent (BOLD) response are used as an indirect but reliable (Ogawa, Lee, and Kay, 1990) measure of neural activity across the brain. The co-variation of the BOLD response between brain regions suggests functional connectivity or synchronization between them (Friston, 1994). Standard univariate fMRI analysis is inadequate for measuring synchronization in that it cannot accurately estimate the variation around the mean BOLD response for individual stimuli (Gotts and Martin, 2012). In order to more accurately measure functional connectivity, I used the multivariate analysis technique Partial Least Squares (PLS) (Lobaugh, West, and McIntosh, 2001; McInstosh, Chau, and Protzner, 2004; Krishnan, Williams, McIntosh, and Abdi, 2011). PLS is a multivariate technique that analyzes correlational relationships between datasets. It was originally applied to neuroimaging data acquired using PET scans, but has since been extended for use with fMRI (McIntosh, Bookstein, Haxby, and Grady, 1996). PLS was developed in response to a major criticism of neuroimaging regarding the considerable overlap in brain regions engaged across multiple cognitive functions (McIntosh, 2000). Criticism was leveled at many research studies that tried to tie a cognitive function to a specific brain region by identifying the region of the brain that showed the greatest local neural activity during a cognitive task. However, there can be overlapping, and in some cases very different, cognitive functions associated with a given brain region. In order to remedy these inconsistencies, the idea of "neural context" was proposed. Neural context postulates that neural activity in response to various tasks may occur within the same region; however, the function of the region at a given time is defined by its connectivity across the brain at that time. In this view, the broader patterns of co-activation among brain regions would differentiate tasks, suggesting a different neural context or networks for specific tasks (McIntosh, 2000).

Unlike typical univariate analyses, PLS does not require any assumptions about the temporal dynamics of the hemodynamic response function (HRF) and eschews multiple comparisons by operating on the entire data structure in a single calculation. There are several different variations of PLS: Task PLS relates patterns of whole-brain covariance to conditions/groups, Seed PLS measures functional connectivity of a seed region over the whole brain, Behavioural PLS associates behavioural variables with brain activity patterns, and Multi-Block PLS associates both behaviour and seed activity to brain activity patterns (Krishnan et al., 2011). In this thesis, I will use Seed PLS to explore the relationship between the functional connectivity/synchronization of category preferential regions and the repetition of stimuli from a preferred category.

Category-Preferential Regions

Previous MEG studies did not use functionally defined ROIs for their data analysis. Instead, a priori anatomical ROIs from previous studies were used (Ghuman et al., 2008; Gilbert et al., 2010). However, it has been long known that there are regions within the VOTC that respond preferentially to a specific category of object. As discussed earlier, it remains in question as to what role these regions play in the relationship between behavioural and neural priming. Previous literature regarding the VOTC has established the intrinsic connectivity of category-preferential regions (Stevens et al., 2015, Stevens et al., 2012); it remains unclear if repetition has an impact on the connectivity of category-preferential regions. This thesis will focus on five category-preferential regions: the PPA (scenes), a tool preferential region (VOTC-Tools: tools), the FFA (faces), an animal preferential region (VOTC-Animals: animals) and the visual word form area (VWFA: words).

PPA

The PPA is an area within the posterior parahippocampal gyrus with portions of the PPA extending into the medial fusiform gyrus. The PPA is most involved with the processing of scenes, but is also involved in the processing of large non-manipulable objects (Epistein, Harris, Stanley, and Kanwisher, 1999). The exact nature of scene processing in the PPA is not fully understood. The region has been linked to representations of spatial features, landmark objects that depict local space, and the retrieval of familiar scenes (Kravitz, Peng, and Baker, 2011; Mullally and Macguire, 2011; Epistein, Graham, and Downing, 2003; Epstein, Higgins, Jablonski and Feiler, 2007). Research into the connectivity of the PPA suggests that the region is not a singular monolithic unit, but rather, is composed of subunits with differing connectivity (Baldassano, Beck, and Fei-Fei, 2013; Stevens et al., 2012; Kahn, Andrews-Hanna, Vincent, Snyder, and Buckner, 2008). Resting-state functional connectivity (RSFC) fMRI has shown that the PPA is functionally connected to other scene processing regions (Stevens et al., 2015, Baldassano et al., 2011; Hutchinson, Culham, Everling, Flanagan, and Galliva, 2014), such as the retrosplenial cortex (RSC), believed to be involved in directing one to navigational landmarks that are not in view (Epstein, 2008), and the transverse occipital sulcus (TOS), involved in processing environmental boundaries (Julian, Ryan, Hamilton, and Epstein, 2016). There are reported hemispheric differences, with the left PPA showing stronger functional connectivity to the default network and the frontoparietal control network and the right PPA showing stronger connectivity to posterior visual perception regions (Stevens et al., 2012). Furthermore, an anterior-posterior connectivity gradient has been observed in the PPA, with the anterior portion generally connecting more with the default network and the posterior portion connecting to visual regions in the occipital lobes (Baldassano et al., 2011). However, other studies have found no anterior-posterior differences in the PPA (Epistein and Morgan, 2012; Cant and Xu, 2012) nor hemispheric dissociations (Epistein and Higgins, 2007; Blondin and Lepage, 2005).

VOTC-Tools

The VOTC-Tools is located in the medial fusiform gyrus. Within the literature, this region has shown a preferential response for tools compared to living entities (Stevens et 2015; Beauchamp, Lee, Haxby, and Martin, 2002; Chao, Haxvy, and Martin, 1999; Weisber et al., 2014). This region is located close to, and sometimes overlapping with, the PPA, despite scenes and tools having very little in common in terms of visual properties. The PPA and the VOTC-Tools show a different connectivity pattern across the brain (Stevens et al., 2015). Using RSFC, Stevens et al. (2015) observed that the VOTC-Tools showed connectivity to other tool-related regions, such as the posterior middle temporal gyrus (pMTG), which is involved in processing non-biological motion (Beauchamp et al., 2002), the ventral premotor cortex (vPM), involved in motor execution (Chao and Martin, 2000), and the intraparietal sulcus (IPS) and the inferior parietal lobule (IPL), regions which are critical for reaching and grasping (Chao and Martin, 2000). Both connectivity and activation changes in the VOTC-Tools in response to tools are left lateralized. (Stevens et 2015; Beauchamp et al., 2002; Chao et al., 1999)

FFA

The FFA is a region found within the lateral portions of the fusiform gyrus that shows preferential activity for faces. The FFA was one of the first category-preferential regions identified in the VOTC (Kanwisher, McDermott and Chun, 1997). FFA activity is bilateral, but is usually greater in the right hemisphere (Kanwisher et al., 1997; McCarthy, Puce, Gore, and Allison, 1997). Faces tend to activate many regions across the brain and it has been suggested that the FFA specifically is involved in the processing of facial identity (Winston, Henson, Fine Goulden and Dolan, 2004; Rotshtein, Henson, Treves, Driver and Dolan, 2005). Studies using RSFC have identified several regions as being key nodes within the face network (O'Neil, Hutchinson, McLean and Köhler, 2014; Turke-Browne, Norman-Haignere, and McCarthy, 2010; Zhang, Tian, Liu, Li, and Lee, 2010); these regions include: the occipital face area (OFA), which is involved in processing facial symmetry (Kietzmann et al., 2014), view point (Kietzmann et al., 2015) and plays a role in recognition (Solomon-Harris, Mullin, and Steeves, 2013); and the posterior superior temporal sulcus (pSTS) and amygdala, both of which are associated with the processing of gaze and facial expressions (Deen, Koldewyn, Kanwisher, and Saxe, 2015; Whalen et al., 1998) .

VOTC-Animals

The VOTC-Animals is located on the lateral portions of the fusiform gyrus; a region that has shown preferential activation for both faces and animals. However, animals tend to have widespread activity across lateral portions of the fusiform gyrus, whereas face processing tends to involve a more clustered activation in the FFA (Chao et al., 1999). A reason for this may be that animal species are more variable than human faces (Martin, 2007). The neural representation of animals and faces relies on similar regions across the brain (Chao et al., 1999). Animal preferential portions of the fusiform gyrus show a similar connectivity pattern as the FFA (Stevens et al., 2015, Chao et al., 1999). Previous work has demonstrated that living entities such as animals and human faces tend to activate the lateral regions of the VOTC, whereas non-living entities, such as tools, activate the medial portions of the VOTC (Martin, 2007). Regions associated with the animal processing include the pSTS, amygdala and extrastriate body area (EBA), which is involved with the processing of non-facial body parts (Urgesi, Berlucchi and Aglioti, 2004).

Visual Word Form Area

The VWFA is a brain region within the left occipito-temporal sulcus that is involved in the visual processing of words (Cohen et al., 2000). This region is thought to play a key role in the neural mechanisms of reading. However, there is debate surrounding the role of the VWFA and its preference for words. The VWFA has also been associated with the processing of visual objects and faces (Price and Devlin, 2003; Davies-Thompson, Johnston, Tashakkor, Pancaroglu and Barion, 2016; Mei et al., 2010), and other high spatial frequency stimuli (Vogel, Petersen, and Schlaggar, 2012a; Vogel, Petersen, and Schlaggar, 2014). It is expected that if the VWFA is involved in reading mechanisms, it should show stronger connectivity to the language regions.

While studies have reported both functional and structural connectivity between the VWFA and temporal and frontal regions, it has not been established that these regions or connections are involved in language processing (Bouhali et al., 2014; Fan, Anderson, Davis, Cutting, 2014; Chai et al., 2016; Li et al., 2013; Koyama et al., 2010; Koyama et al., 2011; Wang, Caramazza, Peelen, Han and Bi, 2015). Other studies have shown the VWFA to have functional connections to visual attention areas, suggesting a completely different role of the VWFA (Vogel, et al., 2012a; Vogel, Miezin, Petersen, and Schlaggar, 2012b; Vogel et al., 2014).

Current Study Overview

In this study, participants completed two scanning sessions. The first session consisted of a multi-category block-design functional localizer used to localize multiple category-preferential cortical ROIs in individual participants. An independent, block-design functional localizer is the most powerful method to localize ROIs (Saxe, Brett, and Kanwisher, 2006).

In the second session (approximately 1 week later), an event-related, semantic classification, repetition priming task was completed. Participants were shown multiple intermixed stimuli from several categories of words and images and were asked to judge if each stimulus was manmade, natural, or neither. Each stimulus was presented 6 times over the course of the scan. Data collected in this experiment were part of a broader study, however, only results from the animals, faces, scenes, tools, and words stimuli were analyzed in this thesis. These categories were chosen because there is a deep literature regarding the processing of each of these categories (Martin; 2007).

Methods

Participants

All data were collected at the National Institutes of Health (NIH) in Bethesda, MD, USA.

In total 27 participants, 15 males and 12 females (mean age = 24.01) completed both sessions of the experiment and will be analyzed. All participants were healthy, right handed, literate, young adults with normal or corrected to normal vision, no history of medical or mental health issues, and no history of substance abuse. All participants gave informed consent in writing and were paid for their participation, observing a NIH Review Board- approved protocol.

Session 1: Functional Localizer

The functional localizer consisted of 10 runs, each containing 14 blocks, one block for each of 14 categories. Each block lasted 20s and contained 20 trials, with each trial (1 s) consisting of a 300 ms stimulus presentation and 700 ms inter stimulus interval. Task blocks were interleaved with fixation blocks lasting 10s. To maintain attention, participants performed a 1-back task to detect stimulus repetition. Repetition was indicated by using the left index finger to press a button. All stimuli were matched in size and were viewed in the MRI via a mirror attached to the head coil.

Stimulus categories for session 1 were: faces, bodies, animals, tools, non-manipulable objects, abstract objects, scenes, scrambled objects, words, motion (moving dots), static dots, biological motion (animated point-light bodies), non-biological motion (animated point-light tools), and motor (slight finger/toe/tongue movement).

Session 2: Semantic Classification Task

In the task session approximately 1 week following the localizer session, participants completed a semantic classification task using a rapid event-related design. Stimuli from 10 categories were shown and results from 6 categories (scenes, tools, animals, faces, real words, and pseudowords) were analyzed in this thesis; each category had 20 exemplars, except for real words. Real words contained 5 sub categories: animal, tools, non manipulable objects, scenes, and body parts; each sub-category of words had 20 exemplars. The sub-categories were collapsed together for a total of 120 real words. Real words were matched with pseudowords for several characteristics including length, number of orthographic neighbours, and bigram frequency by position using the English Lexicon Project (Reference: Balotat et al. 2007). Stimuli from the functional localizer were not used in the task runs. All stimuli were shown in random order over 2 runs, and this was repeated 6 times for total of 12 runs. Stimuli were presented for 300 ms followed by an inter stimulus interval of 1700 ms for total trial length of 2 s. Null trials were randomly interspersed between stimuli to add temporal jitter, as required for rapid event-related designs, and accounted for one third of all trials. Participants were to judge each image or word as man-made, natural, or neither using a button box held in their left hand.

Stimulus categories for session 2 were: faces, bodies, animals, tools, non-manipulable objects, abstract objects, scenes, scrambled objects, real words, and pseudowords. Figure 1 displays sample stimuli from the categories studied in this thesis.

MRI Scanning

All participants were scanned at the National Institutes of Health (NIH) Clinical Center NMR Research Facility. A GE Sigma 3 Tesla whole-body MRI scanner with an 8-channel head coil was used for data collection. Cardiac and respiration data were also recorded to be regressed out during preprocessing. During both sessions, each participant was first scanned for a high resolution T1 weighted anatomical (124 axial slices, slice thickness = 1.2 mm, Field of View (FOV) = 24 cm, acquisition matrix = 256 × 256), followed by a high-resolution resting-state scan for a duration 8 min 10 s (140 TRs). The resting-state scan was obtained using gradient-echo echo-planar fMRI with whole brain coverage; during this scan participants were asked to remain still and fixate on a white cross overlaid on gray background (TR = 3500 ms, TE = 27 ms, flip

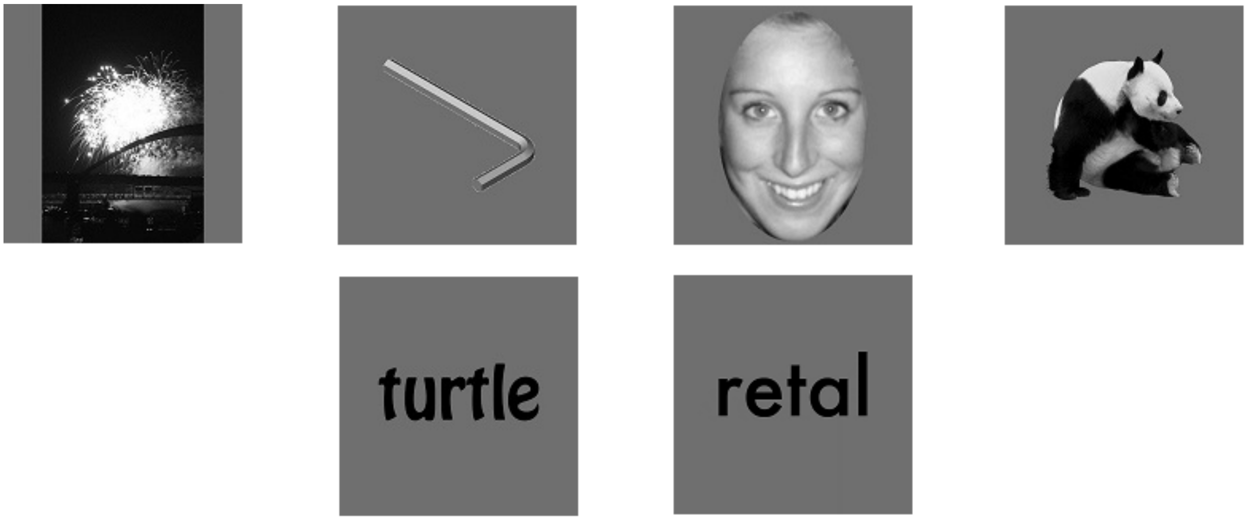

Figure 1. *Sample stimuli for the semantic classification task. Participants were asked if the word or image represented something man-made (e.g., tool), natural (e.g., animal), or neither (pseudoword). Top row from left to right: Scene, Tool, Face, Animal. Bottom row from left to right: Real Word, Pseudoword.*

angle = 90 degrees, 42 interleaved contiguous axial slices per volume, slice thickness = 3.0 mm, FOV = 220 mm, acquisition matrix = 128 × 128 acquisition matrix, single-voxel volume = 1.7mm × 1.7 mm × 3.0 mm). After completing the resting scan, task-evoked brain activity was recorded. During session 1, participants completed a functional localizer (TR = 2000 ms, TE = 27 ms, flip angle = 77 degrees, 41 interleaved contiguous axial slices per volume, slice thickness = 3.0 mm, FOV = 216 mm, acquisition matrix = 72 × 64, single-voxel volume = 3.0mm isotropic), each run of the localizer was 7 min 18s (219 TRs). The session 2 semantic classification task consisted of 12 rapid event related runs (7 min 24s; 222 TRs) and was scanned using the same parameters as the localizer runs.

Preprocessing fMRI Data

All fMRI preprocessing was done with Analysis of Functional Neuroimages (AFNI: Cox,1996). First, the initial four volumes from each run were discarded. Activity outliers (spikes) in each voxel time series were removed and replaced with fitted, smoothed curves. Slice time correction was applied to the data; the functional data were then co-registered to the anatomical image. A modified version of ANATICOR (Jo, Saad, Simmons, Milbury, and Cox, 2010) was used to remove physiological and non-physiological noise. Each participant's anatomical image was run through a FreeSurfer (Fischl, 2012) pipeline in which it was segmented and used to create ventricle, draining vessel, and white matter masks, which were then eroded on the perimeter by 1 voxel to avoid partial volume effects. Masks were applied to the volume registered functional data to obtain nuisance time-series for the ventricles and draining vessels. White matter masks were used to calculate a local estimate of average white mater BOLD activity within a 15 mm sphere. Noise from cardiac and respiratory systems was regressed out using Retroicor (Glover, Li, and Ress, 2000) and using RetroTS from the AFNI

Matlab regressors for respiration per volume time were generated and removed (Birn, Smith, Jones, and Bandettini, 2008). Nuisance time-series were then de-trended with fourth-order polynomials, and a least squares model fitted time series was generated for each nuisance variable to be subtracted from the voxel time series. All functional data were scaled to percent BOLD signal change.

ROI Definition

The functional localizer was used to define individual ROIs in each subject. Previous research has shown that it is critical to individually localize ROIs for many of the category preferential regions within the VOTC (Glezer and Riesenhuber, 2013; Stevens et al., 2012; Stevens et al., 2015). Localizer data were modeled with a boxcar function convolved with a canonical HRF and were then deconvolved. Table 1 shows the contrasts used to define each ROI; these are standard contrasts found in the literature (Stevens et al., 2015). Peak activation was determined by using the t-statistic, and was localized in both volume and surface space using AFNI and SUMA respectively. A localized ROI contained all voxels with a t-statistic above 2.58 (voxelwise $p < 0.01$) for the given contrast within a 6mm radius sphere centered on the peak voxel. Once localized, all ROIs were spatially transformed into each participant's session 2 native brain space.

PLS

Spatio-temporal PLS was developed for analysis of event-related fMRI data (McIntosh et al., 2004). Spatio-temporal PLS describes the relationship between brain activity and behavioral or design (e.g.: conditions in an experiment) variables, over multiple time points. In the analysis, data is organized into a matrix, **D**, so all operations can be performed in a single calculation. The rows of **D**, represent the observations from the experiment which is equal to $n * m$ were n is the

Table 1 Each ROI with the contrast used to define it

Region	Contrast
PPA	Scenes – Faces
VOTC-Tools	Tools – Animals
FFA	Faces – Scenes
VOTC-Animals	Animals –Tools
VWFA	Words – Nameable Entities

number of participants and m is the number of conditions. It follows then that there are a total of $n * m$ rows of stacked vectors in **D**. The columns of **D**, contain the BOLD signal intensity in each voxel at each time point. There are a total of $i * j$ columns in **D**, where i is the number of voxels and j is the number of time points. All values of **D** are within-condition mean centered; this is done by averaging all trials within a condition, which are then expressed as a voxel by voxel deviation from the grand mean.

Matrix **D** is decomposed using singular value decomposition (SVD), producing latent variables (LV). A LV is a pair of vectors representing the relationship between brain activity and the design. A LV reveals the least squares optimized spatio-temporal brain activity pattern and the conditions most related to this pattern. The total number LVs is equal to the number of conditions in the analysis. A second product of SVD is a vector of singular values used to calculate the proportion of covariance each LV accounts for of matrix **D**; LVs are given in decreasing order based on this value. A voxel salience is calculated for each voxel, which represents how strongly a given voxel relates to the spatio-temporal pattern expressed by the LV. Also given is a design salience which reflects how robustly each condition is related to the given spatio-temporal pattern; this can be seen as an optimized contrast as determined by the analysis. PLS also produces a two aggregate scores, including a brain score and a design score. The brain score for each participant, represents how strongly that participant expresses the spatio-temporal pattern of the LV, which is a weighted sum of all voxel saliences. Similarly, the design score indicates how strongly a participant expresses the contrast determined by the design saliences.

Since the determination of LVs is subject to noise, permutation testing is used to measure the statistical significance of each LV. The permutation test re-orders the conditions for each subject through sampling without replacement. For each permutation the singular values calculated are compared to the original singular values to obtain the probability that a permutated singular value will exceed the observed singular for each LV. This provides a statistical significance measure for the spatial-temporal activity pattern for each LV. Standard PLS protocol conducts 500 permutation tests.

In order to establish the reliability of the voxel saliences, a bootstrap estimation of voxel saliences is conducted. The purpose of this is to determine which voxels show a consistent experimental effect. Bootstrapping samples with replacement, keeping the order of experimental conditions for each subject fixed; reliable voxels saliences should not show large variations regardless of the makeup of the sample. Using the bootstrapped samples, salience standard error can be estimated. With a large bootstrap sample, the bootstrap distribution will be approximately normal, meaning that the ratio of the voxel salience to the bootstrap standard error (bootstrap ratio, BSR) will approximate a z-score. It has been suggested 100 bootstrap samples should be used however this may vary based other factors such as sample size.

Visually, voxels with positive BSR values, which are associated with positive brain score values, are represented by warm colours; and voxels with a negative BSR, which are associated with negative brain scores, are represented by cool colours. The direction of the BSR values is arbitrary for any given PLS analyses. As mentioned, spatio-temporal PLS provides results on brain activity over time. Time points for each LV are indexed by lags referring to the time after the event onset. For example, lag 0 would show the LV's pattern activity over the acquisition of the first brain volume post stimulus. This allows for the observation experimental effects that unfold over time.

Seed PLS analyzes the functional connectivity of an ROI across the whole brain. Activation is extracted from the ROI for each condition and is treated as a behavior variable

(Krishnan et al., 2011). LVs are generated by the method described above, and additionally, brain scores for each participant in each condition are correlated with the extracted activation. Confidence intervals for these correlations are obtained through the bootstrapping resampling procedure in the analysis. The upper and lower limits of the confidence intervals are determined by the 97.5th (upper limit) and 2.5th (lower limit) percentiles of the bootstrap distribution. In this thesis, the mean percent signal change was extracted from the individually localized ROIs for each participant, and was used as a behavioral variable in a seed PLS. Previous work reported significantly stronger and more specific RSFC within participants when using individually localized ROIs compared to group localized ROIs (Stevens et al., 2015; Stevens et al., 2011).

Hypotheses

Behaviour

Reaction time differences across stimulus presentations for each category were analyzed. First and foremost, this was to establish if the paradigm was generating behavioural priming. I hypothesized that I would observe priming (decreasing reaction time) across presentations for all categories. To test the changes in RT across presentations, a 1×6 ANOVA was conducted for each category, followed by t-test between each presentation with false discovery rate (FDR) correction for multiple comparisons.

ROI Repetition Suppression

The main hypothesis in this set of analyses was that there would be category-preference for activity and neural priming within each region for stimuli from the appropriate category. The PPA, FFA and VWFA should show category-preferential activation and neural priming for scenes, faces, and words, respectively. I also hypothesized that the VOTC-Animals and VOTC-Tools would show specificity of neural priming for animals and tools, respectively. Finally, I hypothesized that there would be greater activation and neural priming in the left hemisphere for VOTC-Tools and the right hemisphere for the PPA, FFA, and VOTC-Animals.

Seed PLS

Seed PLS is not typically used to study changes in functional connectivity associated with priming. To this author's knowledge, only one such study has been reported that uses seed PLS in a repetition priming paradigm (Stevens, Spreng, Gaesser, and Schacter, 2011). This analysis measured the functional connectivity of seed ROIs with the rest of the brain. Seed PLS shows how strongly activation within a seeded ROI correlates with brain scores over each repetition. I hypothesized that the functional connectivity of the category-preferential ROIs with other task-relevant brain regions would strengthen across repetitions, including with the PFC, early visual areas, regions of the ventral and dorsal attention networks, and in other category relevant regions. More specifically, I expected the following changes over repetition for each category:

- Scenes: Increased functional connectivity of the PPA with the bilateral RSC, bilateral TOS, bilateral PFC, and primary visual cortex (Epstein et al., 1999; Park and Chun, 2009; Ganaden, Mullin, and Steeves, 2013).
- Tools: Increased functional connectivity of the VOTC-Tools with the left IPS, left IPL, left vPM, left pMTG, left PFC and the primary visual cortex. (Stevens et al., 2015)
- Animals: Increased functional connectivity of the VOTC-Animals with the right pSTS, right amygdala, left PFC and primary visual cortex. (Stevens et al., 2015)
- Real Words: Increased functional connectivity of the VWFA with Wernicke's area, Broca's area, PFC, and primary visual cortex (McCandliss et al., 2003)

- Pseudowords: Increased functional connectivity of the VWFA with the left PFC and primary visual cortex.

All PLS analyses conducted 500 permutation tests and used 100 bootstrap samples.

Results

Behaviour Results

Scenes

The Mauchly's test suggested that the assumption of sphericity had been violated for the main effect of presentation, $W = 0.372$, $p < 0.05$, $\varepsilon = 0.82$. Degrees of freedom were subjected to the Huynh-Feldt estimate. A main effect of presentation on reaction time was observed $F(4.11, 108.84) = 31.61$, $p < 0.001$ (Figure 2). Pairwise t-tests using false discovery rate (FDR) correction for multiple comparisons revealed significant differences between all presentations except the fourth and fifth (Table 2)

Tools

There was no evidence to suggest that the assumption of sphericity had been violated, thus, no corrections were made. A main effect of presentation was found $F(5,130) = 3.04$, $p < .01$(Figure 3). Pairwise t-tests revealed significant differences between presentation one and presentations three and six (Table 3).

Faces

There was no evidence to suggest that the assumption of sphericity had been violated and no corrections were made. There was no main effect of presentation (Figure 4).

Animals

There was no evidence to suggest that the assumption of sphericity had been violated and no corrections were made. A main effect of presentation was observed, $F(5, 130) = 12.36$, p <

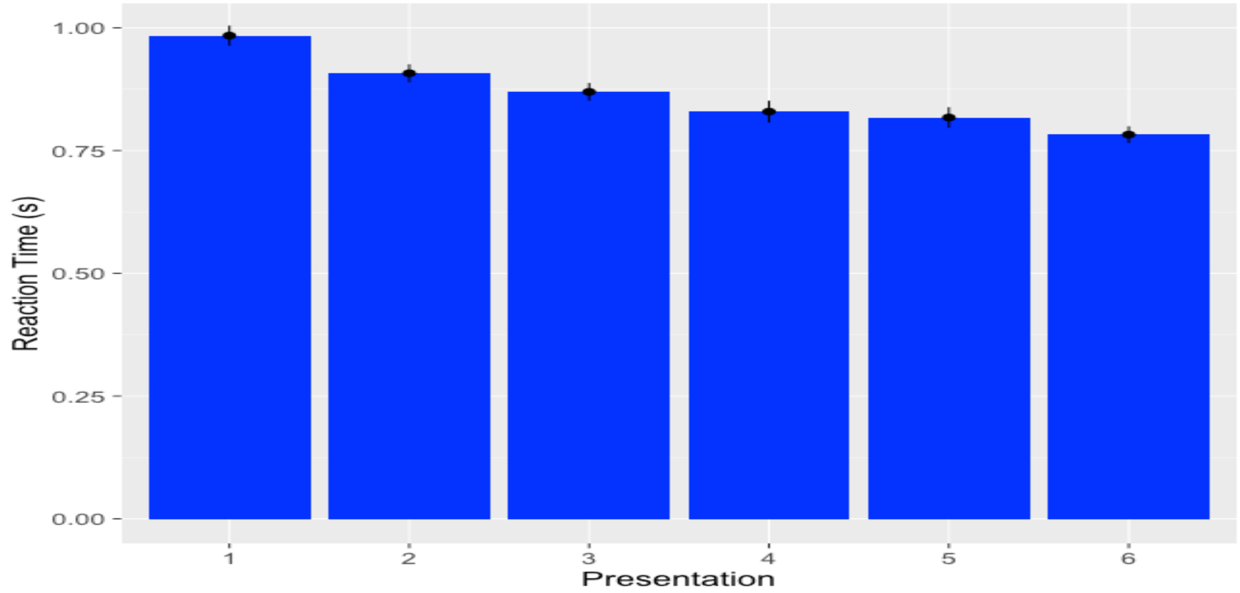

Figure 2. Changes in reaction time across presentation for scene images

Table 2. Pairwise comparisons for reaction time for scene images across presentation. Yellow cells contain statistically significant pairwise comparisons, red cells contain statistically insignificant comparisons, and blue cells indicate invalid or repeated comparisons.

