Research report

Broca's region and Visual Word Form Area activation differ during a predictive Stroop task

Mikkel Wallentin ^{a,b,*}, Claus Højbjerg Gravholt ^{c,d} and Anne Skakkebaek ^{c,e}

^a Center of Functionally Integrative Neuroscience, Aarhus University Hospital, 8000 Aarhus C, Denmark

^b Center for Semiotics, Aarhus University, Denmark

^c Department of Endocrinology and Internal Medicine (MEA), Aarhus University Hospital, 8000 Aarhus C, Denmark

^d Department of Molecular Medicine, Aarhus University Hospital, 8200 Aarhus N, Denmark

^e Department of Clinical Genetics, Aarhus University Hospital, 8200 Aarhus N, Denmark

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ABSTRACT

Competing theories attempt to explain the function of Broca's area in single word processing. Studies have found the region to be more active during processing of pseudo words than real words and during infrequent words relative to frequent words and during Stroop (incongruent) color words compared to Non-Stroop (congruent) words. Two related theories explain these findings as reflecting either “cognitive control” processing in the face of conflicting input or a linguistic prediction error signal, based on a predictive coding approach. The latter implies that processing cost refers to violations of expectations based on the statistical distributions of input. In this fMRI experiment we attempted to disentangle single word processing cost originating from cognitive conflict and that stemming from predictive expectation violation. Participants ($N = 49$) responded to whether the words “GREEN” or “RED” were displayed in green or red (incongruent vs congruent colors). One of the colors, however, was presented three times as often as the other, making it possible to study both congruency and frequency effects independently. Auditory stimuli saying “GREEN” or “RED” had the same distribution, making it possible to study frequency effects across modalities. We found significant behavioral effects of both incongruency and frequency. A significant effect ($p < .05$ FWE) of incongruency was found in Broca's region, but no effect of frequency was observed and no interaction. Conjoined effects of incongruency and frequency were found in parietal regions as well as in the Visual Word Form Area (VWFA). No interaction between perceptual modality and frequency was found in VWFA suggesting that the region is not strictly visual. These findings speak against a strong version of the prediction error processing hypothesis in Broca's region. They support the idea that prediction error processes in the intermediate timeframe are allocated to more posterior parts of the brain.

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* Corresponding author. Center of Functionally Integrative Neuroscience, Aarhus University Hospital, Building 10-G-5, Nørrebrogade, 8000 Aarhus C, Denmark.

E-mail addresses: mikkel@cfni.dk, mikkel@cfni.au.dk (M. Wallentin).

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1. Introduction

1.1. Broca's region

Broca's region (Broca, 1861) is located in the left inferior frontal gyrus (LIFG) and is usually defined as consisting of Brodmann area 44 and 45 (Amunts & Zilles, 2012). It is known to play a key role in speech production as well as in the processing of language input (e.g., see Kristensen & Wallentin, 2015 for a review). The exact function of the region, however, is disputed (Grodzinsky & Santi, 2008; Novick, Trueswell, & Thompson-Schill, 2010). One suggestion has been that activation in Broca's region reflects general linguistic processing costs (Kristensen & Wallentin, 2015), i.e., that whenever a linguistic process for some reason is difficult or challenged, it causes Broca's region to become more active. In support of this hypothesis are well-known findings that syntactic manipulations yield increased Broca's region activation (Ben-Shachar, Palti, & Grodzinsky, 2004; Christensen & Wallentin, 2011; Kristensen, Engberg-Pedersen, Nielsen, & Wallentin, 2013; Tettamanti et al., 2009) and findings showing that Broca's region responds to unpredicted word order, rather than syntactic manipulations per se, as defined by working memory demands (Fiebach, Schlesewsky, Lohmann, VonCramon, & Friederici, 2005; Wallentin, Roepstorff, Glover, & Burgess, 2006), cloze probability (Oleser & Kotz, 2010) or context (Kristensen, Engberg-Pedersen, & Wallentin, 2014).

Broca's region activation is also routinely observed in the absence of word order manipulations (Fedorenko, Duncan, & Kanwisher, 2013; Novick et al., 2010). Single word studies have demonstrated that Broca's region activity is increased whenever a new word is presented (Wallentin, Michaelson, Rynne, & Nielsen, 2014), that it is correlated with working memory demand (Cohen et al., 1997), and displays an inverse correlation with word frequency (Fiebach, Friederici, Müller, & VonCramon, 2002; Kronbichler, et al., 2004), word generation practice (Raichle et al., 1994) and priming (Thompson-Schill, D'Esposito, & Kan, 1999). Pseudo-words, on the other hand, have been found to generate greater activation than real words (Fiebach et al., 2002), again suggesting that unexpected words or words that are difficult to understand yield greater activation. Along the same lines, Broca's region has been found to increase activation to degraded visual word features (van de Meerendonk, Rueschemeyer, & Kolk, 2013) and when words from one perceptual modality (e.g., vision) has to be compared to words from another (e.g., audition) (Wallentin et al., 2014) as well as to decreased plausibility based on world knowledge (van de Meerendonk et al., 2013). More generally, it has been found that Broca's region activation is positively correlated with response time during linguistic processing (Christensen & Wallentin, 2011; Kristensen & Wallentin, in press; Orfanidou, Marslen-Wilson, & Davis, 2006; Wallentin et al., 2006).