	Presentation Condition 1				
Presentation Condition 2	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	t= 5.34, $p < 0.001$				
Presentation 3	t=5.77, $p < 0.001$	t=2.51, $p < 0.05$			
Presentation 4	t=6.65, $p < 0.001$	t=4.22, $p < 0.001$	t=2.63, $p < 0.05$		
Presentation 5	t=7.20, $p < 0.001$	t=5.37, $p < 0.001$	t=3.06, $p < 0.01$	$p > 0.05$	
Presentation 6	t=9.11, $p < 0.001$	t=6.76, $p < 0.001$	t=4.67, $p < 0.001$	t=2.68, $p < 0.05$	t=2.48, $p < 0.05$

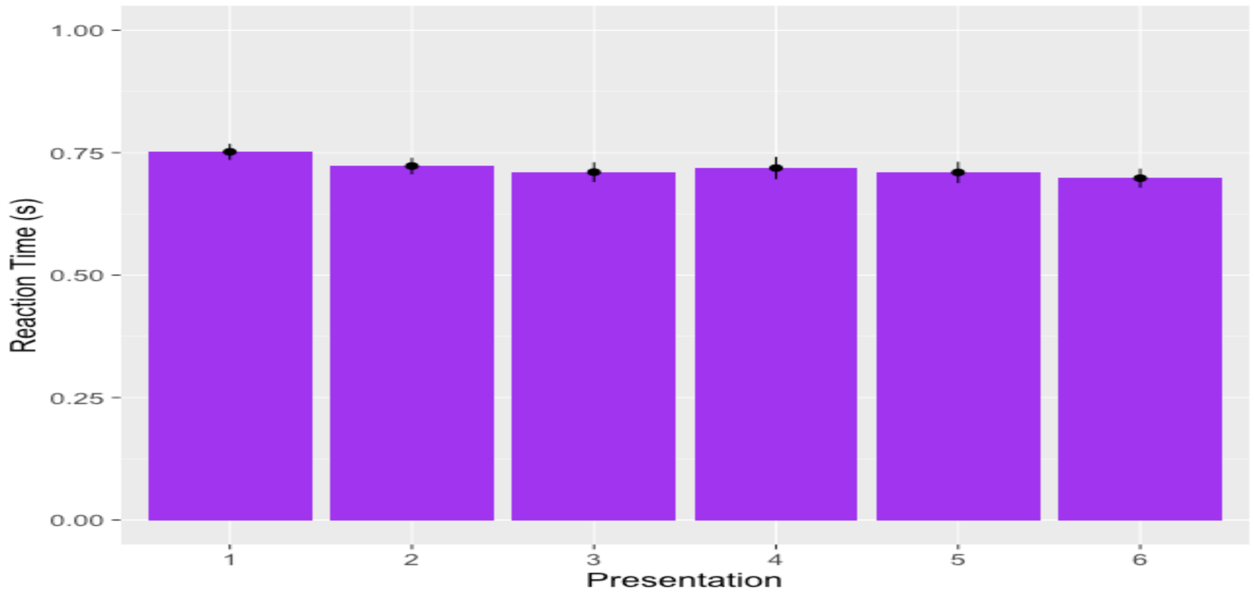

Figure 3. Changes in reaction time across presentation for tool images

Table 3. Pairwise comparisons for reaction time for tool images across presentation. Yellow cells are statistically significant pairwise comparisons, red cells are statistically insignificant comparisons, and blue cells are invalid or repeated comparisons

	Presentation Condition 1				
Presentation Condition 2	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	p > 0.05				
Presentation 3	*t*= 3.04, p < 0.05	p > 0.05			
Presentation 4	p > 0.05	p > 0.05	p > 0.05		
Presentation 5	p > 0.05	p > 0.05	p > 0.05	p > 0.05	
Presentation 6	*t*= 3.29, p < 0.05	p > 0.05	p > 0.05	p > 0.05	p > 0.05

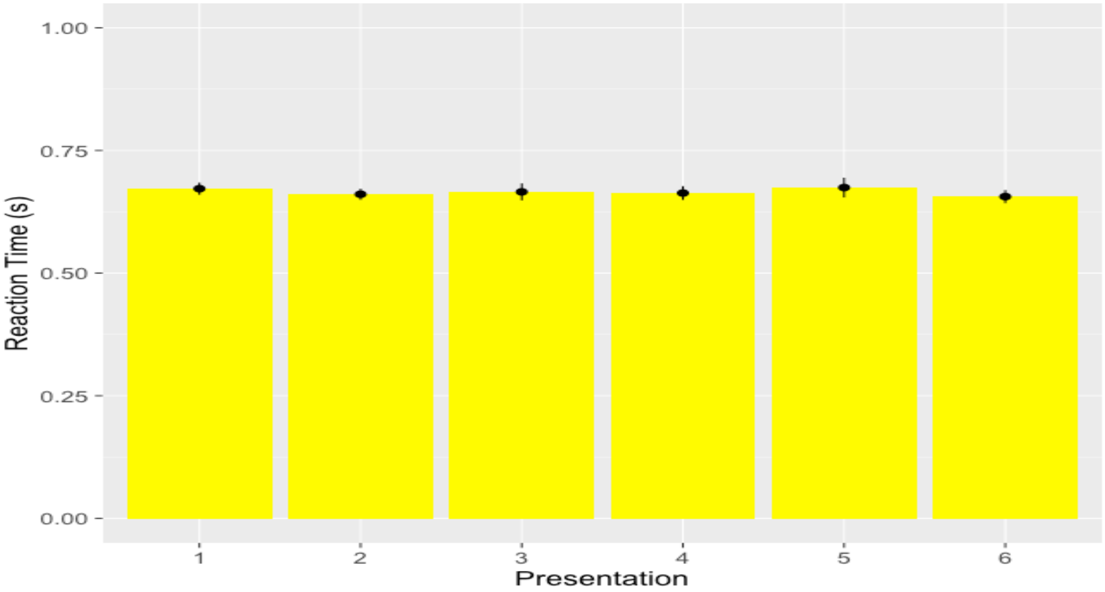

Figure 4. Changes in reaction time across presentation for face images

0.001 (Figure 5). Pairwise t-tests revealed that presentation one was significantly different from all other presentations (Table 4).

Real Words and Pseudowords

When analyzing reaction time data for real words stimuli, there was evidence to suggest that the assumption of sphericity had been violated, $W = 0.095$, $p < 0.001$, $\varepsilon = 0.514$, therefore the degrees of freedom were corrected. A main effect of presentation was found $F(2.57, 66.76) = 30.30$, $p < 0.001$ (Figure 6). Pairwise t-tests revealed that the first presentation was significantly different from every other presentation (Table 5).

For pseudowords, there was no evidence to suggest that the assumption of sphericity was violated. A main effect of presentation was observed $F(5,130) = 50.16$, $p < 0.001$ (Figure 7). Pairwise t-tests revealed a significant difference between all presentations except the fifth and sixth (Table 6).

ROI Neural Priming Results

PPA

A 1×6 ANOVA was used to determine if neural priming occurred in the PPA in response to repeated presentation of scenes; this was done for both the left and right PPA. Data from both the left and right PPA showed there was no evidence to suggest that the assumption of sphericity was violated. A main effect of presentation was observed in both the left ($F(5,130) = 6.93$, $p < 0.001$, $\eta^2 = 0.06$) and right ($F(5,130) = 6.27$, $p < 0.001$, $\eta^2 = 0.051$) PPA (Figure 8). Pairwise t-tests on the data from the left PPA found that presentation one was significantly different from all other presentations (Table 7); pair-wise t-tests on the data from the right PPA found that presentation one was significantly different from presentations three, four, five and six (Table 8).

A 2×6 ANOVA was used to identify laterality differences in the response to images of

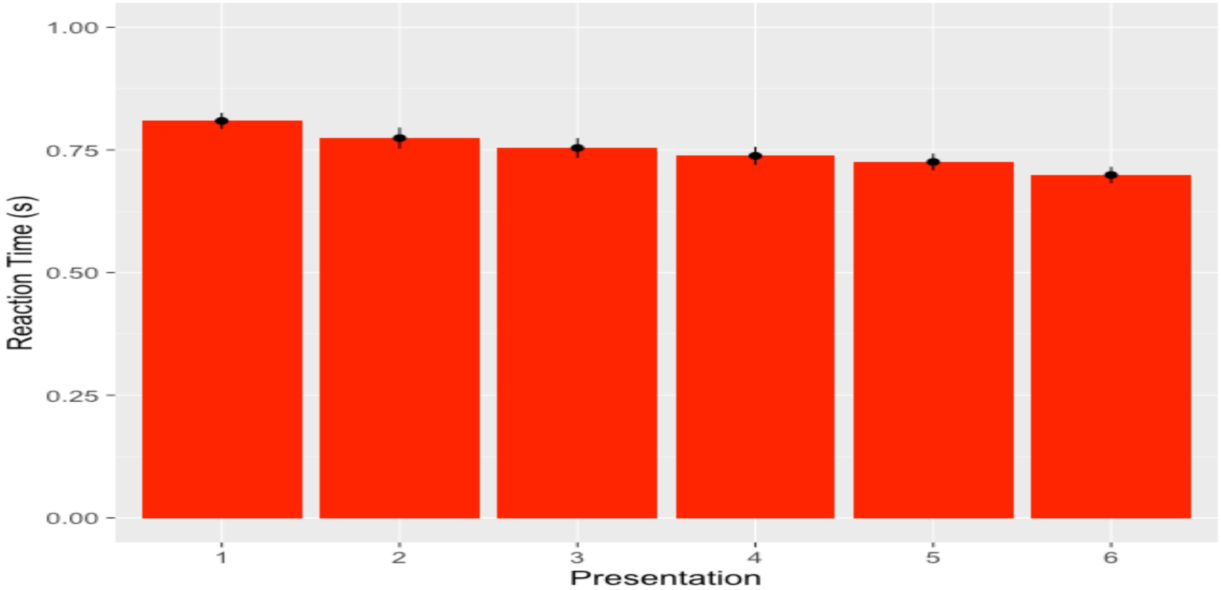

Figure 5. Changes in reaction time across presentation for animal images

Table 4. Pairwise comparisons for reaction time for animal images across presentation. Yellow cells are statistically significant pairwise comparisons, red cells are statistically insignificant comparisons, and blue cells are invalid or repeated comparisons

Presentation Condition 2	Presentation Condition 1				
	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	*t*= 2.43, $p < 0.05$				
Presentation 3	*t*= 2.81, $p < 0.05$	$p > 0.05$			
Presentation 4	*t*= 4.87, $p < 0.001$	*t*= 2.30, $p < 0.05$	$p > 0.05$		
Presentation 5	*t*= 4.55, $p < 0.001$	*t*= 2.87, $p < 0.05$	*t*= 2.27, $p < 0.05$	$p > 0.05$	
Presentation 6	*t*= 5.87, $p < 0.001$	*t*= 4.49, $p < 0.001$	*t*= 3.62, $p < 0.01$	*t*= 2.64, $p < 0.05$	*t*= 2.18, $p < 0.05$

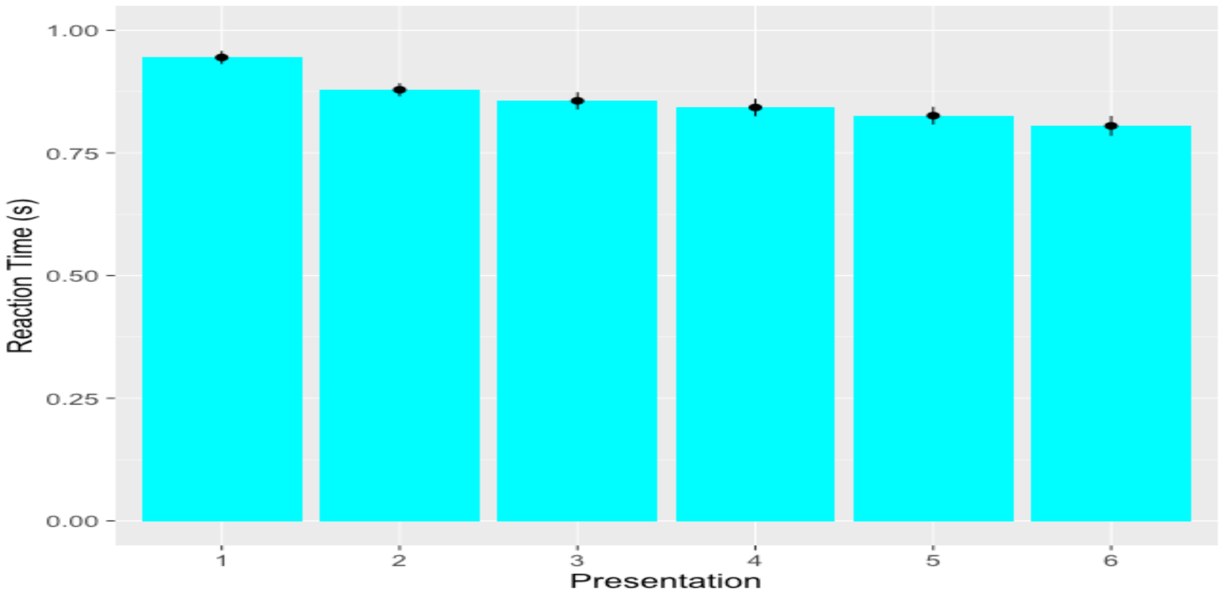

Figure 6. Changes in reaction time across presentation for real words

Table 5 Pairwise comparisons for reaction time for real words across presentation. Yellow cells are statistically significant pairwise comparisons, red cells are statistically insignificant comparisons, and blue cells are invalid or repeated comparisons

	Presentation Condition 1				
Presentation Condition 2	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	t= 8.13, $p < 0.001$				
Presentation 3	t= 2.27, $p < 0.001$	$p > 0.05$			
Presentation 4	t= 5.76, $p < 0.001$	t= 3.20, $p < 0.01$	$p > 0.05$		
Presentation 5	t= 6.53, $p < 0.001$	t= 3.85, $p < 0.01$	t= 3.29, $p < 0.01$	$p > 0.05$	
Presentation 6	t= 6.88, $p < 0.001$	t= 4.95, $p < 0.001$	t= 4.73, $p < 0.001$	t= 3.85, $p < 0.05$	$p > 0.05$

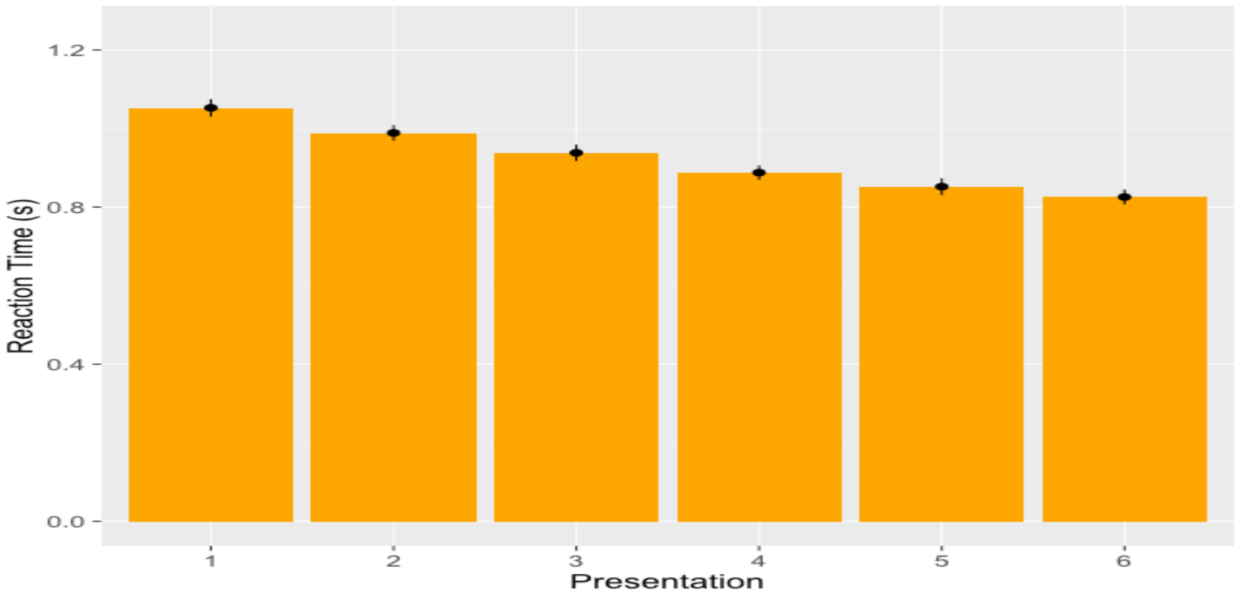

Figure 7. Changes in reaction time across presentation for pseudowords

Table 6. Pairwise comparisons for reaction time for pseudowords across presentation. Yellow cells are statistically significant pairwise comparisons, red cells are statistically insignificant comparisons, and blue cells are invalid or repeated comparisons

	Presentation Condition 1				
Presentation Condition 2	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	t= 4.09, $p < 0.001$				
Presentation 3	t= 5.64, $p < 0.001$	t= 3.32, $p < 0.01$			
Presentation 4	t= 6.99, $p < 0.001$	t= 5.58, $p < 0.001$	t= 4.35, $p < 0.001$		
Presentation 5	t= 8.71, $p < 0.001$	t= 8.05, $p < 0.001$	t= 5.22, $p < 0.001$	t= 2.59, $p < 0.05$	
Presentation 6	t=10.01,$p < 0.001$	t= 9.95,$p < 0.001$	t= 9.44, $p < 0.001$	t= 5.21, $p < 0.001$	$p > 0.05$

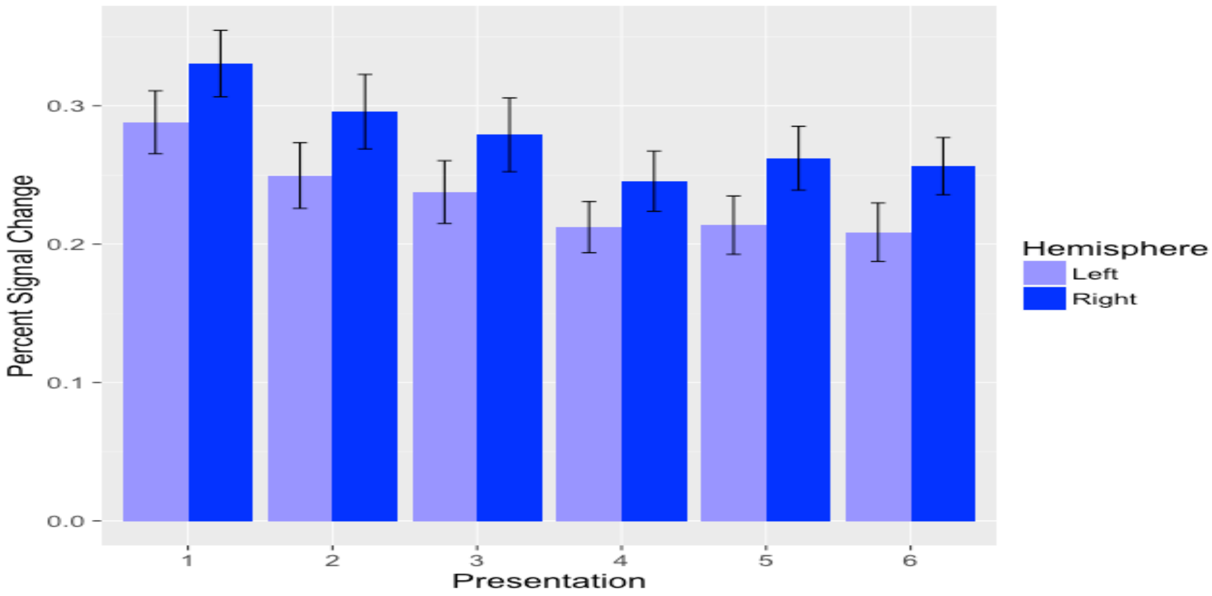

Figure 8. *Neural activation across presentation for scene images in the left and right PPA*

Table 7. *Pairwise comparisons for neural activation for scene images across presentation in the right PPA. Yellow cells are statistically significant pairwise comparisons, red cells are statistically insignificant comparisons, and blue cells are invalid or repeated comparisons*

	Presentation Condition 1				
Presentation Condition 2	*Presentation 1*	*Presentation 2*	*Presentation 3*	*Presentation 4*	*Presentation 5*
Presentation 2	$p > 0.05$				
Presentation 3	$t = 2.77, p < 0.05$	$p > 0.05$			
Presentation 4	$t = 5.97, p < 0.001$	$t = 2.91, p < 0.05$	$p > 0.05$		
Presentation 5	$t = 3.92, p < 0.01$	$p > 0.05$	$p > 0.05$	$p > 0.05$	
Presentation 6	$t = 4.02, p < 0.01$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$

Table 8. Pairwise comparisons for neural activation for scene images across presentation in the left PPA. Yellow cells are statistically significant pairwise comparisons, red cells are statistically insignificant comparisons, and blue cells are invalid or repeated comparisons

	Presentation Condition 1				
Presentation Condition 2	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	*t*= 3.48, $p <0.01$				
Presentation 3	*t*= 2.97, $p < 0.05$	$p > 0.05$			
Presentation 4	*t*= 5.71, $p < 0.001$	*t*= 2.56, $p < 0.05$	$p > 0.05$		
Presentation 5	*t*= 4.56, $p < 0.001$	$p > 0.05$	$p > 0.05$	$p > 0.05$	
Presentation 6	*t*= 4.95, $p < 0.001$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$

scenes between the left and right PPA across presentations of scenes (Figure 8). There was no evidence to suggest that the assumption of sphericity was violated. Significant main effects of hemisphere ($F(1, 26) = 5.30$, $p = 0.003$, $\eta^2 = 0.03$) and presentation ($F(1, 130) = 7.32$, $p < 0.001$, $\eta^2 = 0.05$) were found; the interaction between presentation and hemisphere was not significant. The right PPA showed greater local neural activity in response to scene images than the left PPA; there was no difference in neural priming between the left and right PPA.

To establish the preference of the defined PPA for scene images, a 2×6 ANOVA was conducted (Figure 9) comparing the activation for scenes and animals (a non-preferred category) across had been violated in the presentation factor, $W=0.25$, $p = 0.02$, $\varepsilon = 0.81$, therefore the degrees of freedom were corrected. Significant main effects of category, $F(1, 26) = 150.44$, $p < 0.001$, $\eta^2 = 0.577$, and presentation, $F(1,26) = 150.44$, $p = 0.001$, $\eta^2 = 0.04$, were observed. The interaction between presentation and category was also significant, $F(5,130) = 4.90$, $p < 0.001$, $\eta^2 = 0.023$. A 1×6 ANOVA comparing activation for animal stimuli over presentations found a significant main effect for presentation, $F(5,130) = 2.31$, $p = 0.05$, $\eta^2 = 0.051$. The left PPA demonstrated category-preferential activity and neural priming for images of scenes.

Within the right hemisphere (Figure 10), there was no evidence that sphericity had been violated. Significant main effects of category, $F(1, 26) = 166.21$, $p < 0.001$, $\eta^2 = 0.626$, and presentation, $F(5,130) = 7.84$, $p < 0.001$, $\eta^2 = 0.05$, were observed. The interaction between category and presentation was also significant, $F(5,130) = 2.81$, $p = 0.001$, $\eta^2 = 0.014$. A 1×6 ANOVA comparing the neural activation from animal stimuli over presentation found a significant main effect of presentation, $F(5,130) = 4.98$, $p < 0.001$, $\eta^2 = 0.111$. The right PPA demonstrated category-preferential activity and neural priming for images of scenes.

A 3×6 ANOVA was used to compare activation in the PPA for scenes, tools, and non-

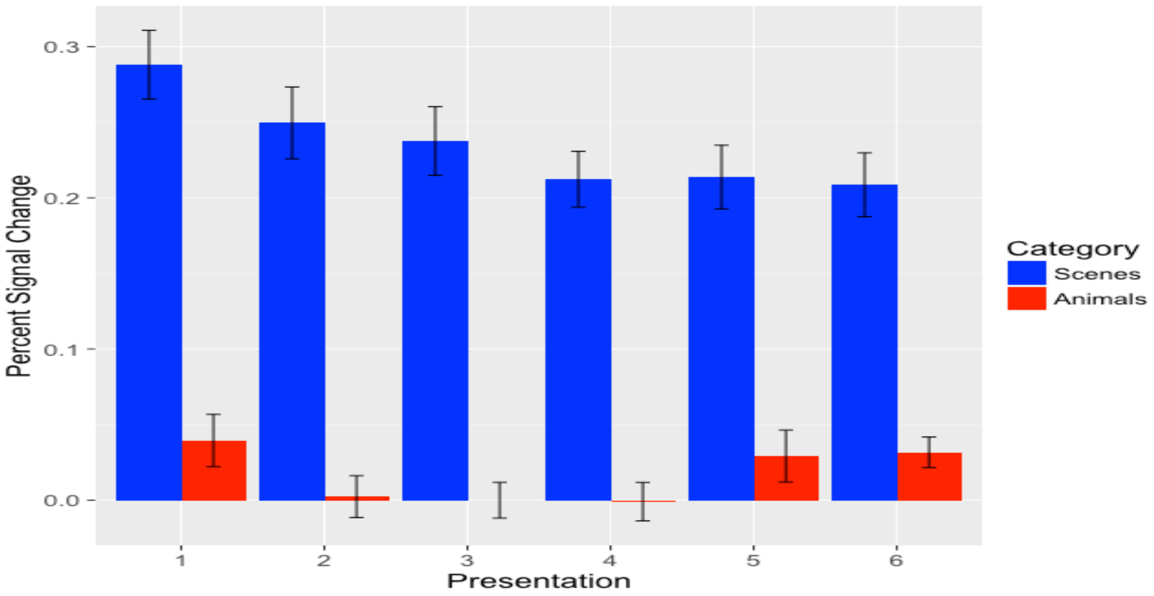

Figure 9. *Neural activation across presentation for scene and animal images in the left PPA*

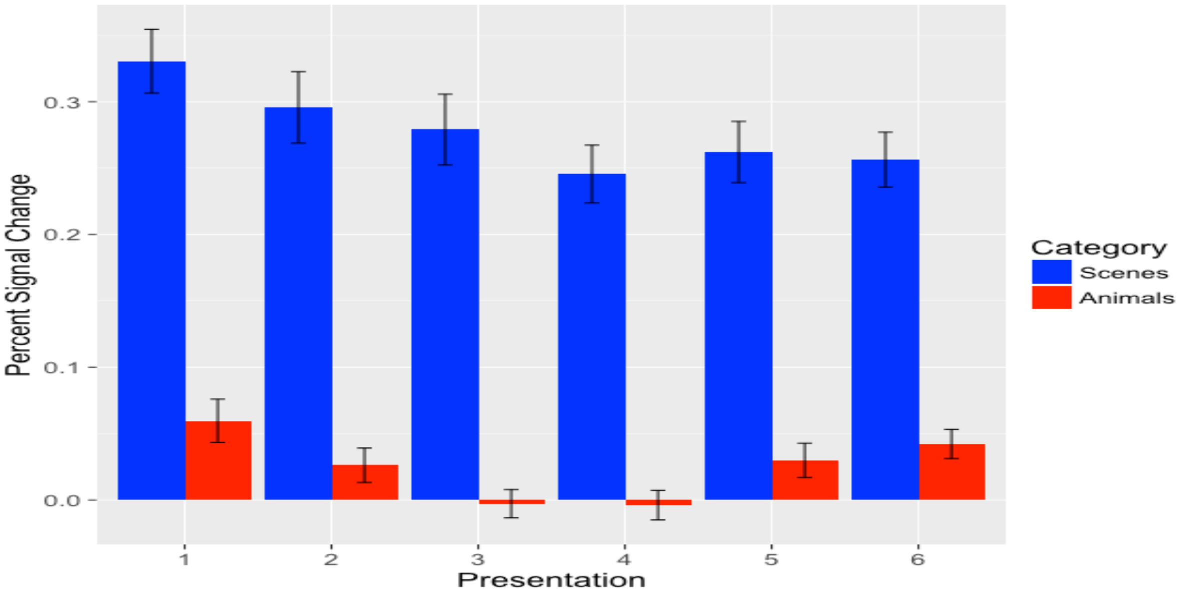

Figure 10. *Neural activation across presentation for scene and animal images in the right PPA*

manipulable data from the left and right PPA. Tools and non-manipulable objects were chosen because these categories have been associated with increased activity in the PPA. Within the left PPA (Figure 11), there was evidence to suggest that the assumption of sphericity had been violated in the category factor, W=0.64, $p = 0.004$, $\varepsilon = 0.77$, therefore the degrees of freedom were corrected. Significant main effects of category, $F(1.53,39.87) = 101.20$, $p < 0.001$, $\eta^2 = 0.395$, and presentation, $F(5, 130) = 8.25$, $p < 0.001$, $\eta^2 = 0.04$, were observed. There was a significant interaction between presentation and category, $F(10, 260) = 2.07$, $p = 0.002$, $\eta^2 = 0.014$. A 1×6 ANOVA comparing the neural activation from tool stimuli across presentations was insignificant. A 1×6 ANOVA comparing the neural activation from non-manipulable object stimuli across presentations found a significant main effect of presentation, $F(5, 130) = 7.38$, $p < 0.001$, $\eta^2 = 0.07$. The left PPA demonstrated category-preferential activity and neural priming for images of scenes and non-manipulable objects.

Within the right PPA (Figure 12) there was evidence that to suggest the assumption sphericity was violated in the category, W=0.57, $p < 0.001$, $\varepsilon = 0.73$, and the interaction between presentation and category, W=0.04, $p < 0.05$, $\varepsilon = 0.93$, therefore the degrees of freedom were corrected. Significant main effects of category, $F(1.46, 37.96) = 101.84$, $p < 0.001$, $\eta^2= 0.48$, and presentation, $F(5, 130) = 9.55$, $p < 0.001$, $\eta^2= 0.05$, were observed. There was no significant interaction. A 1×6 ANOVA comparing the neural activation from tool stimuli across presentations found a significant main effect of presentation, $F(5, 130) = 3.43$, $p < 0.001$, $\eta^2= 0.07$. A 1×6 ANOVA comparing the neural activation from non-manipulable object stimuli over presentation found a significant main effect of presentation, $F(5, 130) = 5.20$, $p - 0.02$, $\eta^2 = 0.07$

VOTC-Tools

It was not possible to localize the right VOTC-Tools in 2 participants; these participants

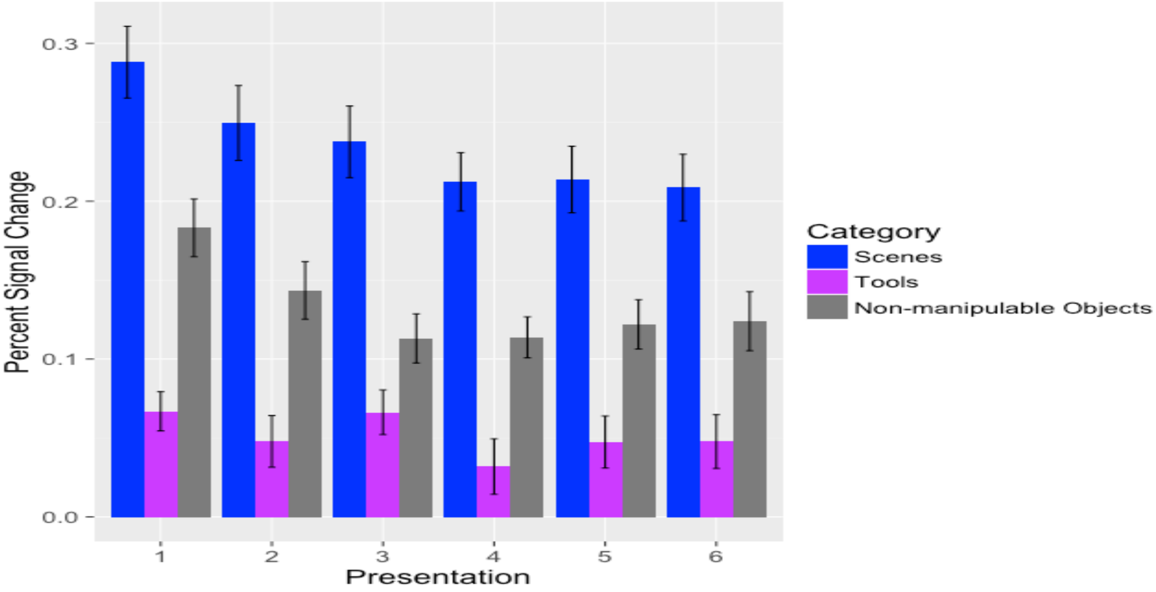

Figure 11. Neural activation across presentation for scene, tool and non-manipulable object images in the left PPA

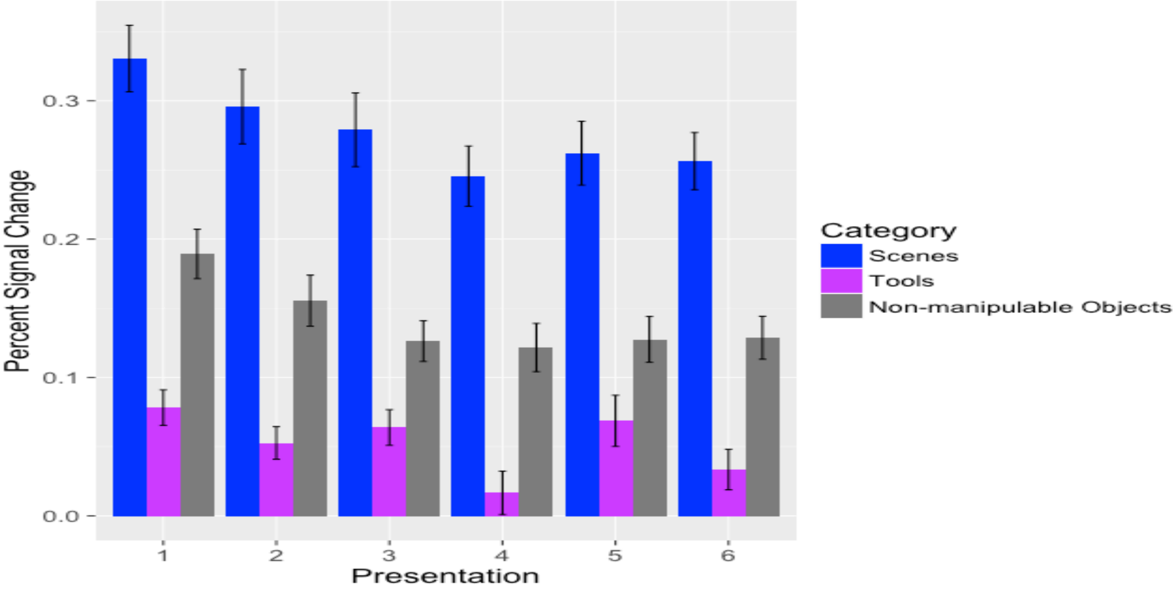

Figure 12. Neural activation across presentation for scene, tool and non-manipulable object images in the right PPA

were not included in any analysis that involved the right VOTC-Tools. A 1×6 ANOVA was used to determine if neural priming occurred in the VOTC-Tools in response to repeated presentation of tool; this was done for both the left and right VOTC-Tools. No significant main effect of presentation was found in the left or right VOTC-Tools. A 2×6 ANOVA was used to identify laterality differences in the response to images of tools between the left and right VOTC-Tools across presentations (Figure 13). No significant effects were observed.

To examine the preference of the VOTC-Tools for the tools category, a 2×6 ANOVA comparing activation for tools and scenes images across presentations was conducted, using data from the left and right VOTC-Tools. Scenes were chosen since scene images activate a region (PPA) near or overlapping the VOTC-Tools. Within the left VOTC-Tools (Figure 14), there was no evidence to suggest that the assumption of sphericity was violated. A significant main effect of category, $F(1, 26) = 25.76$, $p < 0.001$, $\eta^2 = 0.10$, was observed. A 1×6ANOVA comparing the neural activation from scene images across presentations found a significant main effect of presentation, $F(5, 130) = 5.98$, $p < 0.001$, $\eta^2 = 0.07$.

Within the right VOTC-Tools (Figure 15), there was no evidence to suggest that the assumption of sphericity was violated. Significant main effect of presentation, $F(5, 120) = 2.81$, $p < 0.01$, $\eta^2 = 0.02$, and category, $F(1, 26) = 28.54$, $p < 0.001$, $\eta^2 = 0.11$, were observed. A 1×6 ANOVA comparing the neural activation from scene stimuli across presentations did not find a significant main effect of presentation.

To further explore if there was any preference for tools in the defined VOTC-Tools activation for tools in the VOTC-Tools and PPA were compared with a 2×6 ANOVA, using data from both hemispheres. Within both hemispheres, there was no evidence to suggest the assumption of sphericity had been violated. A main effect of region was observed in both the

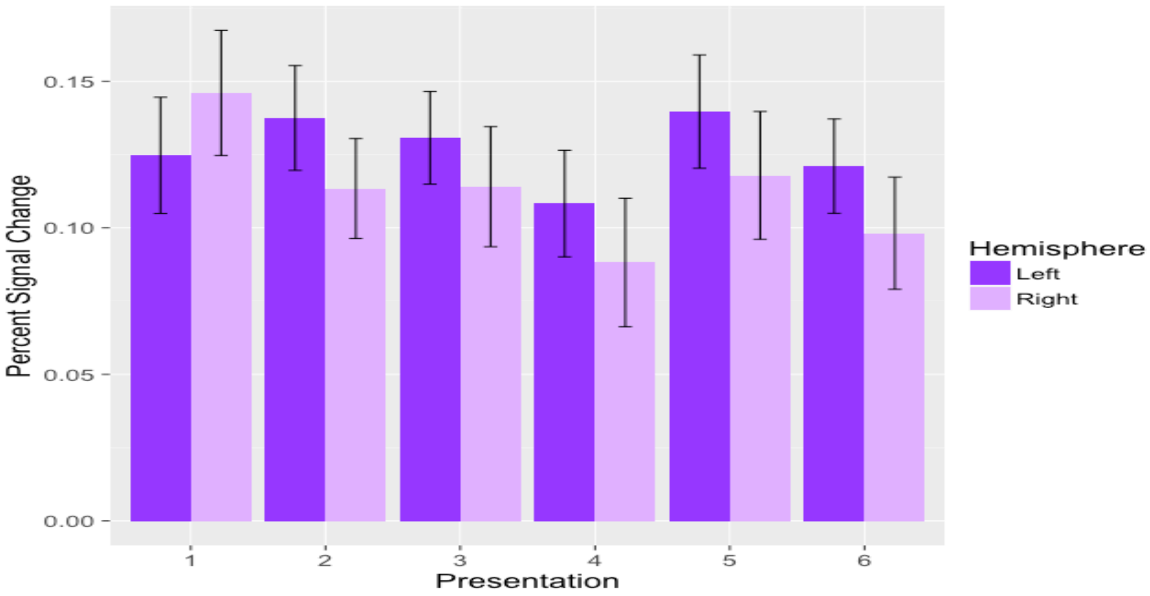

Figure 13. *Neural activation across presentation for tool images in the left and right VOTC-Tools. 2 participants did not have an identifiable right VOTC-Tools based on the functional definition used in this study. These participants were not included in the above graph but were not omitted in analyses that did not require a right VOTC-Tools ROI.*

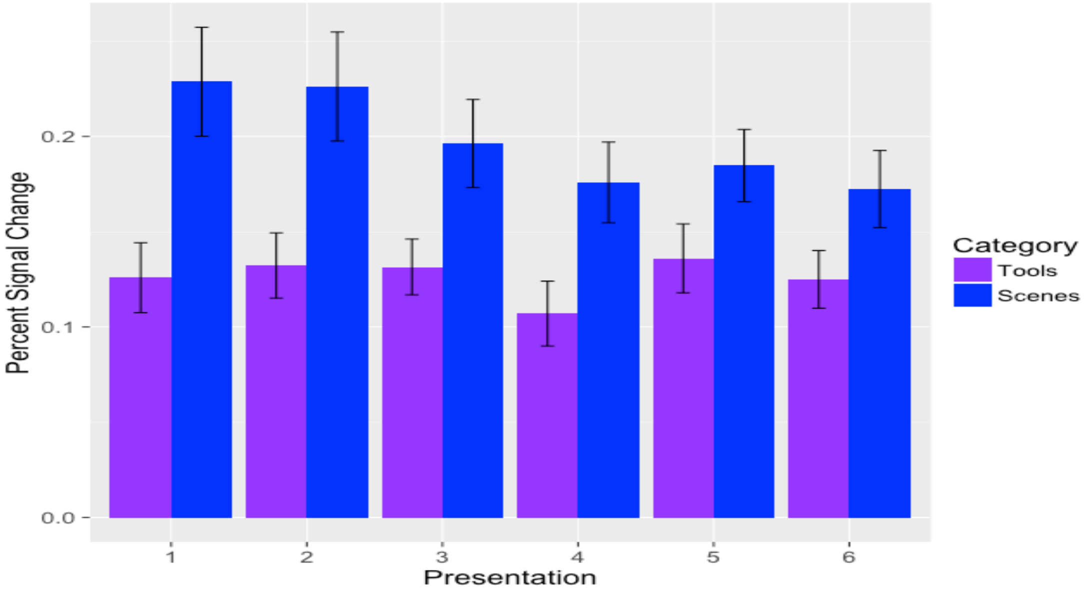

Figure 14. *Neural activation across presentation of tool and scene images in the left VOTC-Tools*

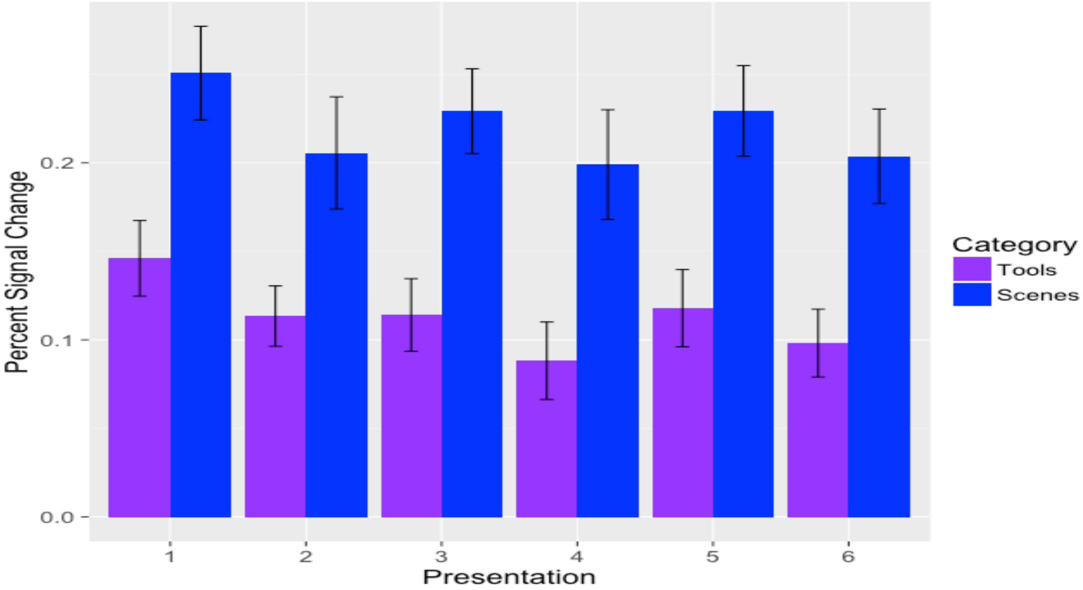

Figure 15. Neural activation across presentation of tool and scene stimuli in the right VOTC-Tools

left, $F(1, 26) = 34.25$, $p < 0.001$, $\eta^2 = 0.17$ (Figure 16), and right hemisphere, $F(1, 26) = 10.45$, $p < 0.001$, $\eta^2 = 0.10$ (Figure 17). The bilateral VOTC-Tools demonstrated greater activation in response to tool images than other regions.

FFA

A 1×6 ANOVA was used to determine if neural priming occurred in the FFA in response to repeated presentation of faces; this was done for both the left and right FFA. Within both the left and right FFA, there were no significant effects. A 2×6 ANOVA was used to identify laterality differences in the response to faces between the left and right FFA across presentations. No significant laterality differences were observed; however, a main effect of hemisphere was trending with $p = 0.066$ (Figure 18).

A 3×6 ANOVA was used to compare activation in the FFA for faces, animals, and scenes across presentations, using data from the left and right FFA. These categories were chosen because animals have been associated with increased activity in the FFA, and scenes are a non-preferred category of the FFA.

Within the left FFA (Figure 19), there was no evidence to suggest that the assumption of sphericity had been violated. A main effect of category, $F(2, 52) = 52.45$, $p < 0.001$, $\eta^2 = 0.30$, was observed; there was not a significant difference between the activation for faces and animals during the first presentation. A 1×6 ANOVA comparing neural activation from animal images across presentations found a significant main effect of presentation, $F(5, 130) = 3.29$, $p = 0.007$, $\eta^2 = 0.05$. A 1×6 ANOVA comparing neural activation from scene images across presentations did not find any significant effects. The left FFA demonstrated greater activation for preferred categories.

Within the right FFA (Figure 20), there was evidence to suggest that the assumption of

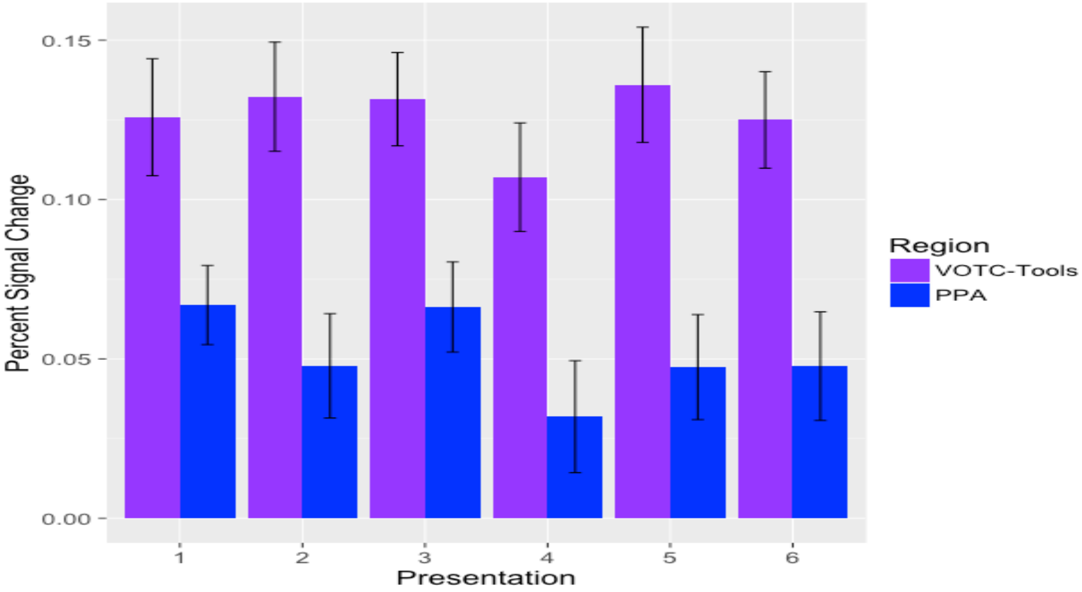

Figure 16. Neural activation in response to tool images in the left VOTC-Tools and left PPA across presentation

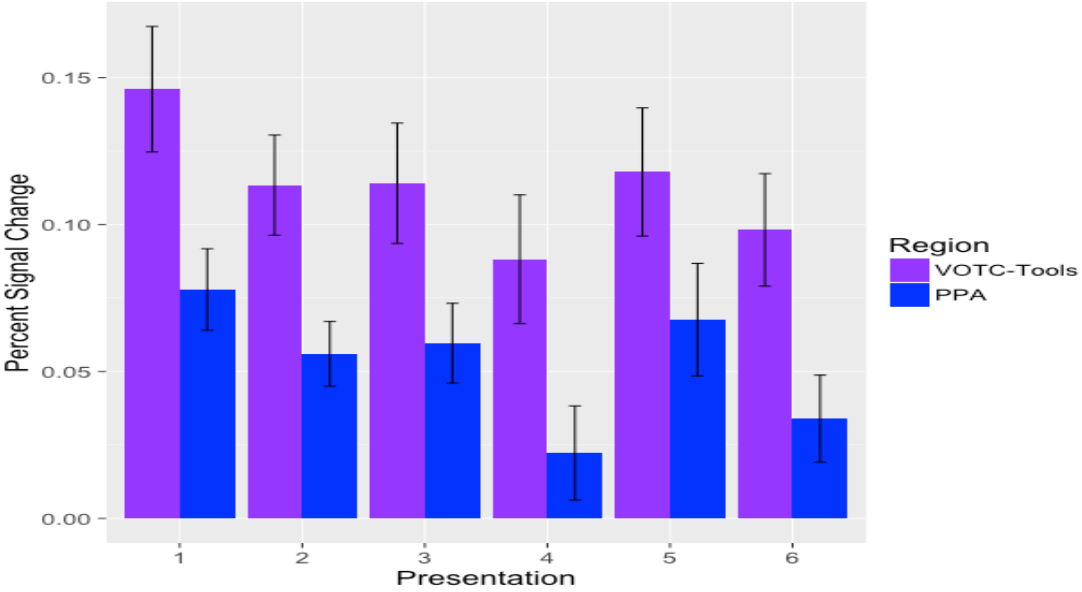

Figure 17. Neural activation in response to tool images in the right VOTC-Tools and right PPA across presentation

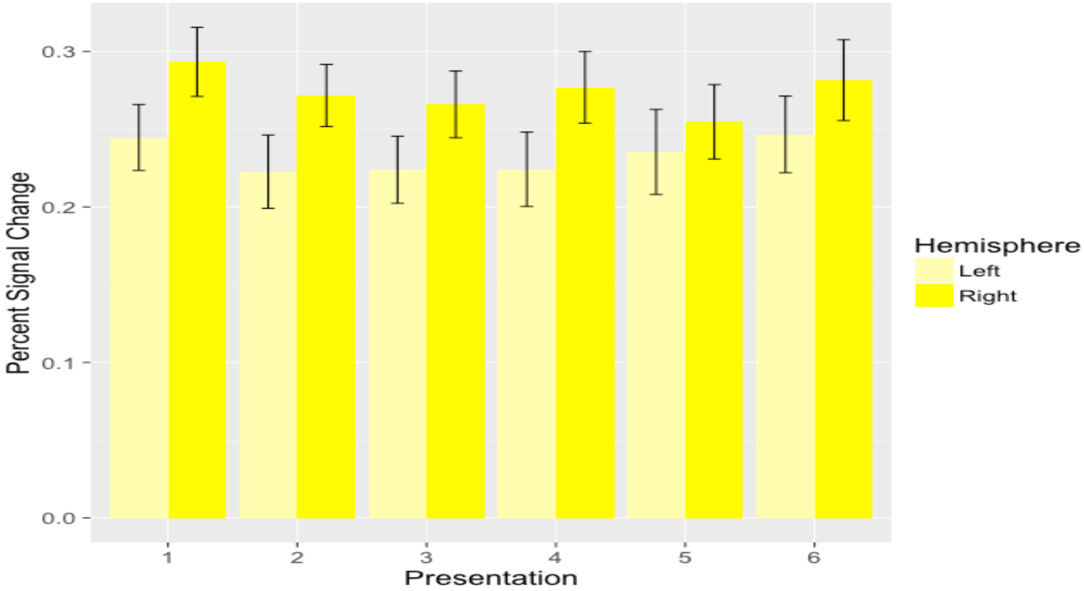

Figure 18. Neural activation across presentation for face images in the left and right FFA.

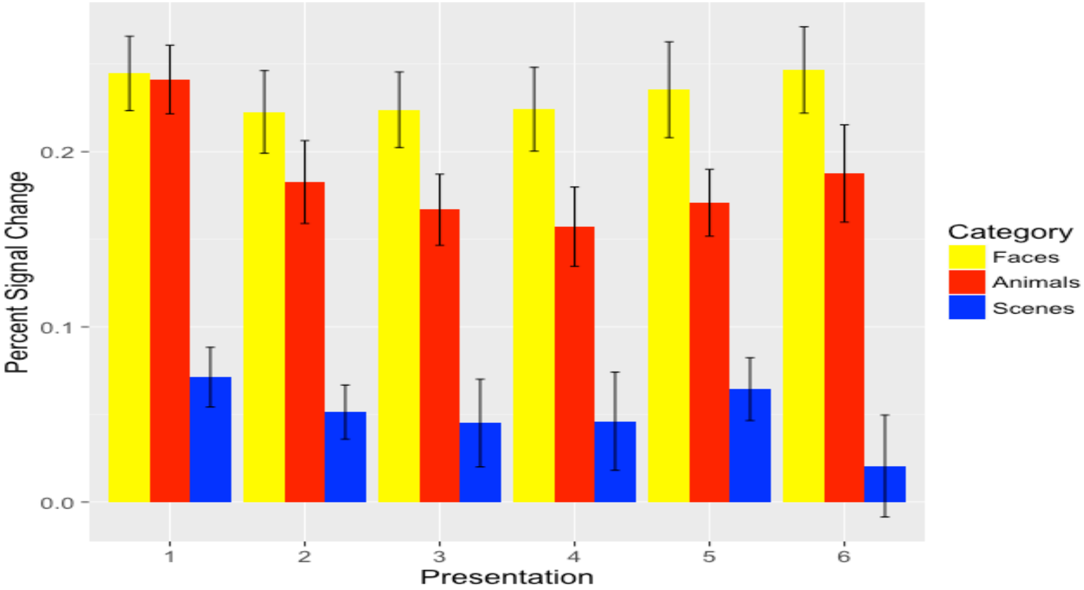

Figure 19. Neural activation across presentation for face, animal and scene images in the left FFA

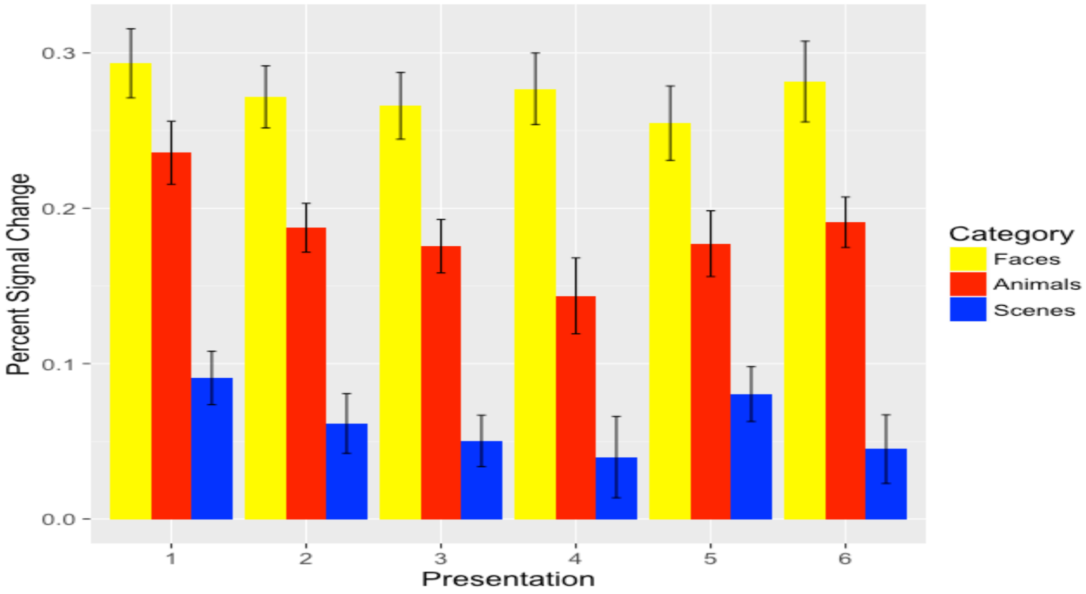

Figure 20. *Neural activation across presentation for face, animal and scene images in the right FFA*

sphericity had been violated in the category factor, $W = 0.47$, $p < 0.001$, $\varepsilon = 0.67$, therefore the degrees of freedom were corrected. A significant main effect of category, $F(2, 52) = 52.45$, $p < 0.001$, $\eta^2 = 0.30$ was observed; there was no significant difference between faces and animals at the first presentation A 1×6 ANOVA comparing neural activation from animal images across presentations found a significant main effect of presentation, $F(5, 130) = 4.46$, $p < 0.001$, $\eta^2 = 0.07$. A 1×6 ANOVA comparing neural activation from scene images across presentations did not find any significant effects. The right FFA demonstrated greater activation for preferred categories.

VOTC-Animals

There were three participants in which the left VOTC-Animals could not be identified and one in which the right lateral VOTC-Animals could not be identified. These participants were omitted from analyses that required the appropriate ROI.

A 1×6 ANOVA was used to determine if neural priming occurred in the VOTC-Animals in response to repeated presentation of animals; this was done for both the left and right VOTC-Animals. Data from both the left and right VOTC-Animals showed there was no evidence to suggest that the assumption of sphericity was violated. A main effect of presentation was observed in the right VOTC-Animals ($F(5, 125) = 5.48$, $p < 0.001$, $\eta^2 = 0.07$). Pair-wise t-tests on the data from the right VOTC-Animals found that presentation one was significantly different from presentations three, four, and five (Table 9). A main effect of presentation was trending in the left lateral fusiform gyrus, $p = 0.054$. A two-way ANOVA analysis did not find a significant interaction between hemisphere and presentation (Figure 21). A 2×6 ANOVA was used to identify laterality differences in the response to faces between the left and right FFA across presentations. No significant laterality differences were observed.

Table 9. Pairwise comparisons for neural activation for animal images across presentation in the right VOTC-Animals. Yellow cells are statistically significant pairwise comparisons, red cells are statistically insignificant comparisons, and blue cells are invalid or repeated comparisons

	Presentation Condition 1				
Presentation Condition 2	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	p >0.05				
Presentation 3	*t*= 3.40, p < 0.01	p > 0.05			
Presentation 4	*t*= 4.66, p < 0.01	p > 0.05	p > 0.05		
Presentation 5	*t*= 3.41, p < 0.01	p > 0.05	p > 0.05	p > 0.05	
Presentation 6	*t*= 4.29, p < 0.01	p > 0.05	p > 0.05	p > 0.05	p > 0.05

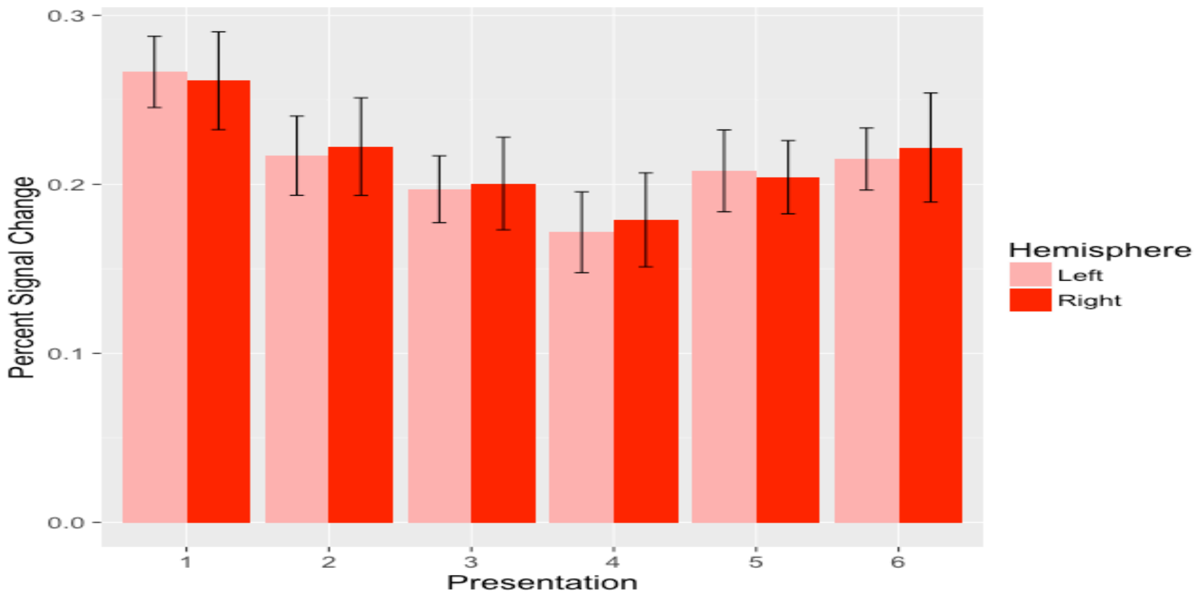

Figure 21. Neural activation across presentation of animal stimuli in the left and right VOTC-Animals. 3 participants did not have an identifiable right VOTC-Animals and one other participant did not have an identifiable left VOTC-Animals based on the functional definition used in this study. These participants were not included in the above graph but were not omitted in analyses that did not involve appropriate missing ROI.

A 3×6 ANOVA was used to compare activation in the VOTC-Animals for animals, faces, and scenes across presentations, using data from the left and right VOTC-Animals. These categories were chosen because faces have been associated with increased activity in the VOTC-Animals, and scenes are a non-preferred category of the VOTC-Animals.

Within the left VOTC-Animals (Figure 22), there was no evidence to suggest that the assumption of sphericity had been violated. A main effect of category, $F(2, 46) = 35.74$, $p < 0.001$, $\eta^2 = 0.19$, was observed. There was no significant difference between the activation for animals and faces at the first presentation. A 1×6 ANOVA comparing neural activation from face images across presentations did not find any significant effects. A 1×6 ANOVA comparing neural activation from scene images across presentations did not find any significant effects. The left VOTC-Animals showed greater activation and neural priming for preferred categories.

In the right VOTC-Animals (Figure 23), there was evidence to suggest that the assumption sphericity had been violated in the category factor, $W=0.47$, $p < 0.001$, $\varepsilon = 0.67$, therefore the degrees of freedom were corrected. A main effect of category, $F(1.34, 33.5) = 37.44$, $p < 0.001$, $\eta^2 = 0.29$, was observed. There was no significant difference between the activation for animals and faces at the first presentation. A 1×6 ANOVA comparing neural activation from face images across presentations did not find any significant effects. A 1×6 ANOVA comparing neural activation from scene images across presentations did not find any significant effects. The right VOTC-Animals showed greater activation and neural priming for preferred categories.

VWFA

A particular question regarding the VWFA was if the region displayed dissociable responses to real words and pseudowords over multiple presentations. To test this a 2×6

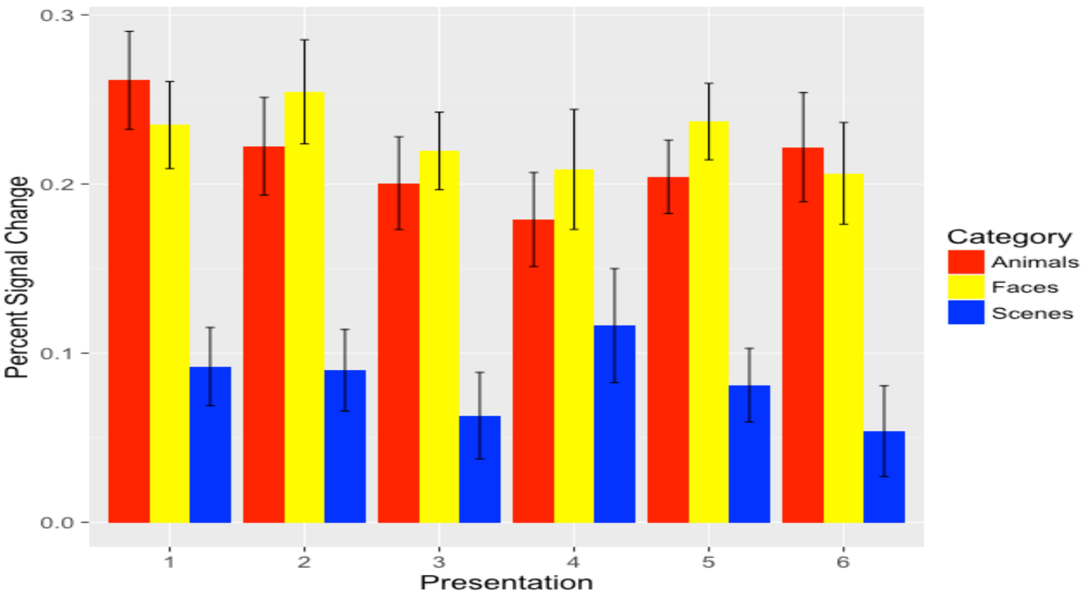

Figure 22. *Neural activation across presentation for animal, face and scene images in the left VOTC-Animals*

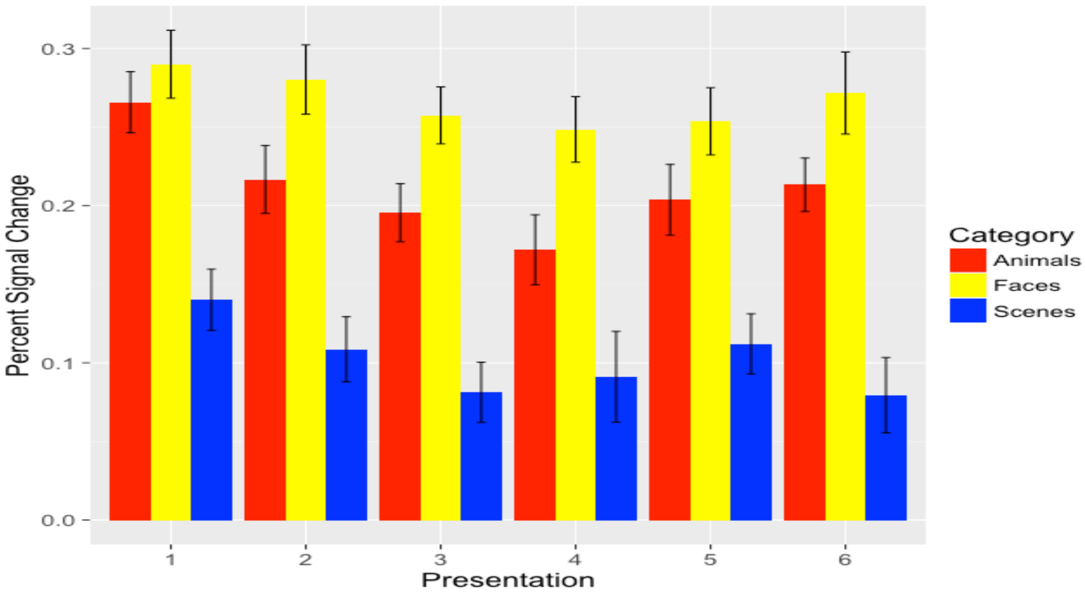

Figure 23. *Neural activation across presentation for animal, face and scene images in the right VOTC-Animals*

ANOVA was used to determine if neural priming occurred in the VWFA in response to repeated presentation of real words and pseudowords (Figure 24). Within the VWFA, there was no evidence to suggest that the assumption of sphericity had been violated. Significant main effects of presentation, $F(5,130) = 4.34$, $p < .01$, $\eta^2 = 0.04$, and category, $F(1,26) = 58.86$, $p < .001$, $\eta^2 = 0.14$, were observed. There was a significant interaction between presentation and category, $F(5,130) = 3.46$, $p < .01$, $\eta^2 = 0.01$, were observed. Pseudowords activated the VWFA more than real words at every presentation. Pair-wise t-tests on the data from real words found that presentation one was significantly different from presentations two, three, five, and six (Table 10). Pair-wise t-tests on the data from pseudowords found that presentation one was significantly different from presentations four, five, and six (Table 11).

To examine the preference of the VWFA for letter strings, activation for real words, pseudowords, and faces was compared using a 3×6 ANOVA (Figure 25). Faces were chosen for this analysis because of the debate within the literature regarding the VWFA's preference for letter strings compared to faces. Within the VWFA, there was evidence to suggest that the assumption sphericity was violated for the category factor, $W = 0.67$, $p < 0.01$, $\varepsilon = 0.79$, and the interaction between presentation and category, $W = 0.02$, $p < 0.001$, $\varepsilon = 0.78$). A main effect of category was observed, $F(1.58,41.08) = 109.42$, $p < .001$, $\eta^2 = 0.42$. There was a significant interaction between presentation and stimulus category, $F(7.80,202.80) = 2.606$, $p < .01$, $\eta^2 = 0.02$. Pair-wise t-tests found that real words and pseudowords evoked significantly greater activity than faces at every presentation. A 1×6 ANOVA comparing neural activation from face images across presentations did not find any significant effects. The VWFA demonstrated greater activation and neural priming for the preferred letter string categories.

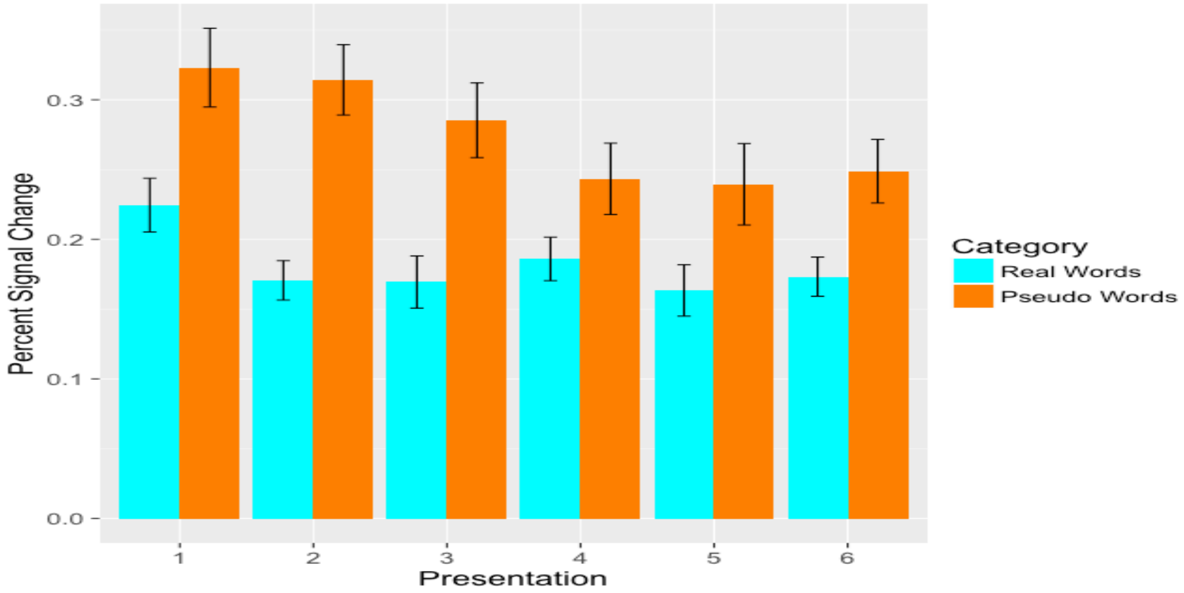

Figure 24. Neural activation across presentation for real words and pseudowords in the VWFA

Table 10. Pairwise comparisons for neural activation for real words across presentation in the VWFA. Yellow cells are statistically significant pairwise comparisons, red cells are statistically insignificant comparisons, and blue cells are invalid or repeated comparisons

	Presentation Condition 1				
Presentation Condition 2	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	*t*= 3.63, $p < 0.01$				
Presentation 3	*t*= 3.39, $p < 0.05$	$p > 0.05$			
Presentation 4	$p > 0.05$	$p > 0.05$	$p > 0.05$		
Presentation 5	*t*= 4.01, $p < 0.01$	$p > 0.05$	$p > 0.05$	$p > 0.05$	
Presentation 6	*t*= 2.92, $p < 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$

Table 11. Pairwise comparisons for neural activation for pseudowords across presentation in the VWFA. Yellow are statistically significant pairwise comparisons, red are statistically insignificant comparisons, and blue are invalid or repeated comparisons

	Presentation Condition 1				
Presentation Condition 2	Presentation 1	Presentation 2	Presentation 3	Presentation 4	Presentation 5
Presentation 2	$p > 0.05$				
Presentation 3	$p > 0.05$	$p > 0.05$			
Presentation 4	$p < 0.05$	$p < 0.05$	$p > 0.05$		
Presentation 5	$p < 0.05$	$p < 0.05$	$p > 0.05$	$p > 0.05$	
Presentation 6	$p < 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$

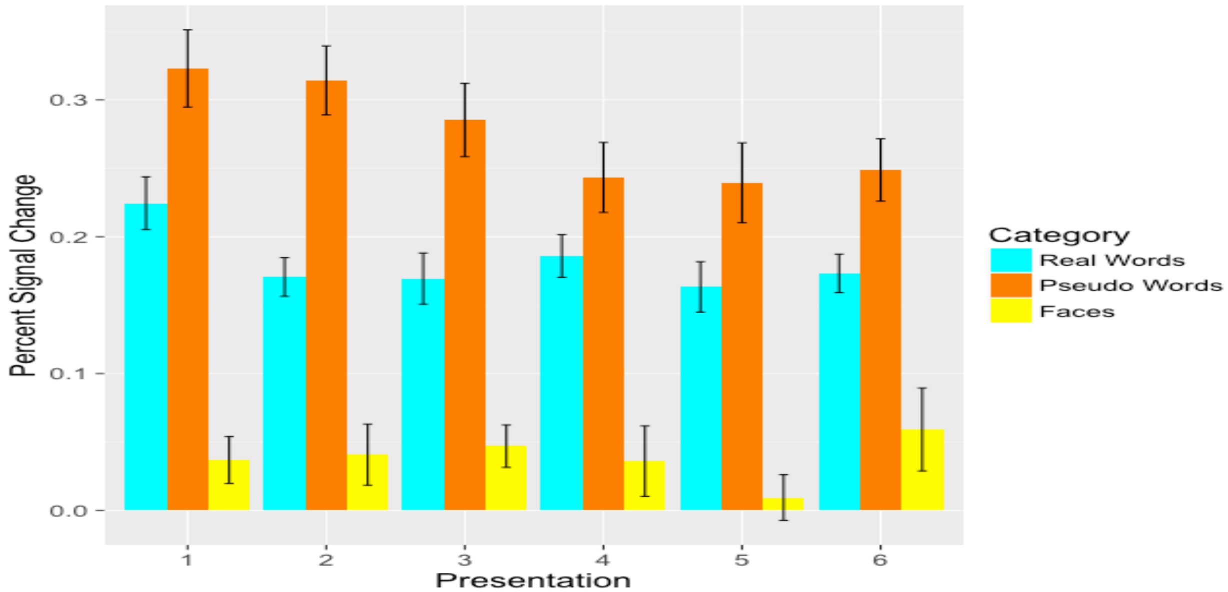

Figure 25. Neural activation across presentation for real words, pseudowords and face images in the VWFA

To further explore if the preference for real words in the VWFA, activation for real words in the VWFA and left FFA were compared with a 2×6 ANOVA (Figure 26). There was no evidence to suggest that the assumption sphericity had been violated. Significant main effects of region, $F(1,26) = 6.63$, $p = .002$, $\eta^2 = 0.07$, and presentation, $F(5,130) = 4.32$, $p = .001$, $\eta^2 = 0.04$, were observed. There was no significant interaction between region and presentation.

To further explore if the preference for pseudowords in the VWFA, activation for pseudowords in the VWFA and left FFA were compared with a 2×6 ANOVA (Figure 27). A significant main effect for region ($F(1,26) = 13.65$, $p = .001$, $\eta^2 = 0.14$) and presentation ($F(5,130) = 3.98$, $p = .002$, $\eta^2 = 0.04$) were found. A significant interaction between region and presentation was found, ($F(5,130) = 2.40$, $p = .04$, $\eta^2 = 0.01$).

Correlating Behavioural Priming and Repetition Suppression

Scenes and the PPA

In the left PPA, there were significant differences in RT and neural activity in response to presentation one relative to all subsequent presentations. The correlations between the magnitude of change in RT and the magnitude of change in neural activity between presentation one and every other presentation were not statistically significant.

In the right PPA there were significant differences in RT and neural activity in response to presentation one relative to presentations three, four, five, and six. The correlations between the magnitude of change in RT and the magnitude of change in neural activity between presentation one and every other presentation were not statistically significant.

Animals and the VOTC-Animals

There were no significant differences in neural activity between presentations in the left lateral fusiform gyrus

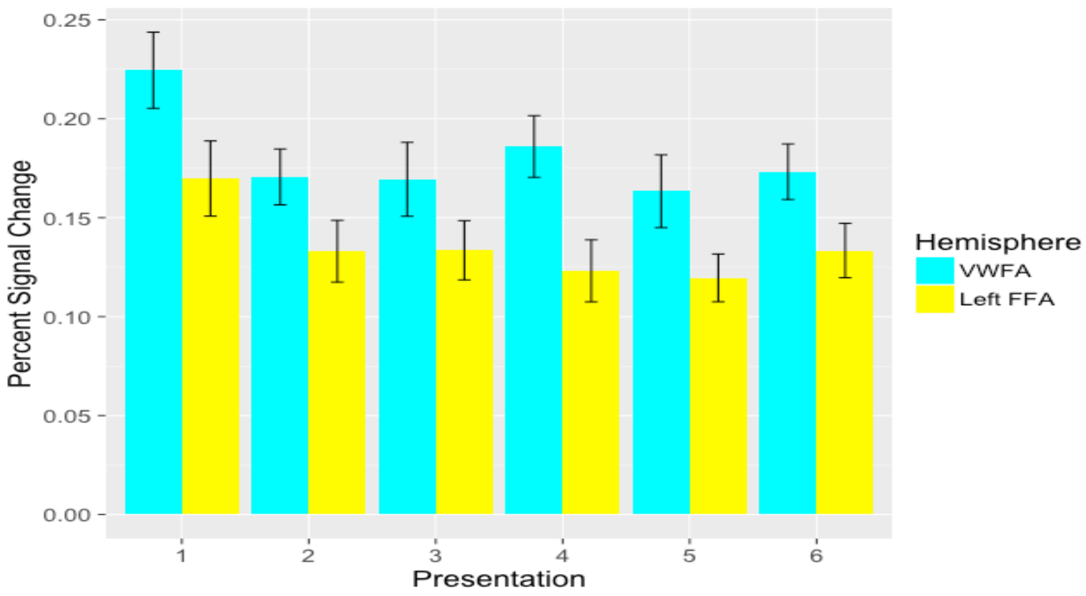

Figure 26. Neural activation for real words across presentation in the VWFA and left FFA

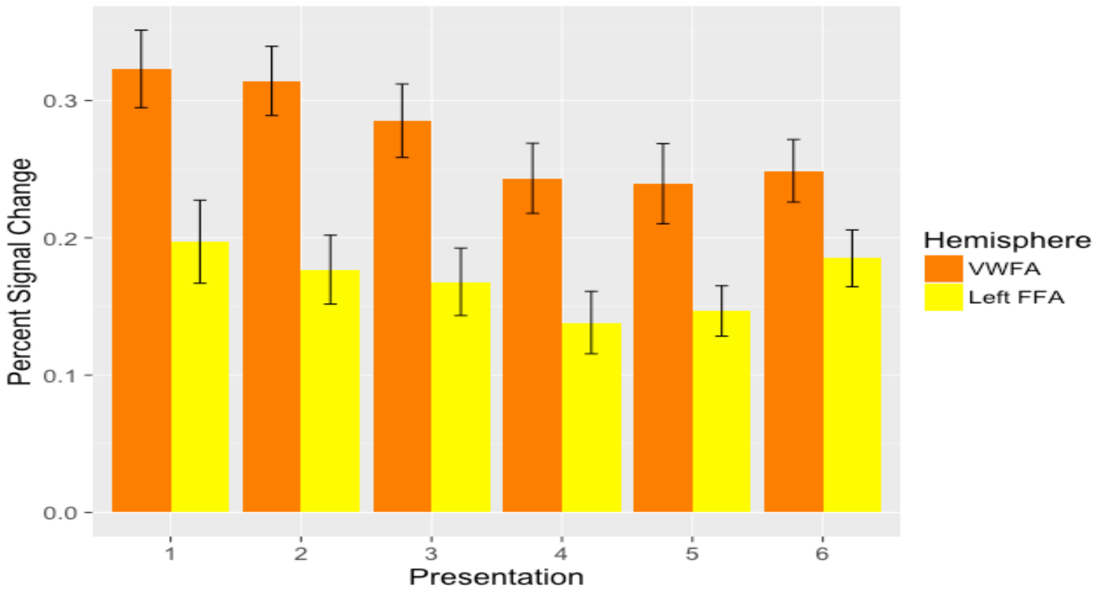

Figure 27. Neural activation for pseudowords across presentation in the VWFA and left FFA

In the right lateral fusiform gyrus, there were significant differences in RT and neural activity in response to presentation one relative to presentations three, four, five and six. The correlations between the magnitude of change in RT and the magnitude of change in neural activity between presentation one and every other presentation were not statistically significant.

Real Words and the VWFA

In the VWFA, there were significant differences in RT and neural activity in response to presentation one relative to presentations two, three, five, and six. The correlation between the magnitude of change in RT and the magnitude of change in neural activity was significant between presentation one and two, $r(25) = 0.44$, $p < 0.05$. There were no other significant correlations.

Pseudowords and the VWFA

In the VWFA, there were significant differences in RT and neural activity in response to presentation one relative to presentations four, five, and six. The correlations between the magnitude of change in RT and the magnitude of change in neural activity between presentation one and every other presentation were not statistically significant.

Tools and the VOTC-Tools

There was no neural priming in the left or right medial fusiform gyrus for tools, hence this a correlation between neural priming and behavioural priming could not be calculated.

Faces and the FFA

There was no repetition suppression in the left or right FFA for faces, hence this analysis was not conducted.

Seed PLS

Right PPA

The seed PLS using activity in the right PPA in response to scene images produced one significant LV ($p = 0.004$, 28.81% of covariance accounted for). All six presentations of scene stimuli had a significant negative correlation between brain scores and seed activity (Figure 28). There were no significant differences between these presentations. Functional connectivity between the right PPA and critical scene processing regions such as the RSC and TOS was observed, but did not change significantly as a function of repetition (Figure 29; Table 12).

Left PPA

The seed PLS using activity in the left PPA in response to scene images produced one significant LV ($p = 0.002$, 26.94% of covariance accounted for). Presentations one, three, five, and six had a significant negative correlation between brain scores and seed activity. There were no significant differences between these presentations. Presentation 4 had a significant positive correlation between brain scores and seed activity, but there were no clusters of voxels corresponding to a positive BSR that were above threshold (Figure 30). Functional connectivity between the left PPA and critical scene processing regions such as the RSC and TOS was observed (Figure 31; Table 13).

Left VOTC-Tools

The seed PLS using activity in the left VOTC-Tools in response to tool images produced one significant LV ($p = 0.008$, 24.66% of covariance accounted for). All six presentations of tool stimuli had a significant negative correlation between brain scores and seed activity (Figure 32). There were no significant differences between the presentations. Functional connectivity between the left VOTC-Tools and critical tool processing regions, such as the IPS and vPM

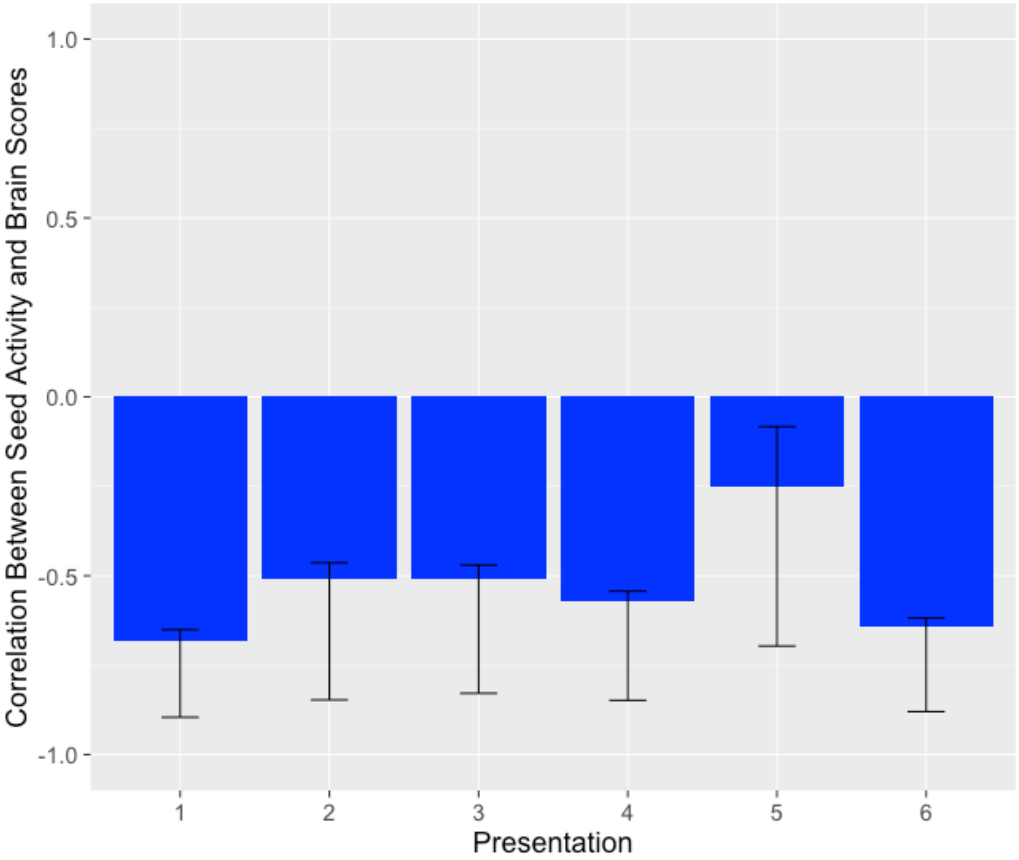

Figure 28. The task-related functional connectivity of the right PPA across presentation (LV1)

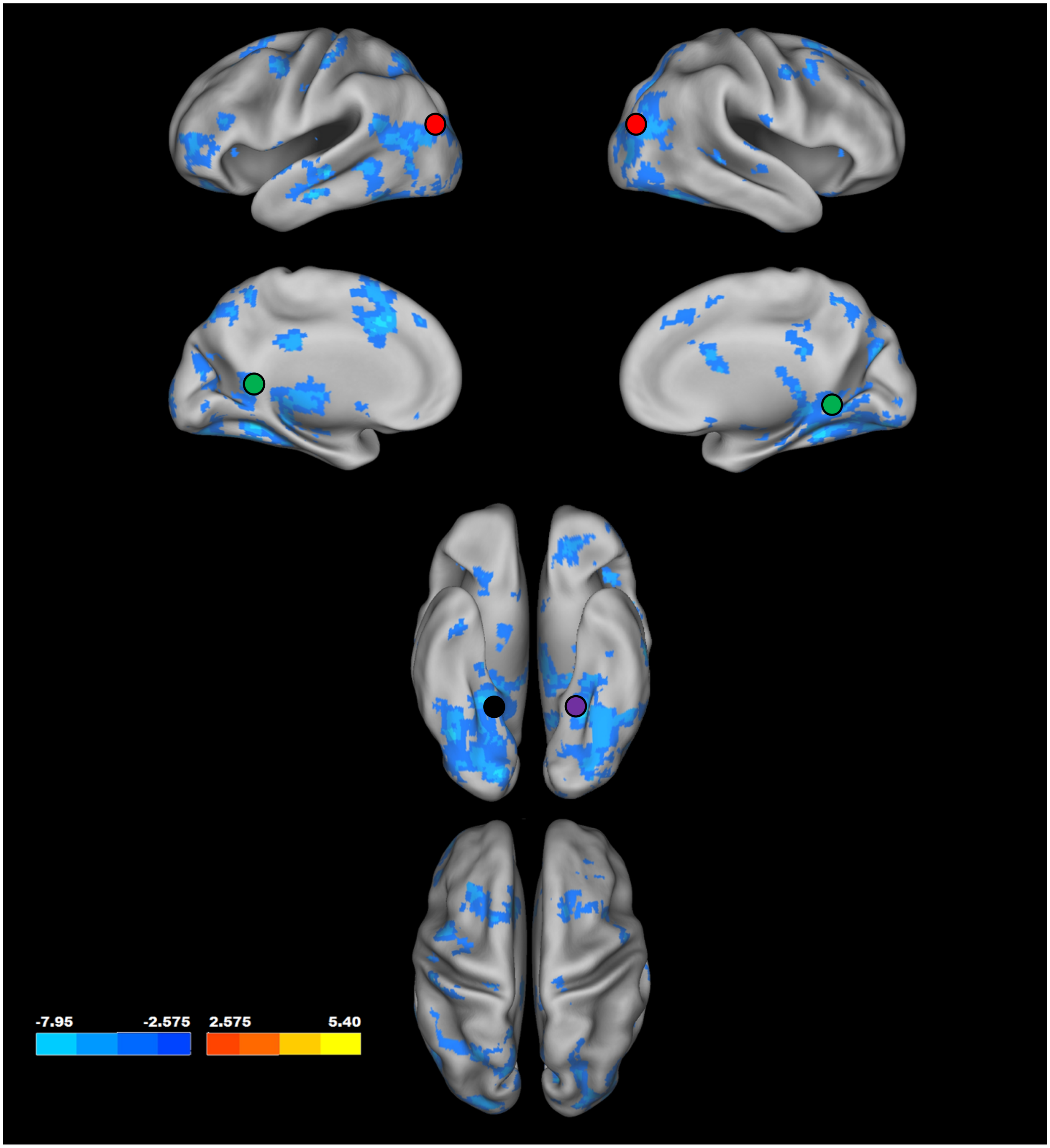

Figure 29. The temporal brain pattern of the right PPA observed at lag 2 (LV1). The brain pattern includes the right PPA (black circle), left PPA (purple circle), bilateral RSC (green circle), and the bilateral TOS (red circle)

Table 12. Cluster report for LV 1 at lag 2 in the right PPA seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01. Of note there were no clusters of voxels associated with a positive BSR above threshold

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one, two three, four, five, six > 0						
Parahippocampal Gyrus	Right	30	-42	-15	-7.86	5554
Inferior Temporal Gyrus	Left	-60	-18	-21	-7.09	242
Anterior Cingulate Cortex	Left	-6	15	36	-6.94	603
Primary Motor Cortex	Left	-12	-24	63	-5.90	41
Superior Frontal Gyrus	Right	21	12	60	-5.76	74
Premotor Cortex	Left	-45	0	48	-5.34	104
Posterior Cingulate Cortex	Left	-3	-30	30	-5.00	94
Putamen	Left	-21	-3	12	-4.80	20
Anterior Cingulate Cortex	Right	6	12	21	-4.79	48
Inferior Frontal Sulcus	Right	36	9	42	-4.71	81
Cerebellum	Left	-6	-72	-39	-4.70	50
Thalamus	Right	18	-9	15	-4.69	29
Ventrolateral PFC	Right	27	24	24	-4.68	57
Primary Somatosensory Cortex	Left	-51	-21	30	-4.59	36
Anterior Insula	Left	-39	15	12	-4.52	111
Posterior Superior Temporal Sulcus	Right	45	-36	3	-4.46	38
Orbitofrontal Cortex	Right	27	21	-24	-4.43	32
Ventrolateral Prefrontal	Left	-42	45	6	-4.40	296
Primary Motor Cortex	Right	15	-21	57	-4.38	55
Transverse Occipital Sulcus	Right	15	-93	27	-4.16	35
Superior Temporal Gyrus	Right	66	-15	12	-4.13	27
Primary Somatosensory Cortex	Right	24	-30	48	-4.08	21
Inferior Temporal Gyrus	Right	36	-3	-45	-3.96	33
Posterior Orbitofrontal Gyrus	Right	3	9	-15	-3.82	41
Hippocampus	Right	30	-15	-9	-3.78	33
Anterior Insula	Right	33	27	6	-3.47	20
Superior Temporal Gyrus	Right	54	-12	-3	-3.28	27

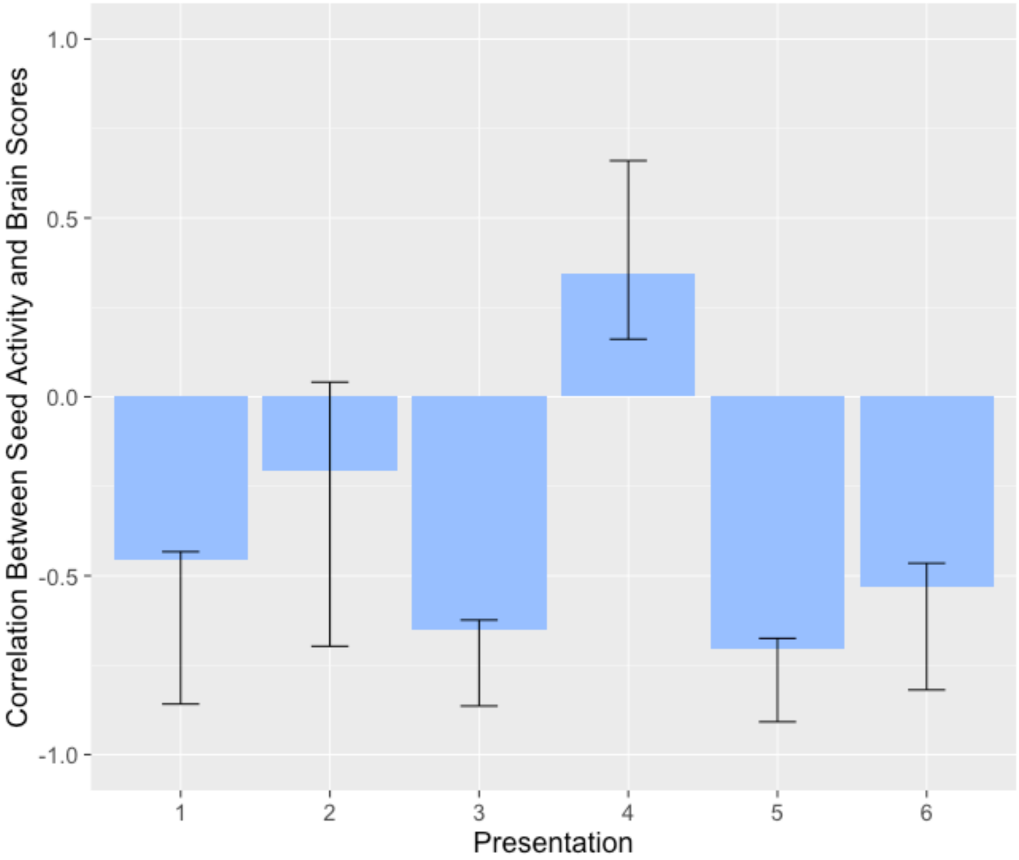

Figure 30. The task-related functional connectivity of the left PPA across presentation (LV1)

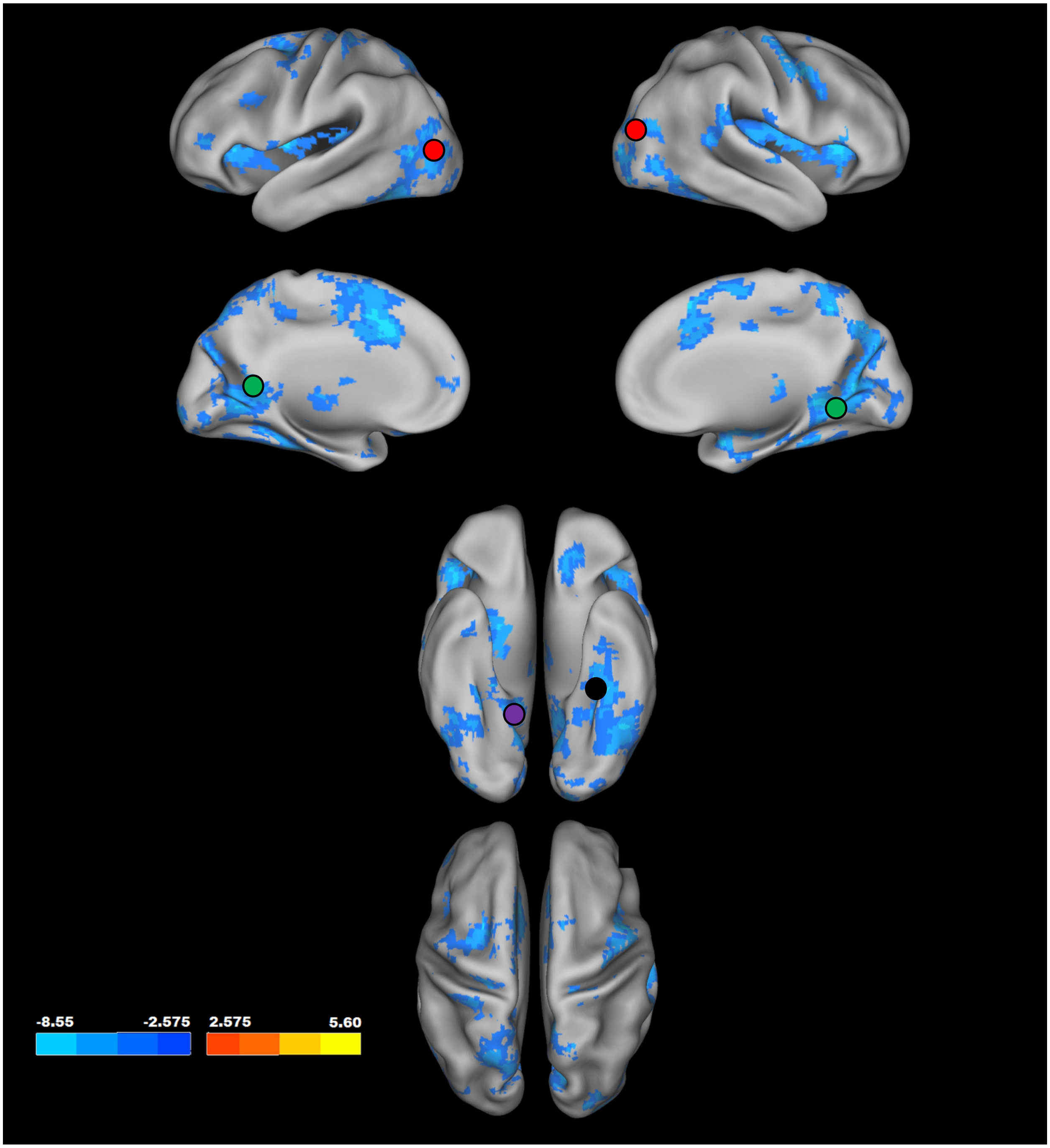

Figure 31. The temporal brain pattern of the left PPA observed at lag 2 (LV1). The brain pattern includes the left PPA (black circle), right PPA (purple circle), bilateral RSC (green circle), and the bilateral TOS (red circle)

Table 13. Cluster report for LV 1 at lag 2 in the left PPA seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01. Of note there were no clusters of voxels associated with a positive BSR above threshold

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one, three, five, six > Presentation four, 0						
Parahippocampal Gyrus	Left	-45	-54	-12	-8.53	2354
Inferior Frontal Gyrus	Right	45	24	9	-7.27	288
Transverse Occipital Sulcus	Right	33	-84	24	-6.61	620
Thalamus	Right	18	-12	18	-6.05	50
Anterior Insula	Left	-33	21	6	-6.01	105
Transverse Occipital Sulcus	Left	-36	-84	9	-5.76	205
Anterior Cingulate Cortex	Right	12	18	39	-4.99	209
Thalamus	Right	15	-30	18	-4.67	43
Intraparietal Sulcus	Left	-39	-42	39	-4.56	24
Supramarginal Gyrus	Right	39	-36	30	-4.52	27
Thalamus	Left	-12	-6	15	-4.36	29
Posterior Superior Temporal Sulcus	Left	57	-45	12	-4.26	30
Anterior Insula	Right	33	3	-21	-4.17	20
Fusiform Gyrus	Left	39	-6	-39	-4.17	29
Inferior Frontal Gyrus	Left	-33	30	-6	-4.05	23
Primary Somatosensory Cortex	Right	66	-15	24	-3.90	84
Inferior Frontal Gyrus	Right	51	-12	-33	-3.80	35
Occipital Pole	Right	-15	-96	-15	-3.74	47
Posterior Insula	Right	39	-9	15	-3.62	34
Premotor Cortex	Left	-54	9	36	-3.53	25
Hippocampus	Right	27	-9	-27	-3.50	41
Inferior Parietal Lobule	Left	-48	-48	54	-3.18	27

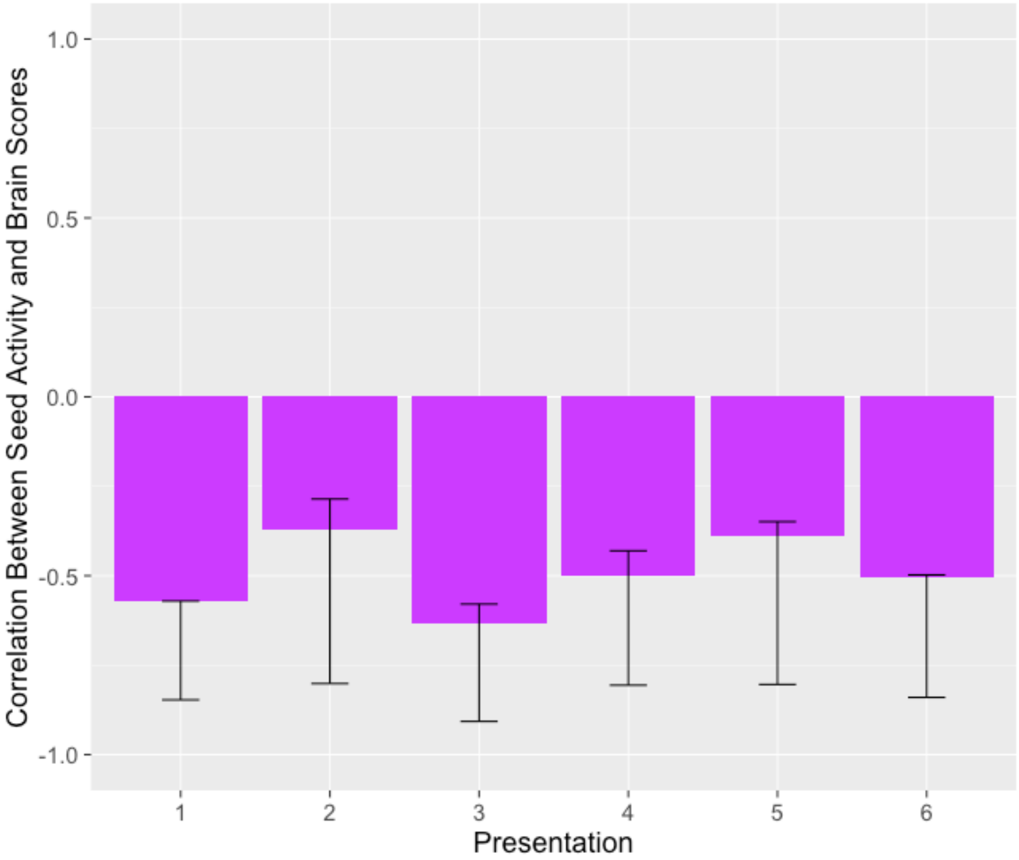

Figure 32. The task-related functional connectivity of the left VOTC-Tools across presentation (LV1)

cortex, was observed, and was heavily left lateralized, though this did not change over repetitions (Figure 33; Table 14).

Right VOTC-Tools

The seed PLS using activity in the right VOTC-Tools in response to tool images produced one significant LV (*p* = 0.002, 27.87% of covariance accounted for). Presentations one, three, and four of tool stimuli had significant correlations between positive brain scores and seed activity. There were no significant differences between these presentations (Figure 34). Functional connectivity between the right VOTC-Tools and critical tool processing regions, such as the IPS and vPM cortex, was observed (Figure 35; Table 15)

Right VOTC-Animals

The seed PLS using activity in the right VOTC-Animals in response to animal images produced one significant LV (*p* = 0.006, 24.65% of covariance accounted for). All six presentations of animal stimuli had significant correlations between negative brain scores and seed activity (Figure 36). There were no significant differences between these presentations. The LV showed functional connectivity between the right VOTC-Animals and critical animals processing regions the amygdala, pSTS, and EBA (Figure 37; Table 16).

Left VOTC-Animals

The seed PLS using activity in the left VOTC-Animals in response to animal images produced two significant LVs. In LV 1 (*p* = 0.002, 26.92% of covariance accounted for), presentations three and five for animal stimuli had significant positive correlation between brain scores and seed activity. There was no significant difference between presentations three and five. Presentations one and six had significant negative correlations between brain scores and

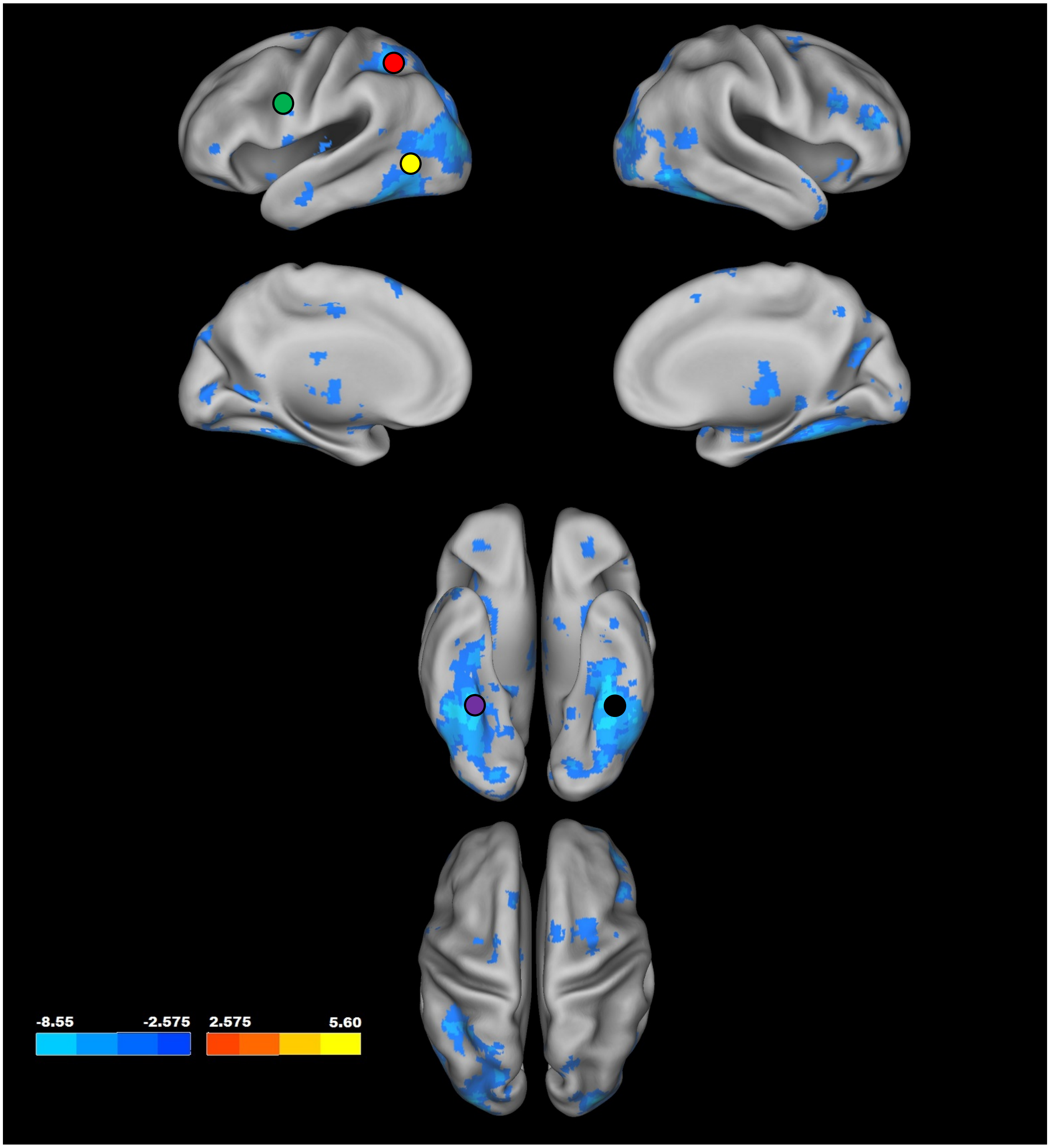

Figure 33. *The temporal brain pattern of the left VOTC-Tools observed at lag 3 (LV1). The brain pattern includes the left VOTC-Tools (black circle), right VOTC-Tools (purple circle), left vPM cortex (green circle), left IPS (red circle) and the left pMTG (yellow circle)*

Table 14. Cluster report for LV 1 at lag 3 in the left VOTC-Tools seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01. Of note there were no clusters of voxels associated with a positive BSR above threshold

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one, two, three, four, five, six > 0						
Medial Fusiform Gyrus	Left	-33	-54	-21	-9.09	2273
Hippocampus	Right	30	-12	-15	-8.91	2634
Intraparietal Sulcus	Left	-36	-90	15	-7.90	834
Medial Orbitofrontal Cortex	Right	18	33	-18	-6.00	43
Ventrolateral PFC	Right	45	42	15	-5.89	57
Posterior Cingulate Cortex	Left	-30	-57	6	-5.70	148
Hippocampus	Right	21	-33	0	-5.53	43
Dorsolateral PFC	Right	33	57	6	-5.17	40
Fusiform Gyrus	Left	-36	-6	-30	-5.10	33
Hippocampus	Left	-21	-6	45	-4.93	25
Ventral Premotor Cortex	Left	-60	3	30	-4.92	99
Inferior Frontal Gyrus	Right	48	21	21	-4.90	103
Cerebellum	Left	-6	-51	-30	-4.52	34
Inferior Frontal Gyrus	Right	42	18	-36	-4.35	55
Superior Frontal Gyrus	Right	18	3	48	-4.29	145
Medial Orbitofrontal Cortex	Left	-42	36	0	-4.10	25
Premotor Cortex	Left	-21	-3	66	-4.07	51
Anterior Middle temporal Gyrus	Left	-63	-6	-18	-4.06	47
Supplementary Motor Area	Left	-6	21	63	-4.03	53
Medial Orbitofrontal cortex	Left	-24	36	-12	-3.82	25
Premotor Cortex	Right	48	0	39	-3.63	41

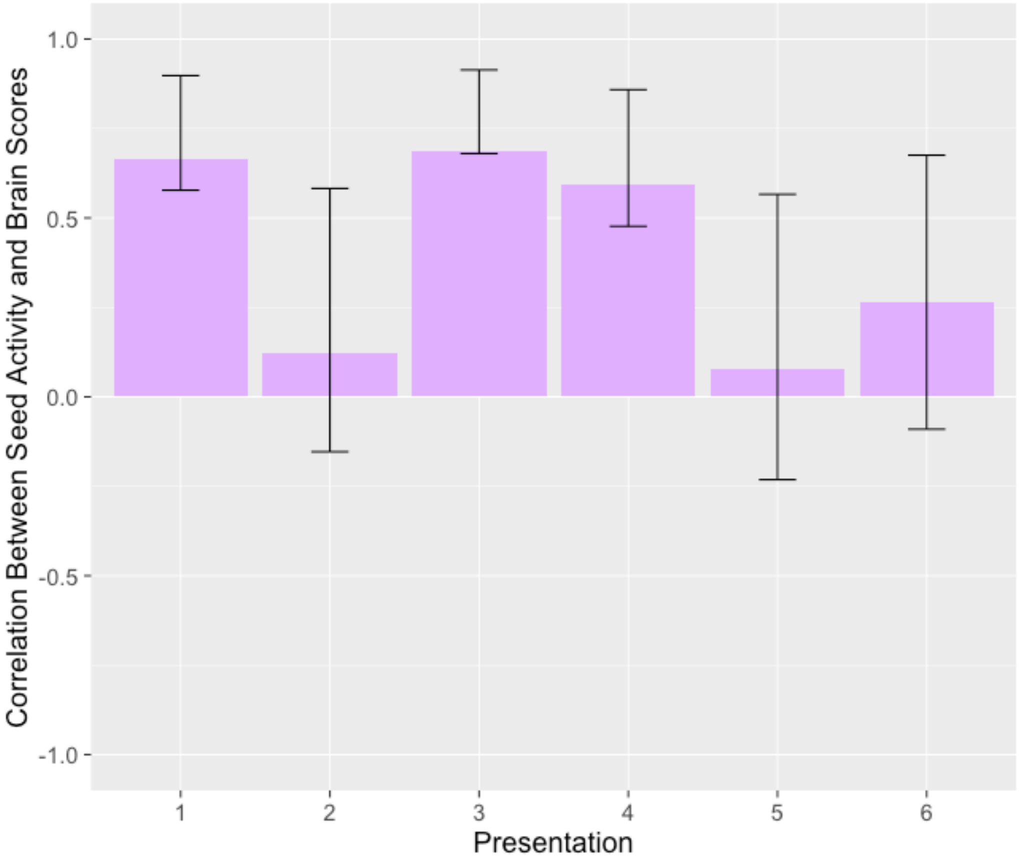

Figure 34. The task-related functional connectivity of the right VOTC-Tools across presentation (LV1)

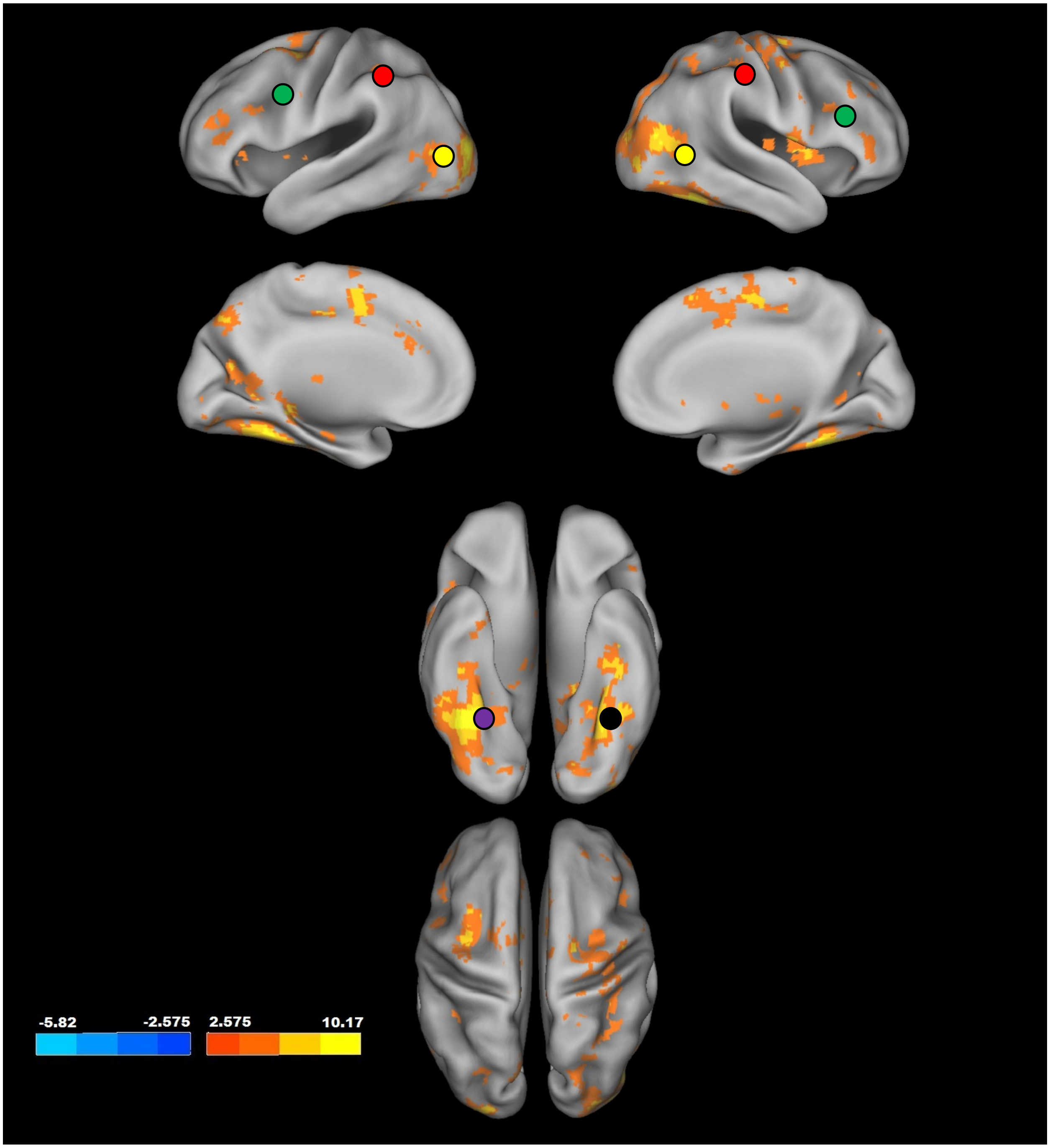

Figure 35. The temporal brain pattern of the right VOTC-Tools observed at lag 3 (LV1). The brain pattern includes the right VOTC-Tools (black circle), left VOTC-Tools (purple circle), bilateral vPM cortex (green circle), bilateral IPS (red circle) and the bilateral pMTG (yellow circle)

Table 15. Cluster report for LV 1 at lag 3 in the right VOTC-Tools seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01. Of note there were no clusters of voxels associated with a negative BSR above threshold

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one, three, four > 0						
Medial Fusiform Gyrus	Right	27	-54	-15	10.17	1643
Medial Fusiform Gyrus	Left	-33	-48	-18	8.17	1989
Posterior Cingulate Cortex	Right	6	-27	-36	6.16	47
Hippocampus	Right	24	-27	0	6.05	410
Posterior Insula	Right	42	-3	6	5.60	40
Cerebellum	Right	9	-57	-30	5.59	39
Anterior Cingulate Cortex	Left	-9	3	39	5.52	58
Anterior Insula	Right	33	30	3	4.83	75
Putamen	Left	-21	21	-6	4.82	249
Posterior Insula	Left	-39	-30	24	4.64	53
Supplementary Motor Area	Right	6	-3	51	4.59	120
Ventral Premotor Cortex	Right	39	-3	57	4.22	118
Putamen	Right	30	-9	-6	4.12	37
Intraparietal Sulcus	Right	27	-54	54	4.09	75
Ventrolateral PFC	Right	45	39	9	4.03	35
Superior Temporal Sulcus	Right	54	-30	24	3.92	22
Caudate Nucleus	Right	21	9	12	3.74	32
Anterior Superior Temporal Gyrus	Right	57	-6	-9	3.49	27
Precuneus	Right	6	-66	54	3.47	21
Inferior Parietal Lobule	Right	33	-36	48	3.39	48

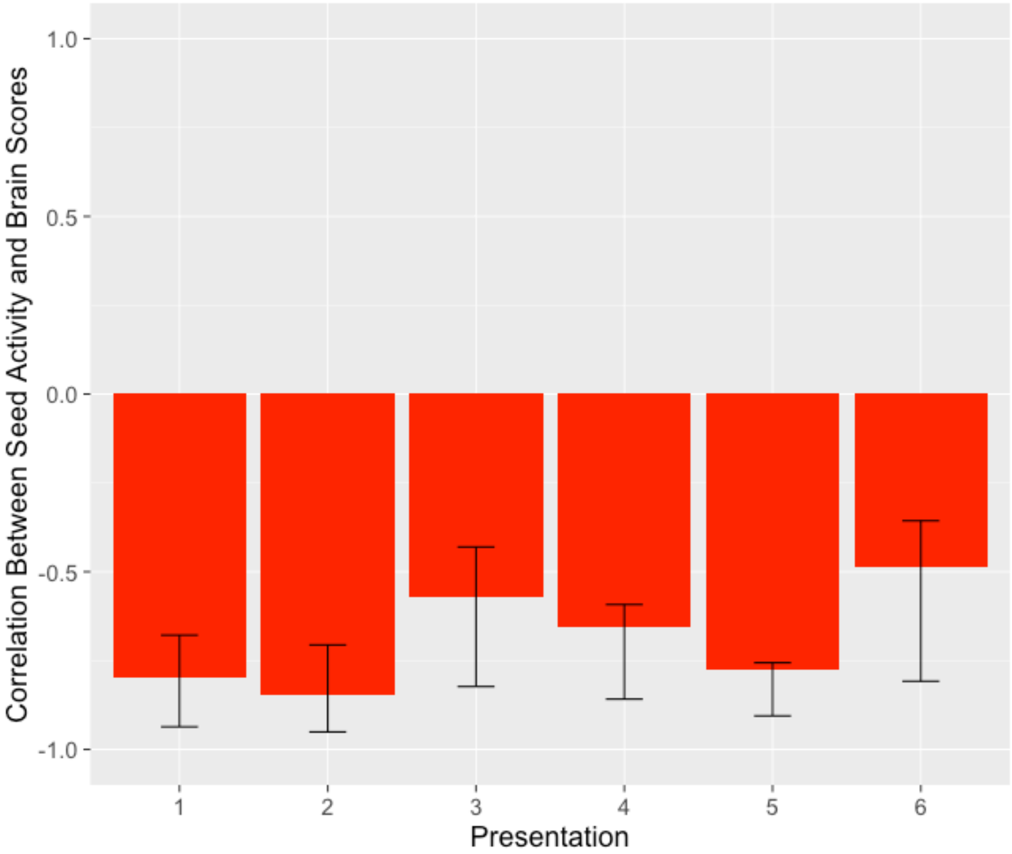

Figure 36. The task-related functional connectivity of the right VOTC-Animals across presentation (LV1)

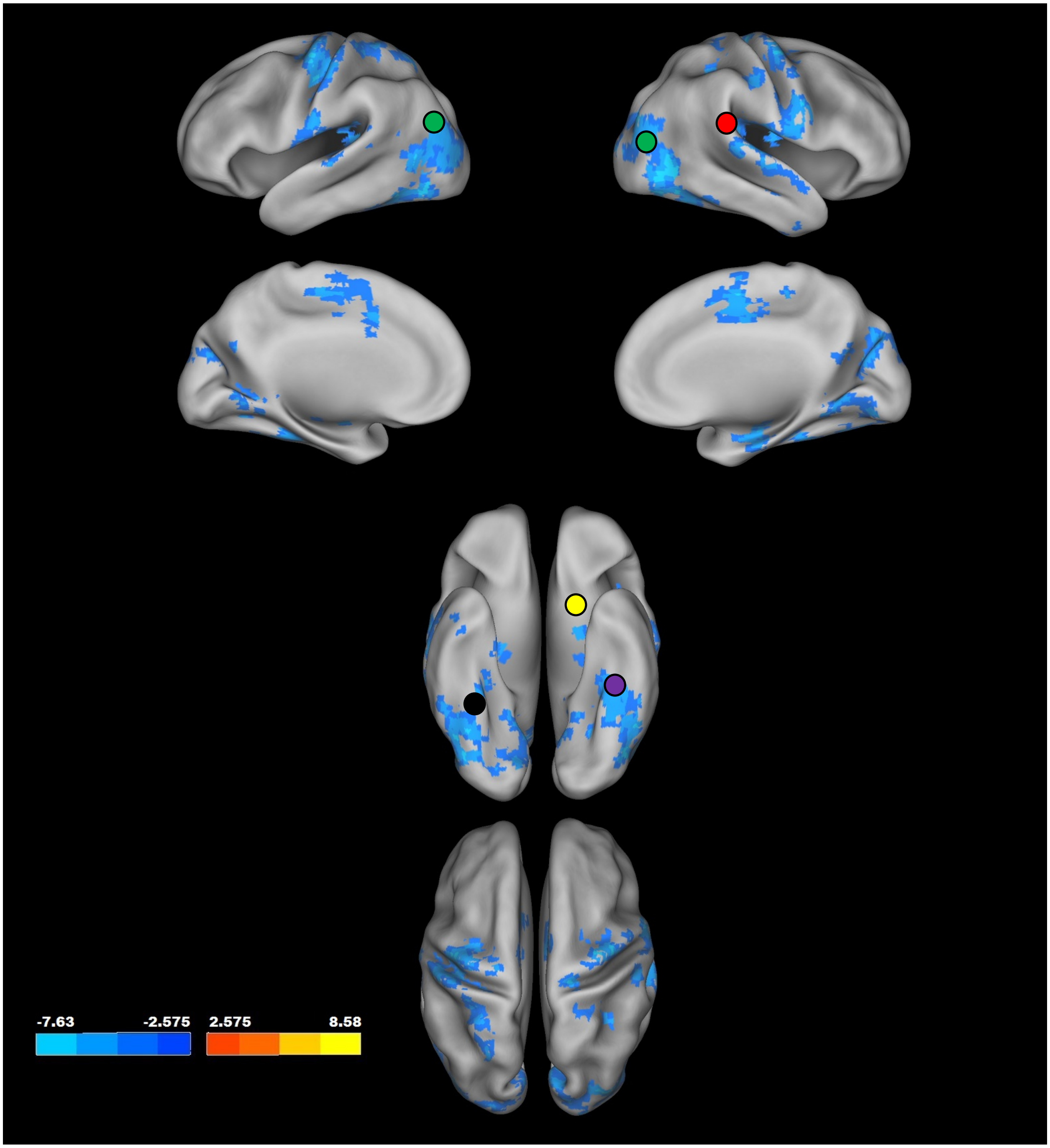

Figure 37. *The temporal brain pattern of the right VOTC-Animals observed at lag 2 (LV1). The brain pattern includes the right VOTC-Animals (black circle), left VOTC-Animals (purple circle), bilateral EBA (green circle), right pSTS (red circle) and the left amygdala (yellow circle)*

Table 16 Cluster report for LV 1 at lag 2 in the right VOTC-Animals seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01. Of note there were no clusters of voxels associated with a positive BSR above threshold

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one two, three, four, five six > 0						
Lateral Fusiform Gyrus	Right	45	-57	-6	-7.05	3051
Cerebellum	Right	0	-63	-24	-6.63	384
Supplementary Motor Cortex	Right	33	-12	57	-6.31	242
Superior Parietal Lobule	Right	21	-48	54	-6.26	168
Hippocampus	Right	18	-15	-15	-6.19	127
Posterior Insula	Right	39	-36	24	-6.14	743
Primary Motor Cortex	Left	-45	-15	54	-5.93	1497
Primary Motor Cortex	Right	18	-24	66	-5.82	87
Posterior Superior Temporal Sulcus	Right	42	0	-33	-4.46	29
Middle temporal Gyrus	Left	-39	-54	15	-4.24	27
Amygdala	Left	-9	-9	-15	-4.10	28
Thalamus	Left	-18	-21	3	-4.05	25
Inferior Frontal Gyrus	Left	-39	12	15	-4.03	21
Primary Somatosensory Cortex	Right	54	-18	42	-3.80	53

seed activity, but no clusters were above threshold (Figure 38). The left VOTC-Animals showed connectivity with the left superior temporal sulcus (Figure 39; Table 17).

In LV 2 (*p* = 0.03, 20.89% of covariance accounted for), all six presentations of animal stimuli had a significant positive correlation between positive brain scores and seed activity (Figure 40). There were no significant differences between these presentations. Functional connectivity between the left VOTC-Animals and critical animals processing regions, such as the amygdala, pSTS, and EBA was observed (Figure 41; Table 18).

Visual Word Form Area

The seed PLS with the VWFA using activity in response to real words produced one significant LV (*p* = 0.004, 25.51% of covariance accounted for). Presentation six had a significant positive correlation between brain scores and seed activity. All other presentations had a significant negative correlation brain scores and seed activity. There were no significant differences between them (Figure 42). The VWFA showed connectivity with regions from the dorsal attention network in the early presentations and then showed connectivity with default network regions at presentation six (Figure 43; Table 19).

A second trending LV (p = 0.0818, 18.32% of covariance accounted for) was also observed. In this LV all six presentations had a significant positive correlation between brain scores and seed activity (Figure 44). There were no differences between these presentations. Functional connectivity between the VWFA and critical reading/language processing regions, such as Broca's area, angular gyrus, and middle temporal gyrus was observed (Figure 45; Table 20).

The seed PLS using activity in the VWFA in response to pseudowords produced one significant LV (*p* = 0.018, 25.36% of covariance accounted for); presentation six had a

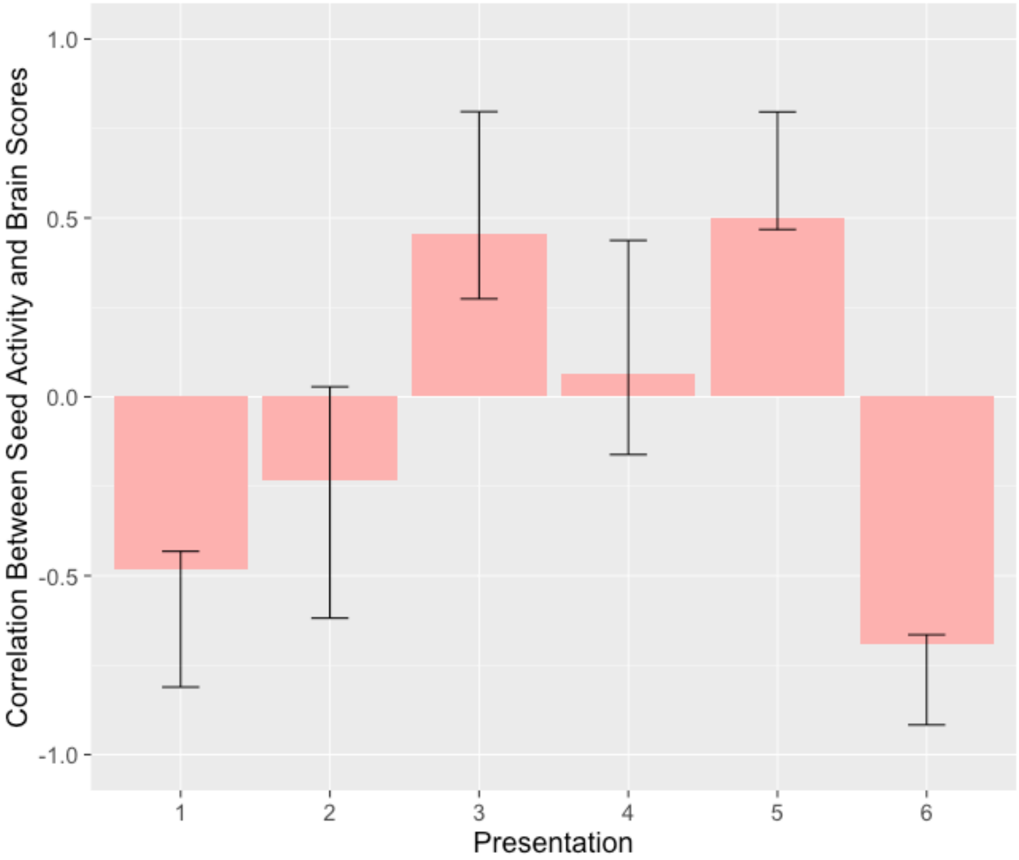

Figure 38. The task-related functional connectivity of the left VOTC-Animals across presentation (LV1)

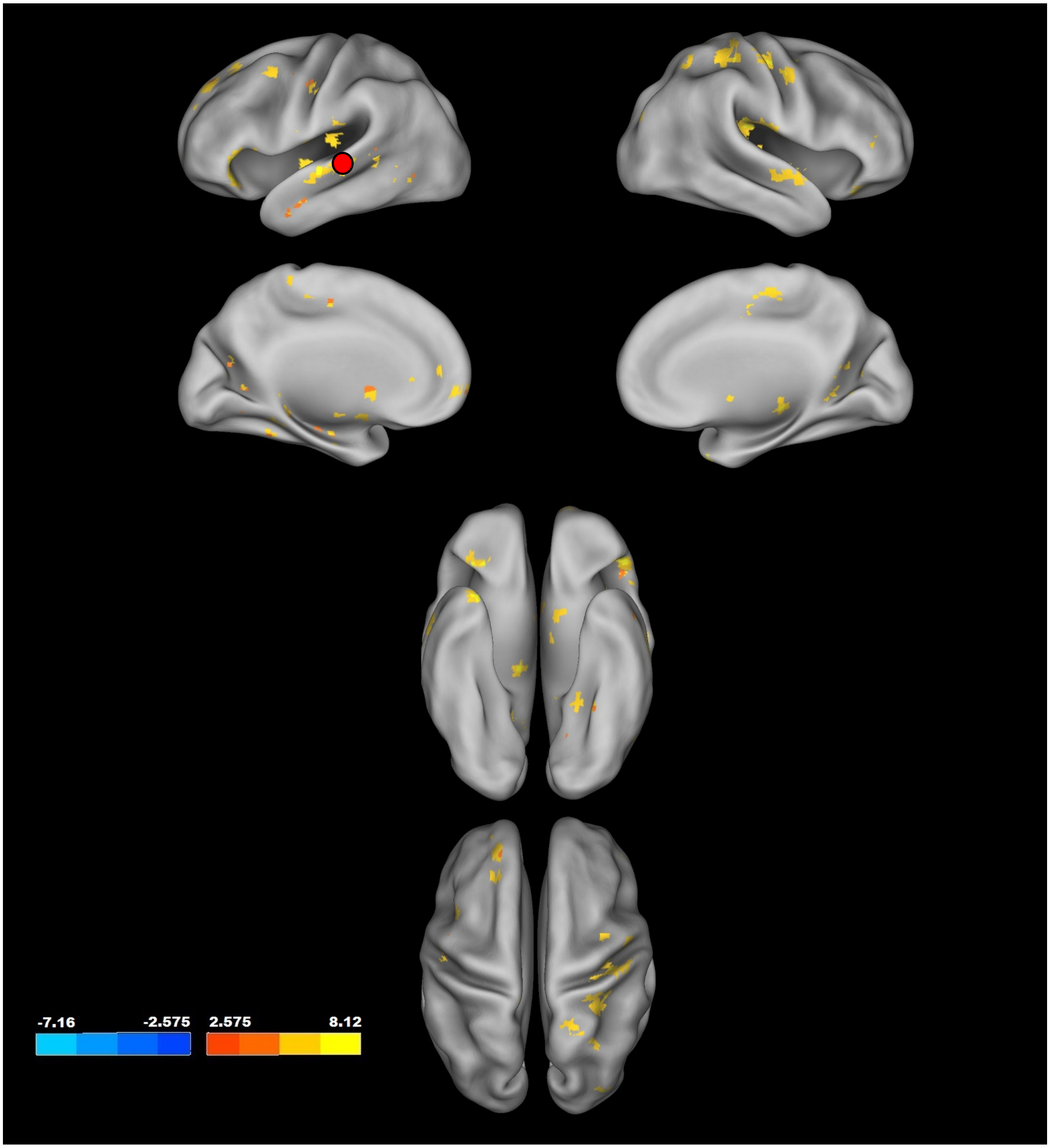

Figure 39. *The temporal brain pattern of the right VOTC-Animals observed at lag 2 (LV1). The brain pattern includes the left VOTC-Animals (black circle) and the left superior temporal sulcus (red circle).*

Table 17. Cluster report for LV 1 at lag 2 in the left VOTC-Animals seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01. Of note there were no clusters of voxels associated with a negative BSR above threshold

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one, six > Presentation three, five						
Superior Temporal Sulcus	Left	-66	-15	-6	6.53	160
Inferior Frontal Gyrus	Left	-48	24	-3	6.51	197
Inferior Middle Temporal gyrus	Right	33	15	-36	5.94	26
Primary somatosensory cortex	Right	27	-33	51	5.66	758
Anterior Cingulate Cortex	Left	-6	33	3	5.30	68
Primary Motor Cortex	Left	-36	6	45	5.17	31
Cerebellum	Left	0	-63	-24	5.02	85
Ventral Medial PFC	Left	-18	36	33	4.86	64
Supramarginal gyrus	Left	-51	-24	24	4.80	94
Superior Parietal Lobule	Right	15	-51	57	4.75	80
posterior middle temporal gyrus	Left	-60	-57	-3	4.72	50
posterior cingulate cortex	Right	12	-60	12	4.66	53
Somatosensory cortex	Right	0	-42	63	4.57	24
Parahippocampal Gyrus	Right	18	-45	3	4.55	22
Putamen	Left	-24	0	18	4.55	40
Medial orbitofrontal cortex	Left	-12	63	-3	4.54	56
Supplementary Motor cortex	Left	-12	-15	48	4.48	20
Thalamus	Right	15	-21	0	4.45	20
Insula	Left	-27	18	15	4.44	25
Somatosensory Cortex	Left	-45	-6	18	4.44	121
Transverse occipital Sulcus	Right	36	-84	27	4.41	33
Anterior Orbitofrontal cortex	Right	30	27	-18	4.38	69
Anterior Superior Temporal Sulcus	Left	-60	-3	-21	4.30	60
Paracentral Lobule	Left	-9	-24	54	4.26	21
Amygdala	Left	-12	0	-12	4.26	23
Superior Frontal Gyrus	Left	-18	24	45	4.18	39
Posterior Insula	Left	-30	-24	12	4.13	41
Hippocampus	Left	-21	-39	3	4.10	116
Thalamus	Right	3	-12	0	4.09	25
Striatum	Left	-9	9	0	4.08	34
Inferior Frontal Gyrus	Right	45	39	3	4.06	34

Superior Temporal Sulcus	Right	63	-3	-9	3.84	56
Calcarine Sulcus	Left	-24	-60	18	3.68	52
Hippocampus	Left	-21	-12	-24	3.37	20

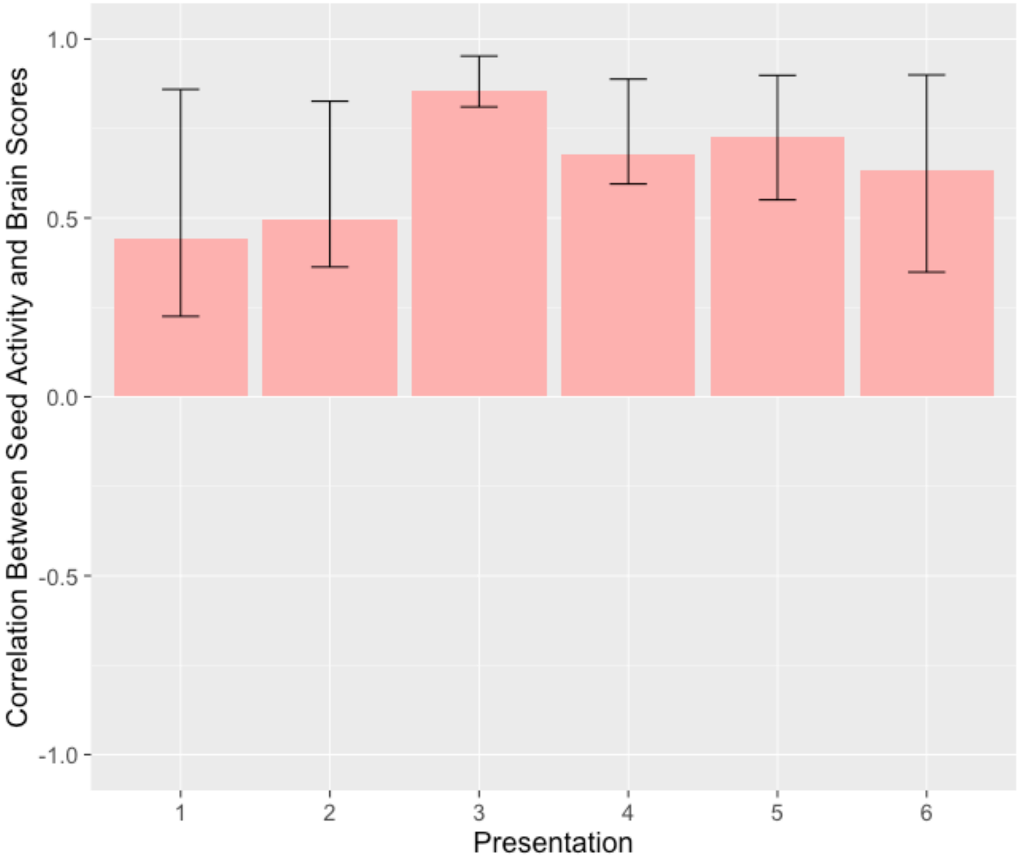

Figure 40. The task-related functional connectivity of the left VOTC-Animals across presentation (LV2)

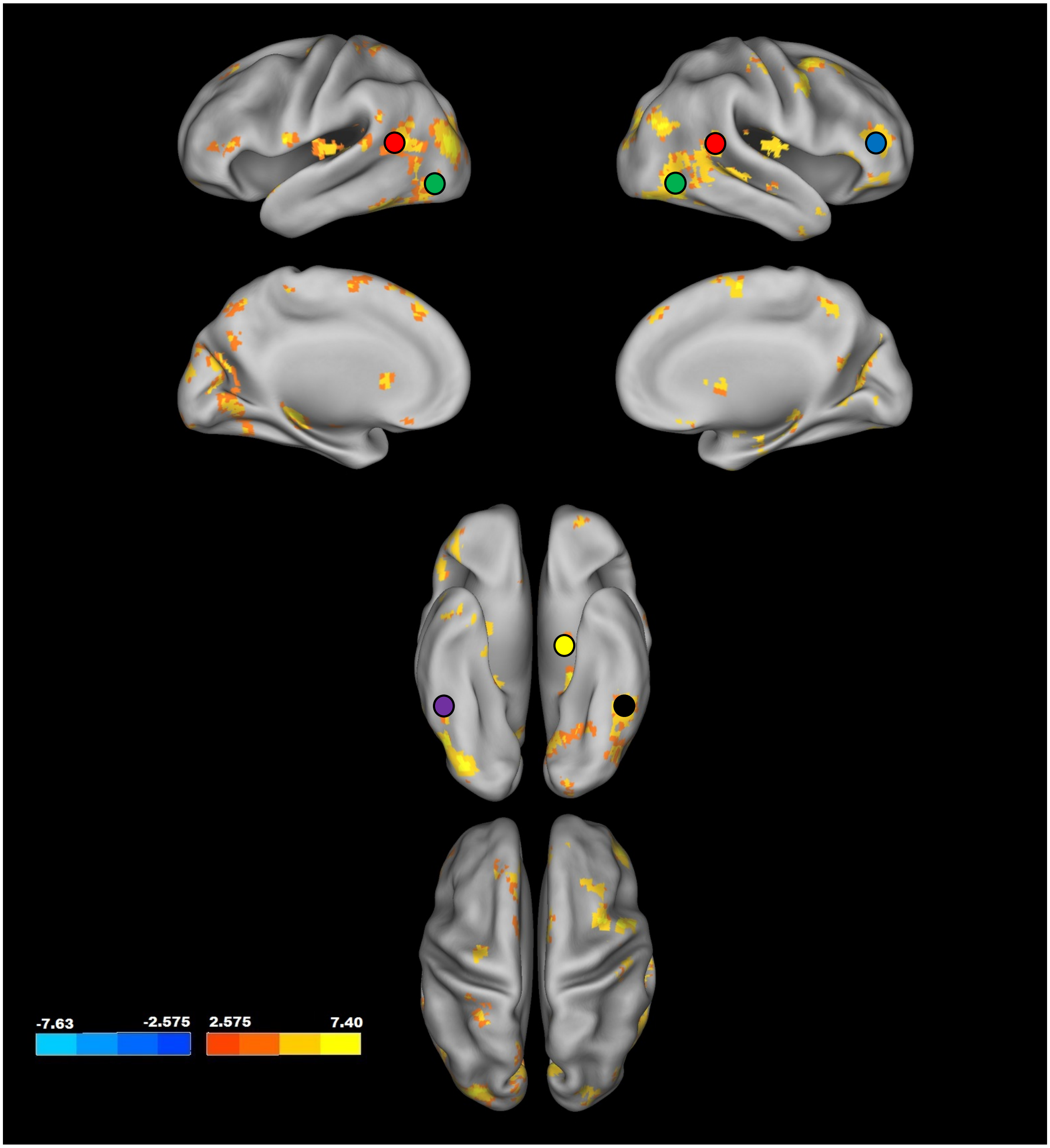

Figure 41. The temporal brain pattern of the left VOTC-Animals observed at lag 2 (LV2). The brain pattern includes the left VOTC-Animals (black circle), right VOTC-Animals (purple circle), bilateral EBA (green circle), bilateral pSTS (red circle), right inferior frontal junction (blue circle) and the left amygdala (yellow circle)

Table 18 Cluster report for LV 2 at lag 2 in the left VOTC-Animals seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01. Of note there were no clusters of voxels associated with a negative BSR above threshold

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one, two, three, four, five, six > 0						
Fusiform Gyrus	Right	42	-60	-6	7.32	1354
Fusiform Gyrus	Left	-45	-45	-24	7.04	298
Lateral Occipital Cortex	Left	-36	-81	15	6.88	1437
Inferior Frontal Gyrus	Right	51	24	-3	5.75	175
Cingulare Sulcus	Right	3	0	66	5.32	116
Premotor Cortex	Left	-24	54	-15	5.00	136
Medial Orbitofrontal cortex	Left	-15	-90	-18	4.84	22
Lingual Gyrus	Right	21	-24	-15	4.80	42
Parahippocampal Gyrus	Left	-27	-15	60	4.61	44
Premotor Cortex	Right	36	-12	12	4.39	48
Posterior Insula	Left	-27	-45	69	4.36	151
Superior Parietal Lobule	Right	0	-42	54	4.34	62
Precuneus	Left	-6	39	48	4.31	51
Medial Superior Frontal Gyrus	Right	27	-3	-15	4.18	118
Amygdala	Right	39	3	-33	4.12	21
Anterior Inferior temporal Gyrus	Left	-54	12	-9	4.05	55
Anterior Superior Temporal Gyrus	Left	-63	-42	15	3.85	24
Posterior Superior Temporal Sulcus	Left	-3	18	6	3.77	46
Caudate Nucleus	Right	42	48	-12	3.69	33
Inferior Orbitofrontal Cortex	Right	51	-12	51	3.67	54
Primary Somatosensory cortex	Left	-51	39	9	3.66	25
Dorsal lateral PFC	Right	33	-6	-45	3.62	46
Inferior frontal Gyrus	Right	0	24	-15	3.59	25
Superior Oribitofrontal Gyrus	Right	33	-15	-18	3.56	28
Hippocampus	Left	-9	-12	-18	3.54	25
Putamen	Left	-48	15	30	3.41	30
Inferior Frontal Sulcus	Left	-24	54	-15	5.00	21

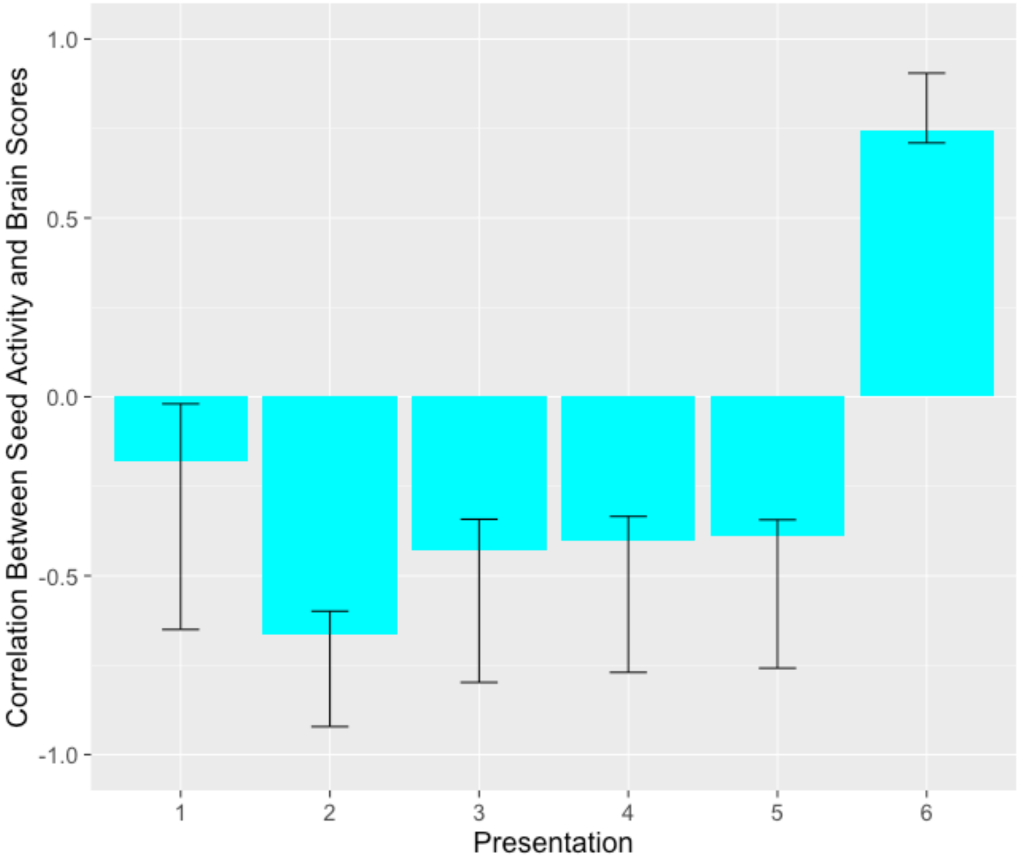

Figure 42. The task-related functional connectivity of the VWFA (real words) across presentation (LV1)

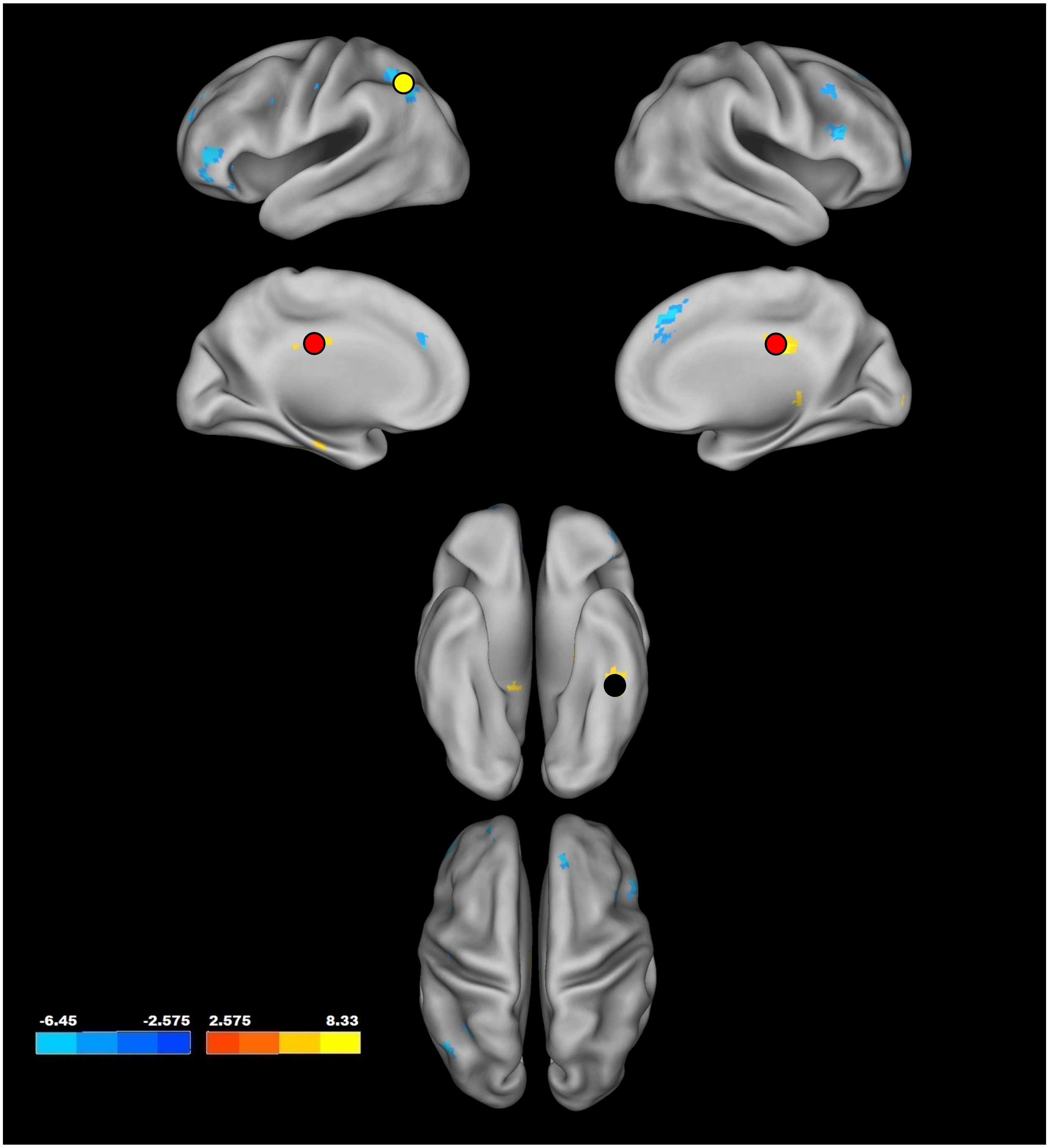

Figure 43. *The temporal brain pattern of the VWFA observed at lag 2 (LV2). The brain pattern includes the VWFA (black circle), bilateral posterior cingulate cortex (red circle), and the left IPS (yellow circle)*

Table 19. Cluster report for LV 1 at lag 2 in the real words VWFA seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01.

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one, two, three, four, five > Presentation six						
Fusiform Gyrus	Left	-42	-33	-21	6.26	35
Posterior Cingulate Cortex	Right	6	-30	30	5.49	55
Cerbellum	Right	9	-72	-39	4.08	53
Hippocampus	Right	15	-33	3	3.82	26
Hippocampus	Left	-9	-6	-15	3.79	37
Calcirine Sulcus	Right	6	-99	3	3.73	43
Cerebellum	Left	-27	-72	-21	3.70	22
Posterior Cingulate Cortex	Left	-21	-48	24	-6.45	23
Presentation six > Presentation one, two, three, four, five						
Medial PFC	Right	9	36	45	-5.77	119
Precuneus	Right	30	-57	18	-5.27	26
Superior Frontal Sulcus	Right	21	54	3	-5.18	66
Inferior Frontal Gyrus	Left	-42	57	0	-4.34	67
Inferior Frontal Gyrus	Right	45	18	15	-4.27	47
Intraparietal Sulcus	Right	24	-45	42	-4.20	26
Intraparietal Sulcus	Left	-30	-51	48	-4.12	30
Angular Gyrus	Left	-45	-63	45	-3.95	38
Superior Fontal Gyrus	Left	-24	51	33	-3.91	33
Middle Frontal Gyrus	Right	42	18	39	-3.80	31
Premotor cortex	Left	-54	9	33	-3.76	31
Anterior Insula	Left	-33	27	3	-3.67	25
Inferior Front Gyrus	Left	-33	-12	33	-3.25	21

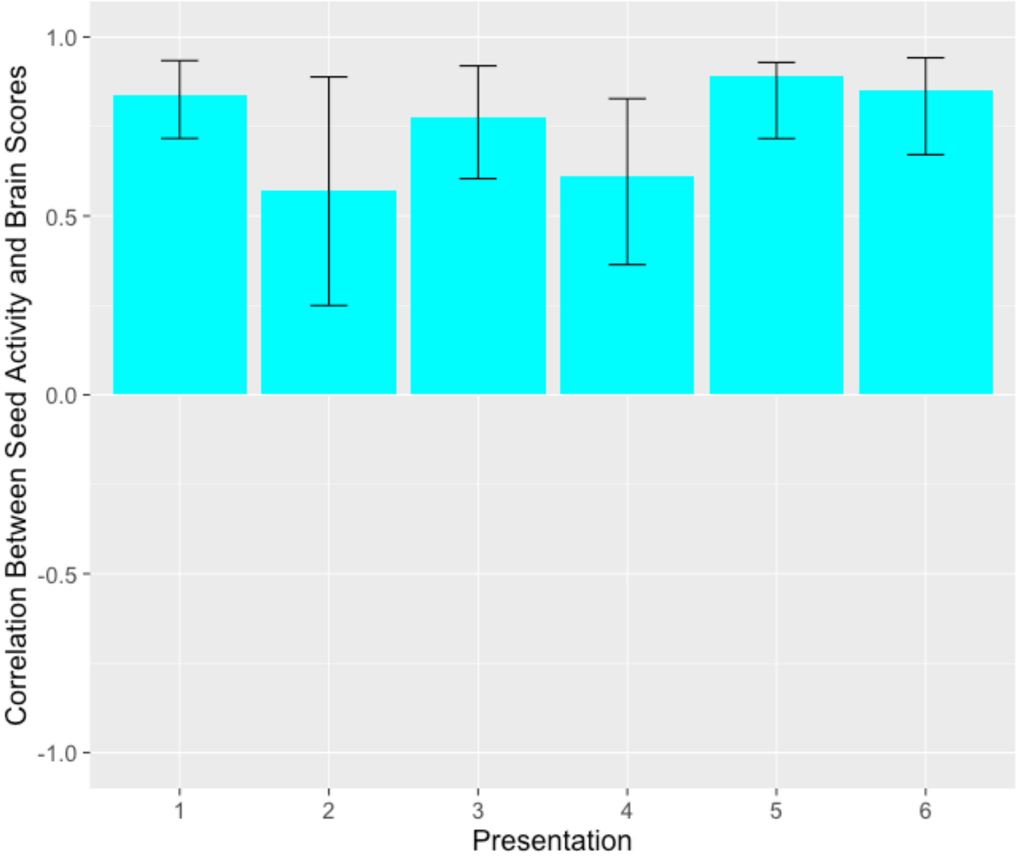

Figure 44. The task-related functional connectivity of the VWFA (real words) across presentation (LV2)

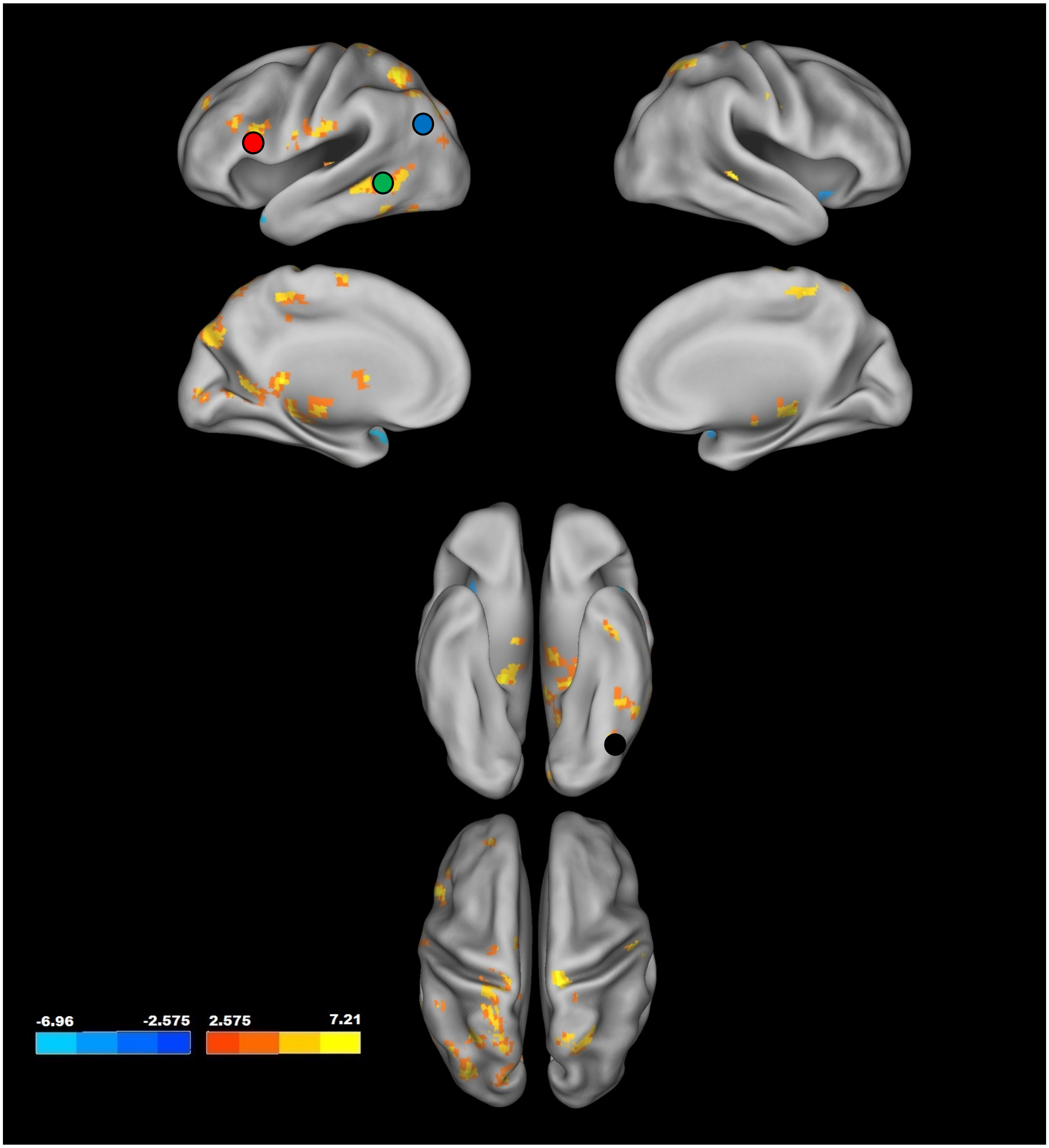

Figure 45. *The temporal brain pattern of the VWFA observed at lag 2 (LV2). The brain pattern includes the VWFA (black circle), frontal operculum (red circle), the middle temporal gyrus (green blue circle), and the left angular gyrus (blue circle)*

Table 20. Cluster report for LV 2 at lag 2 in the real words VWFA seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01.

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation one two, three, four, five, six > 0						
Inferior Frontal Gyrus	Left	-51	15	21	6.22	150
Intraparietal sulcus	Left	-30	-54	51	6.12	326
Posterior cingulate cortex	Left	-6	-39	9	5.95	100
Parietooccipital sulcus	Right	33	-72	6	5.64	25
Hippocampus	Left	-18	-33	-3	5.54	442
Primary Somatosensory cortex	Right	12	-27	69	5.38	112
Fusiform gyrus	Left	-54	-54	-21	5.32	207
Supramarginal Gyrus	Left	-63	-21	24	4.91	105
Posterior Cingulate Cortex	Right	15	-54	-39	4.86	69
Inferior Temporal Gyrus	Left	-39	-9	-42	4.83	34
Anterior inferior temporal Gyrus	Left	-48	-42	57	4.82	36
Angular Gyrus	Left	-30	-84	39	4.80	303
Middle Frontal Gyrus	Right	33	33	21	4.66	34
Superior Parietal Lobule	Right	15	-57	60	4.46	100
Cerebellum	Left	-21	-45	-33	4.42	20
Middle Temporal Gyrus	Right	48	-21	3	4.28	28
Superior Frontal Sulcus	Left	-21	45	33	4.23	22
Calcarine Sulcus	Left	-3	-90	3	4.19	25
Superior Temporal Gyrus	Left	-63	-39	-6	4.03	79
Supplementary Motor Area	Left	-3	-6	66	3.80	40
Angular Gyrus	Right	36	-66	-36	3.52	30
Primary Somatosensory cortex	Right	51	-12	33	3.31	20
Caudate Nucleus	Left	-6	0	15	3.24	21

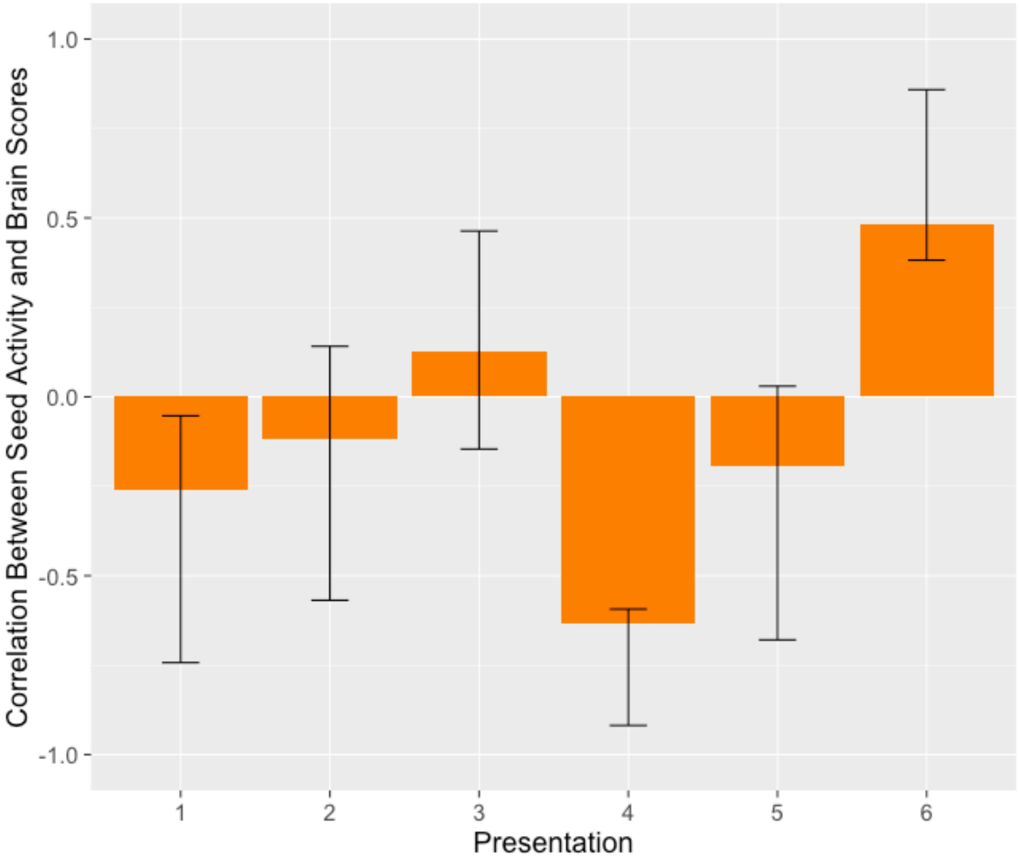

Figure 46. The task-related functional connectivity of the VWFA (pseudowords) across presentation (LV1)

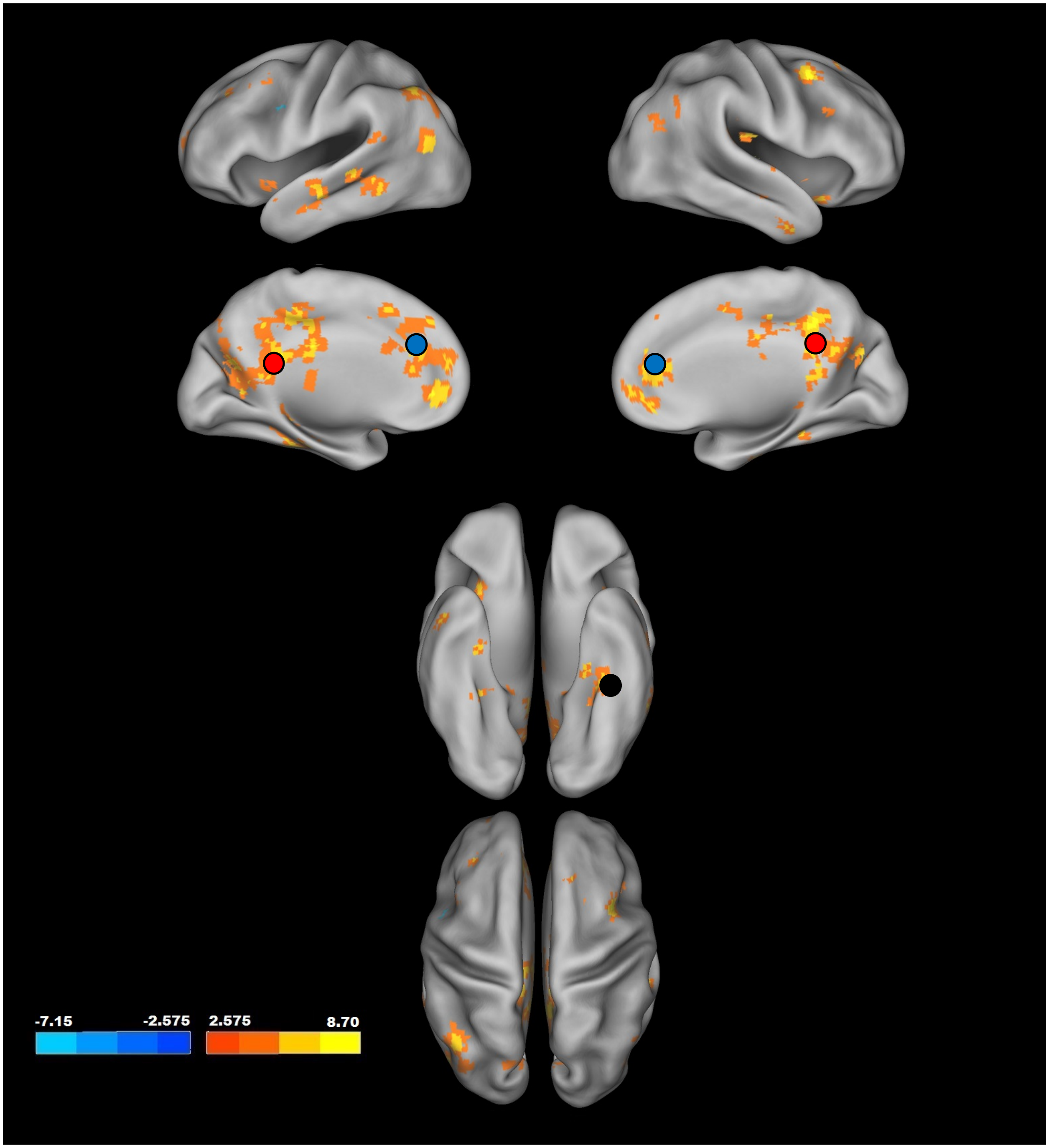

Figure 47. *The temporal brain pattern of the VWFA (pseudowords) observed at lag 3 (LV1). The brain pattern includes the VWFA (black circle), bilateral posterior cingulate cortex (red circle), and the bilateral medial PFC (blue circle)*

Table 21. Cluster report for LV 1 at lag 3 in the pseudowords VWFA seed PLS. Minimum cluster size was set to 20 voxels with minimum of 10 mm between clusters and p <0.01.

		MNI Coordinates (mm)				
Peak Region	Hemisphere	X	Y	Z	BSR	Cluster Size (in voxels)
Presentation six > Presentation one, four						
Posterior Cingulate Cortex	Left	-9	-45	24	8.70	1348
Middle Frontal Gyrus	Right	36	12	42	7.11	123
Anterior Cingulate cortex	Left	-12	42	-3	6.51	669
Anterior Insula	Left	-42	15	-9	6.09	67
Hippocampus	Left	-24	-39	-3	5.96	142
Posterior Inferior Temporal Gyrus	Left	-63	-48	-9	5.95	213
Inferior Parietal Lobule	Left	-48	-72	18	5.72	239
Hippocampus	Right	27	-36	9	4.98	34
Posterior Insula	Right	36	-24	3	4.98	34
Middle Frontal Gyrus	Left	-27	27	36	4.74	35
Middle Temporal Gyrus	Left	-57	-18	-18	4.72	90
Cingulate Cortex	Right	12	-3	45	4.46	22
Superior Temporal Pole	Right	33	12	-24	4.31	36
Mid Brain	Left	-6	-21	-24	4.16	28
Cerebellum	Right	27	-45	-33	4.15	21
Inferior Temporal Gyrus	Right	51	-6	-30	4.09	26
Anterior Insula	Right	45	6	-6	4.07	72
Posterior Insula	Right	36	-21	21	4.07	34
Superior Temporal Gyrus	Right	54	-30	15	4.03	43
Superior Temporal Gyrus	Left	-63	-42	18	3.96	28
Fusiform Gyrus	Right	30	-18	-33	3.88	23
Superior Frontal Gyrus	Right	15	24	51	3.79	29
Superior Frontal Gyrus	Left	-12	24	45	3.76	39
Fusiform Gyrus	Right	33	-39	-18	3.72	36
Cingulate Cortex	Left	-12	0	33	3.59	37
Middle Temporal Gyrus	Right	57	-15	-18	3.49	21
Inferior Frontal Sulcus	Left	-48	18	30	3.49	41
Superior Fontal Sulcus	Left	-21	57	12	3.41	27
Inferior Frontal Sulcus	Right	42	18	27	3.14	29
Presentation one, four > Presentation six						
Inferior Frontal Sulcus	Left	-42	0	30	-4.10	20

significant positive correlation between brain scores and seed activity (Figure 46). Presentations one and four had a significant negative correlation between brain scores and seed activity. There was no significant difference between these presentations. The VWFA showed connectivity to default network regions (Figure 47; Table 21)

Discussion

The neural mechanisms of priming remain unclear. Repetition suppression has been shown to be related to priming, but it does not account for all of the neural changes that occur from repeated stimuli. In this study, I focused on a neural synchrony model that has found support through computational models and MEG studies. The current study adds to this burgeoning body of research by using fMRI, which offers better spatial resolution than MEG and allows for the simultaneous measurement of local neural activity, inferred through the BOLD signal, and functional connectivity, a correlate of neural synchrony. Furthermore, I individually localized several category-preferential regions within the VOTC to examine potential repetition-related changes in their functional connectivity across the whole brain. I hypothesized that there would be a relationship between repetition and changes in functional connectivity. Using Seed PLS to measure task-related functional connectivity I did not find a consistent or predicted pattern of changes in functional connectivity of the category-preferential regions across presentations. However, several findings of interest emerged regarding neural priming and the organization of the VOTC.

Behavioral and Neural Priming

The behavioural analyses demonstrated priming for scenes, tools, animals, real words, and pseudowords, but there was no priming for faces. Each of the defined category-preferential ROIs showed some level of specificity for their preferred category. The FFA and VOTC-Tools were the only regions that did not display neural priming for their respective preferred categories in either hemisphere. There were two significant correlations between the magnitude of behavioural priming and neural priming in the category preferential regions. However, these might have been spurious results, and cases of a type I error across multiple comparisons. Overall, the lack of correlation between behavioural and neural priming in these regions is unsurprising and consistent with previous literature (Maccotta and Buckner, 2004; Bunzeck et al., 2006; Dobbins et al., 2004).

Effects of Stimulus Timing on Priming

I expected to observe behavioural priming for faces and concomitant neural priming in the FFA. The faces used as stimuli in this study were non-famous, i.e., unfamiliar faces; other studies have reported that anonymous faces elicited neural priming in the FFA in the form of neural enhancement over the first several presentations, followed by repetition suppression in later presentations (Henson, Shallice and Dolan, 2000; Ishai, Pessoa, Bikle, and Ungerleider, 2004). Neural priming for faces is heavily modulated by the lag between stimulus presentations (Henson et al., 2000; Henson et al., 2004). Stimulus lag effects have mostly been studied using faces (both familiar and unfamiliar). Lag timing has been reported to have an influence on neural and behavioural priming; increased lag between repeated presentations of a stimulus reduces both priming effects when using familiar or unfamiliar faces (Henson et al., 2000; Henson et al., 2004). Long lags between unfamiliar face repetitions do not produce neural priming in the FFA, however, short lags have been reported to do so (Henson et al., 2000). In this study, there was no set lag between stimulus presentations, and significant delays between presentations would be expected. Given this paradigm, it seems likely that the average time between presentations was great enough to eliminate priming effects for unfamiliar faces.

Different Categories Show Different Priming Qualities

It can be postulated that priming mechanisms are not identical across stimulus categories, since faces show an interaction between familiarity, lag-time, and priming (Henson et al., 2000; Henson et al., 2004), which is not consistent across other categories. In the present study, I found a category difference, as faces did not show neural or behavioural priming, while the other categories did. As previously discussed, this may be related to lag effects. If true, this suggests that the maximum lag-time in which priming effects may still occur varies based on the category of stimuli used, however lag effects were not manipulated in this study so a definitive claim cannot be made. Differentiation between stimulus categories has been found in research examining the effect of repetition probability on repetition suppression, where repetition suppression is modulated by expectancy for face stimuli (Summerfield, Trittschuh, Monti, Mesulam and Egner, 2008) but not for object stimuli (Kaliukhovich and Vogels, 2011; Kovács, Kaiser, Kaliukhovich, Vidnyánszky and Vogels, 2013). One hypothesis is that stimulus category differences are the result of familiarity with stimuli and are not rooted in the categories themselves (Kovács et al., 2013). This would be in line with modification theories of priming, which suggest that priming cannot occur for unfamiliar stimuli; in contrast acquisition theories postulate that unfamiliar stimuli can be primed (Henson, 2003). Several studies have found priming for unfamiliar stimuli (Henson et al., 2000; Ishai et al, 2004), and in the present study using pseudowords (i.e. unfamiliar stimuli), I did observe behavioural priming and neural priming in the VWFA. This suggests that when processing a category of unfamiliar stimuli, it may be possible to access pre-existing representations of similar categories. (Henson 2003; Stevens et al., 2008). In the case of the present study, it may be that pseudowords were learned and became familiar stimuli over the course of the experiment. Real words and pseudowords might be processed at a similar, more superordinate hierarchal level than faces, which might allow one to access representations of real words when processing pseudo words. I postulate that this might enable for pseudowords to be familiarized faster than anonymous faces. Under the theory of hierarchy of object processing, categories such as animals can be processed at a basic level, whereas faces are processed on an individual level (Riesenhuber and Poggio, 2002; Grill-Spector, 2003). This would suggest that face processing occurs at a subordinate level of object recognition compared to animals (Grill-Spector, 2003); for example, pictures of two turtles are more likely to be perceived as similar/the same than two pictures of unfamiliar human faces. I postulate that categories that require subordinate processing, such as unfamiliar faces, may be more influenced by lag or other effects that influence priming.

Category-Related Organization and Neural Priming within the VOTC

The PPA was significantly more active for scenes than other categories. This region also showed increased response to non-manipulable objects, relative to other categories, consistent with previous literature (Cate, Goodale, and Köhler, 2011; Konkle and Olivia, 2012). Neural priming was observed for scenes in both the left and right hemispheres, however we did not find an interaction between the hemispheres and neural priming. There was also a main effect of repetition on activation for animal stimuli in the PPA, however, the pattern of BOLD signal changes across repetitions was not consistent with neural priming; activation for animals was minimal in the PPA and did not change monotonically, but rather, fluctuated up and down across repetitions. The significant main effect was driven by presentations three and four, which did not activate the PPA in both hemispheres; however, subsequent presentations generated a reactivation of the PPA to the point of no longer being significantly different from the first presentation. With no consistent pattern of repetition-related change, it is doubtful that the observed changes reflect neural priming, but more likely they reflect random fluctuations. Factors affecting the specificity of priming will be discussed later.

Previous research has suggested that the PPA plays a role in landmark-based navigation (Epstein and Vass, 2014; Yoder, Clark, and Taube, 2011). It has been postulated that the PPA is critical for landmark recognition (Epstein and Vass, 2014), and large non-manipulable objects may serve as landmarks for navigating landscapes (Aguirre, Zarahn, and D'esposito, 1998; Cate et al., 2011, Konkle and Olivia, 2012). Furthermore, the non-manipulable objects (most of which were large objects, such as buildings) in this study elicited neural priming in the PPA, whereas tools did not. This observation is consistent with previous studies that have shown that the PPA responds more to large than small objects (Konkle and Olivia, 2012). Category-specific neural priming in the PPA for both scenes and non-manipulable objects, a result which has not been previously reported, suggests a relationship between the processing of large non-manipulable objects and scenes, adding to the evidence that the PPA is critical for landmark based spatial navigation (Epstein and Vass, 2014).

As mentioned, the PPA responds more to scenes and large objects than to small objects; however, the VOTC-Tools, which typically overlaps with the PPA in whole or in part, has shown evidence of a preference for tools compared to living entities (Beauchamp et al., 2002; Chao et al., 1999; Stevens et al., 2015). I observed significantly greater activation for tools in the VOTC-Tools than the PPA in both hemispheres. However, I did not however observe the left lateralization of this response that has been previously reported (Chao et al., 1999). There was no evidence of neural priming for tools in this region. However, it is important to note that the VOTC-Tool region is not as robustly or reliably identifiable across individuals as other category-preferential regions, and the analyses revealed large within-subject variability of activation in the VOTC-Tool region.

The FFA was defined using a face-scene contrast in the localizer, and the region showed the same preference for faces compared to scenes during the task. There was a nearly significant effect of lateralization, with greater activity in the right hemisphere, which is consistent with established literature (Kanwisher and Yovel, 2006; Kanwisher et al., 1997). There was no difference between animals and faces at the first presentation in both the right and left FFA, and interestingly, animal stimuli elicited neural priming in the left and right FFA. Similarly, in the VOTC-Animals, animals were the preferred category of this region compared to non-animate entities such as scenes and tools. Activation for faces in this region was not significantly different from animals, but only animals elicited neural priming in this region. I did not observe the expected right lateralization of activation for animals in the VOTC-Animals. The results here corroborate previous work that has suggested that animate entities activate the lateral portion of the VOTC, while inanimate objects activate the medial portions (Martin, 2007).

The lack of dissociation between faces and animals in the VOTC-Animals was unsurprising. Many animal faces have a similar facial structure to humans faces and this is reflected in the pattern of neural response. Further, previous work has shown that both faces and animals activate the lateral portions of the fusiform gyrus compared to objects (Grill-Spector, 2003; Grill-Spector, Knouf, and Kanwisher, 2004). It has also been reported that animals elicit more widespread activation across the lateral fusiform gyrus than faces (Chao et al., 1999, Martin, 2007). Observation of this dissociation might not be expected in this study based on the way ROIs were defined. The FFA was defined using a face-scene contrast, and the VOTC-Animals was defined using an animals-tools contrast. Since there was no direct contrast between animals and faces, there is a great deal of overlap between the ROIs, making small differences between these two similar categories undetectable. As discussed earlier, the lack of neural priming in response to faces in the FFA and VOTC-Animals is most likely related to lag effects and/or differential responses to familiar vs. unfamiliar stimuli, rather than the category preference of the ROIs.

Activation within the VWFA showed preference for both words and pseudowords over faces. Both real words and pseudowords showed neural priming in the VWFA There has been debate over role of the left fusiform gyrus, and the VWFA specifically, regarding preference for lexical stimuli versus other categories (Price & Devlin, 2003; Mei et al., 2010). Several other studies have postulated and provided evidence that the left fusiform gyrus is specialized for processing high spatial frequency stimuli and/or feature detection (Mei et al., 2010; Kitterle and Selig, 1991; Grill-Spector, 2001; Robertson and Lamb, 1991). The results observed in this study offer support for the hypothesis that the VWFA is specific for text, since both pseudowords and real words activated the region significantly more than faces. Further evidence comes from the observation that the activity for both text types was significantly greater in the VWFA than the left FFA. This finding is consistent with recent work by Saygin et al. (2016) in which the individually identified VWFA in 8-year-old participants showed greater activation for words than faces, whereas the left FFA was preferential for faces. The study by Saygin et al. (2016) is part of a growing literature which examines the effect of experience on the development of the VWFA and its dissociation from the FFA (Xue, Chen, Jin and Dong, 2006; Baker et al., 2007; Dehaene et al., 2010; Davies-Thompson et al., 2016). Saygin et al., found evidence that the VWFA develops with reading experience, as the functional dissociation in processing between the VWFA and left FFA was not observed in participants at 5 years of age but was at 8 years of age after children had learned to read. It should be noted that I did not show a complete dissociation between these regions, since real words elicited neural priming in the left FFA, suggesting that there is some degree of overlap in the neural substrate required for the processing of words and faces. This is consistent with a theoretical perspective recently proposed by Behrmann and Plaut (2013, 2014), arguing that face and word processing mechanisms are mediated by brain-wide networks that are not completely independent.

The results also revealed a distinction in the VWFA between real words and pseudowords. Real words elicited immediate, maximal neural priming - with a significant, substantial suppression of activity for the first repetition - which plateaued thereafter, as subsequent presentations generated the same level of activation as the second presentation. In contrast pseudowords did not show any neural priming over the first three presentations, though there was a significant suppression between the third and fourth presentations, which was maintained over subsequent presentations. Neural priming for pseudowords has previously shown repetition enhancement followed by repetition suppression in VOTC (without localizing the VWFA: Fiebach, Gruber, and Supp, 2005). This same pattern has been observed for anonymous faces as well, suggesting a consistent pattern of initial neural enhancement, followed by repetition suppression, across different types of unfamiliar stimuli (Henson et al., 2000). In this study, repeated pseudowords did not show neural enhancement in the VWFA, but importantly, they did not show suppression until the fourth and subsequent presentations. It is possible that after the fourth presentation, an accessible representation of pseudowords had developed, leading to subsequent priming.

Results in the VWFA stress the importance of using individually identified regions, as the disparity in results between studies using group localization vs. individual localization suggests a significant amount of inter-subject variability in the location of the VWFA, consistent with the findings of Glezer and Riesenhuber (2013). When collapsing across subjects by using group localization, results may become less accurate. Previous work using group localization of the VWFA did not find that the VWFA consistently differentiated real words from pseudowords (Liu et al., 2013; Boylan, Trueswell and Thompson-Schill, 2014). Conversely, a study that individually localized the VWFA in all participants demonstrated that it differentiates real words from pseudowords (Glezer, Jiang, and Riesenuber, 2009), consistent with the results obtained in this study.

Specificity of Neural Priming in Category Preferential Regions

Our results indicate a general trend towards greater neural priming for repeated stimuli from the preferred category in category-preferential regions. However, some degree of neural priming for stimuli from non-preferred categories was evident as well, such as for scenes in the left VOTC-Tools and for words in the left FFA. An explanation for the latter might be that there is potentially substantial overlap of the tool- and scene-preferential ROIs and the word- and face-preferential ROIs (Stevens et al., 2015; Behrmann and Plaut, 2013; Behrmann and Plaut, 2014). Within the literature, category-specificity of neural priming has been reported in some studies (Bunzeck et al., 2006; Mahon, Milleville, Negri, Rumiati, Caramazza and Martin, 2007; Pourtois, Schwartz, Spiridon, Martuzzi, and Vuilleumier, 2009) but not in others (Weiner, Sayres, Vinberg and Grill-Spector, 2010; De Baene and Vogels, 2010;). It has been shown that the magnitude of neural priming, in the form of repetition suppression, is greater for preferred category stimuli, and that preferred categories are less susceptible to lag effects (Weiner et al., 2010). Based on previous literature and results of this study, it is likely that category-specificity of neural priming is heavily dependent on the priming task, stimulus lag, and the number of intermittent stimuli between presentations.

Category-Related Networks

The task-related connectivity of the category-preferential regions (i.e. the category-related networks) observed in this study is consistent with reported intrinsic connectivity of the category-preferential regions (Stevens et al., 2015). Both the right and left PPA showed preferential connectivity to key scene processing areas, such as the RSC and TOS bilaterally. However, I did not find parallel laterality effects using measures of task-related functional connectivity as those reported by Stevens et al. (2012) for intrinsic functional connectivity, as I did not observe strong differentiation of connectivity between the right and the left PPA with non-scene-related networks. As with the PPA, the seeded VOTC-Tools regions showed connectivity consistent with previous RSFC results (Stevens et al., 2015). I replicated the left lateralization of tool processing, as both the left and right VOTC-Tools showed connectivity to the left ventral premotor cortex, inferior parietal lobule, intraparietal sulcus, and the pMTG. Stevens et al. (2015) found stark differences in the intrinsic connectivity of the PPA and VOTC-Tools; the distinct task-related functional connectivity of these overlapping regions observed here provides further evidence that category-specialization in the VOTC is not entirely a function of local neural properties, but is also driven by the distinct connectivity of these functionally dissociable regions. Further corroborating the findings of Stevens et al. (2015), the VOTC-Animals showed preferential connectivity to animal associated regions, such the EBA, occipital face area, pSTS, and amygdala. Both the right and left VOTC-Animals had stronger connections to other regions within the right hemisphere. In response to real words, the VWFA, showed functional connectivity with a left lateralized network consisting of regions that have been associated with reading, including the frontal operculum (Broca's area: Hampson et al., 2006; Georgiewa et al., 1999), the mid-middle temporal gyrus (Indefrey & Levelt, 2004; Gaillard, Balasamo, Ibrahim, Sachs, and Xu, 2003), and the angular gyrus (Damasio & Geschwind, 1984; Segal & Petrides, 2013). However, I did not observe functional connectivity between the VWFA and the posterior superior temporal gyrus (Wernicke's area).

Consistent with Stevens et al. (2015), there was category-specific lateralization of these networks. The tool-related and word-related networks were strongly left lateralized, the animal related network was right lateralized, and the scene related network was bilateral. Furthermore, these lateralization effects were not mirrored by asymmetrical activation of the bilateral pairs of category-preferential ROIs across hemispheres. This adds to the growing evidence that the category-related organization of VOTC is driven by both connectivity and local neural activity.

Connectivity between Category Preferential Regions and Attention Networks

The bilateral PPA and VOTC-Tools, and right VOTC-Animals showed functional connectivity with regions of the dorsal attention network, including the middle temporal motion complex, superior parietal lobule, and the IPS (Fox, Corbetta, Snyder, Vincent & Raichle, 2006; Vossel, Weidner, Driver, Friston and Fink, 2012). The dorsal attention network is thought to be involved in goal directed cognition, spatial attention, and orienting attention to a target, and is considered to be a top-down pathway (Spreng, Sepulcre, Turner, Stevens and Schacter, 2013; Vossel, Geng, and Fink, 2014). Conversely, the left VOTC-Animals showed greater connectivity with regions of the ventral attention network. The ventral attention network comprises the temporoparietal junction and the ventral frontal cortex, among other regions, and is heavily right lateralized (Fox et al., 2006; Vossel et al., 2012). This network is mostly involved in attending to salient or unexpected stimuli, and is considered to be a bottom-up pathway (Vossel et al., 2014).

Connectivity to the dorsal attention network was not an unexpected result, given the role of this network in goal directed cognition. The ventral stream may have shown privileged connectivity to the left VOTC-Animals in response to animals because animals may be a very salient category, relative to the others. The lateralization difference in the VOTC-Animals can be interpreted in the context how these two networks interact to orient attention. It is hypothesized that the dorsal attention network modulates activity in the ventral attention network with task-relevant signals, however the ventral attention network may override this process in response to a particularly salient stimulus (Corbetta and Shulman, 2002). In this task, it can be speculated that the bilateral VOTC-Animals was associated with the interaction between the dorsal attention network and the ventral attention network.

Attention Not Awareness Modulates Neural Priming

Connectivity to the attention networks highlights the importance of attention for repetition effects. Previous work has shown that attention modulates neural priming (Eger, Henson, Driver, and Dolan, 2004; Yi, Kelley, Marois, and Chun, 2006), and in some contexts, is required for neural priming (Henson and Mouchliantis, 2007). The results provide evidence that the attention networks are connecting to regions that show neural priming. I hypothesize that through these connections, the attention networks modulate neural priming; however, further evidence will be required in order to substantiate this possibility. It is important to distinguish between awareness and attention. Attention alone does not imply awareness; it is possible to attend to a point without being aware of the presence of a stimulus (Henson, 2016). For example, Kouider et al., (2009) displayed a face stimulus between forward and backwards masks to manipulate awareness and found that even without awareness of the presentation of a face stimulus, neural priming effects were evident.

VWFA Connectivity to the Default Network

The VWFA showed increased connectivity to regions of the default network during presentation six of real words and pseudowords. The core nodes of the default network are the ventromedial PFC, posterior cingulate, IPL, lateral temporal cortex, dorsal medial PFC and the hippocampal formation (Buckner, Andrews-Hanna, and Schacter, 2008; Andrews-Hanna, 2012). Activation of the default network is associated with mind wandering, self-reference or reflection, recalling the past or imagining the future, and the recall of autobiographical information (Buckner et al., 2008; Andrews-Hanna, 2012; Spreng et al., 2013; Spreng, Stevens, Chamberlain, Gilmore, and Schacter, 2010). Importantly, it has been shown that default network activity is suppressed during tasks that involve attending to a stimulus (Buckner et al., 2008; Andrews-Hanna, 2012). This suggests that by presentation six, participants did not require as much attention to complete the task for pseudowords. Similar changes in the connectivity of the VWFA across presentation of real words was observed. During presentations one through five, there was VWFA connectivity with dorsal attention network regions, and at presentation six, the VWFA was functionally connected with the posterior cingulate, a core node of the default network. These observations may reflect that the semantic judgment task became easier over repetitions of words, hence requiring less attentional load, which in turn increased default network connectivity. It should be noted that this is a speculative claim and further exploration is required in order to determine if increased connectivity of the VWFA with the default network associated with text repetition is a robust phenomenon.

Connectivity of the Left VOTC-Animals

In a similar vein, interpretation of LV1 of the left VOTC-Animals can only be speculative given the limited clusters of activation across the brain. There was a large cluster surrounding the anterior portions of superior temporal cortex, a region that has been associated with the recognition of facial expression and gaze direction (Engell and Haxby, 2007; Narumoto, Okada, Sadato, Fukui, and Yonekura, 2001). There was also connectivity between the VOTC-Animals and the left amygdala and inferior frontal gyrus, which are other regions that have been implicated in recognition of facial expression (Gorno-Tempini et al., 2001; Iidaka, Omori, Murata, Kosaka, Yonekura, Okada, and Sadato, 2001). This suggests that the left VOTC-Animals is connecting to regions involved in recognizing facial expression and only presentations three and five were correlated with this pattern; however, connectivity in this LV was found to be very left lateralized, whereas in the literature, recognition of facial expression is more right lateralized (Engell and Haxby, 2007; Narumoto et al., 2001).

Changes in Functional Connectivity of Category-Preferential Regions

The PLS analysis I conducted used category-preferential regions as a seed to find category-related networks for scenes, tools, animals, and real words. I defined the networks based on the functional connectivity between category-preferential VOTC regions and other regions associated with processing their preferred category. Based on the synchrony model, I hypothesized that there would be increased functional connectivity between category-preferential regions and other associated regions within a category-related network with repeated presentation. The results revealed none of the hypothesized changes in functional connectivity of the category-preferential regions that were related to the neural synchrony hypothesis. While the current study did not find evidence to support the neural synchrony hypothesis, there are several limitations that may have contributed to the null findings.

Limitations of Using PLS to Examine Repetition Effects

Previous studies indicate that neural priming and synchrony changes associated with repetition are subtle effects (Stevens et al., 2008; Ghuman et al., 2008). When there are large brain-wide effects, they account for a large proportion of the variance in the data, and smaller/subtler effects may not be detected. The PLS analysis used in this study calculated between-subject correlations between seed activity and brain wide activity. These correlations were used to determine whether the functional connectivity of differed across presentations. Using this method, the analysis is susceptible to the Simpson's paradox, which is occurs when group-level effects are either absent or reversed within individual subjects. The paradox can occur when large sets of data are aggregated together; such is the case in the present study (Roberts, Hach, Tippett and Addis, 2016).

Future Directions

While this study did not find evidence for the synchrony model of priming, several follow up analyses may shed more light on connectivity changes from repetition. Using the current dataset, future work could use behaviour PLS, as an exploratory tool to specifically identify regions that covary together as a function of response time, and thus behavioural priming, without a priori hypotheses. This study focused exclusively on the functional connectivity of category-preferential regions in the VOTC; however, frontal regions have shown correlations between neural and behavioural priming. Thus, a follow up analysis examining the functional connectivity of selected frontal regions may provide evidence of increased neural synchrony. Frontal regions could be selected based on behavioural PLS results, a whole brain univariate analysis for neural priming, or from previous literature.

Further, analyses should explore other techniques that measure functional connectivity. Alternative methods include psychophysiological interactions (PPI) analysis and structural equation modelling (SEM). An advantage of these methods is that they measure effective connectivity instead of functional connectivity. Effective connectivity analyses allow for inferences as to the direction and causality of neural interactions across brain regions. However, PPI analysis makes assumptions about the HRF and lacks power in event-related designs (O'Reilly, Woolrich, Behrens, Smith and Johansen-Berg, 2012); SEM techniques are constrained by the substantial limits of known neuroanatomical connectivity in the human brain (McIntosh, Gonzalez-Lima, 1994). For these reasons, I propose that the best method for measuring functional connectivity for this data set is a within subject PLS (Roberts et al., 2016). Comparisons between standard seed PLS and within-subjects seed PLS found that the results of between-subjects analyses showed a Simpson's paradox effect and were less robust than results from a within-subjects PLS (Roberts et al., 2016). I believe that a combination of a within-subjects PLS and individually localized ROIs, including a broader and more comprehensive set of brain regions, is the soundest and most promising analytic approach to this dataset going forward.

Conclusion

The exact neural mechanisms of priming remain underspecified. Repetition suppression has been shown to be related to priming, but it does not account for all of the neural and behavioural changes that occur from repeated stimuli. A neural synchrony model has found support through computational models and MEG studies. The present project attempted to identify the critical yet elusive interrelationship between neural synchrony, neural priming, and behaviour. However, I did not find any meaningful changes in functional connectivity across stimulus presentation of category-preferential regions. However, several interesting properties of the category-preferential regions emerged from the analyses. The category-preferential regions showed some evidence of specificity in neural priming for a preferred category. The task-related connectivity of these regions was similar to previously reported intrinsic connectivity. Finally, the VWFA showed a preference for text and a dissociation between real words and pseudowords, and displayed functional connectivity with language regions in response to real words. I did not find evidence to support the neural synchrony model of priming with the chosen analytical methods, however there are several future directions that may reveal more about the neural mechanisms of priming.

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