1.2. The Stroop task and cognitive control

Due to this broadening of the scope of tasks that yield increased Broca's region activity, it has been suggested that its function is not limited to linguistic processes, but serves a

broader function in cognitive control (Novick, Trueswell, & Thompson-Schill, 2005; Novick et al., 2010). Cognitive control refers to the mental ability to guide and adjust one's attention and actions in accordance with current goals (Novick et al., 2010), often in the face of conflicting information. Cognitive control has classically been thought of as a slow and strategic process (Shiffrin & Schneider, 1977) that is initiated in a top-down (i.e., internal, goal-driven) fashion. According to this theory, LIFG is thought to be involved when individuals must resolve conflicting information about how to characterize a stimulus, or how best to respond to that stimulus (Novick et al., 2010). One clear example of a situation requiring elevated levels of cognitive control is the well-known Stroop task (MacLeod, 1991; Stroop, 1935). The Stroop task involves naming the ink color of printed color words, and it involves cognitive control when the written word and the color of the letters are not the same, because the instruction to name the color of the letters conflicts with the overly practiced response of reading the word. The Stroop task has repeatedly been found to yield activation in LIFG (Chen, Lei, Ding, Li, & Chen, 2012; Derrfuss, Brass, Neumann, & von Cramon, 2005; MacDonald, Cohen, Andrew Stenger, & Carter, 2000; Milham, Banich, & Barad, 2003; Van 't Ent, Den Braber, Rotgans, De Geus, & De Munck, 2014; van Veen & Carter, 2005). The fact that the Stroop task yields LIFG activation excludes the possibility of LIFG function being exclusively tied to working memory demand (Fiebach et al., 2005; Wallentin et al., 2006), as there is no overt working memory component in the Stroop task.

The exact role of the LIFG in the Stroop and in cognitive control in general is not yet fully understood. One suggestion would be to interpret the Stroop effect and cognitive control within the predictive coding paradigm.

1.3. Predictive coding

Predictive coding has been suggested as an overarching framework for how the brain works (Clark, 2013; Friston, 2010; Hickok, 2012; Hohwy, 2013). In short, predictive coding is the process by which the brain is thought to constantly attempt to match incoming sensory inputs with top-down expectations or predictions. The underlying idea is that the brain has a model of the world that it tries to optimize using sensory inputs. In this view, the brain is an inference machine that actively predicts and explains its sensations. Central is a probabilistic model that can generate predictions, against which sensory samples are tested to update beliefs about their causes. According to the theory, this is achieved using a hierarchical generative model that aims to minimize prediction error within a bidirectional cascade of cortical processing. The bottom of the hierarchy are the processes closest to the sensory input, while the top is constituted by the levels that contain models that are abstracted away from a clear relation to a particular sensory stimulus and/or modality (Tenenbaum, Kemp, Griffiths, & Goodman, 2011). Prediction errors can arise at multiple stages in the processing hierarchy whenever a top-down expectation is not met by the bottom-up stimuli from the lower level.

A simple example of a phenomenon thought to reflect predictive coding and prediction error is task shift effects

(Wallentin et al., 2014). In a recent experiment, we used a simple one-back memory task where participants were asked simply to report whether a word in the stimulus row was the same as the previously presented word or not. With this task it was found that new words yielded stronger activation in LIFG than words that were repeats. Along the same lines it was found that words that were presented in a new perceptual modality (e.g., going from a visual word to an orally presented word) also yielded more activation in LIFG than words that remained within the same perceptual modality, suggesting that whenever something new happens in the verbal domain, Broca's region increases its activation. This sort of status quo bias is also reflected in the flip side effect known as repetition suppression where repeated stimuli are found to yield decreased neural responses (Dehaene et al., 2001; Orfanidou et al., 2006; Raichle et al., 1994; Schacter & Buckner, 1998; Summerfield, Wyart, Johnen, & de Gardelle, 2011; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008; Todorovic, van Ede, Maris, & de Lange, 2011). Repetition suppression has been used as an example of how more predicted stimuli yields less neural activation (Friston, 2010). Within the predictive coding framework, this is thought to be based on a statistical sampling of the stimuli over time. The task shift effects and repetition suppression effects thus reflect sampling that happens over a very short period of time, i.e., over the course of two experimental trials (a few seconds). But predictions may of course also be based on intermediate or longer periods of time and reflect the experienced distribution of stimuli and events in the environment. Similar to the notion of abstraction as removed from the concrete perceptual input it may also be conceptualized as removed from the immediate temporal context. We may thus additionally define the bottom of the predictive coding hierarchy in terms of its responsiveness to short-term changes in predictability. Along these lines, all experiences and actions that are novel or untrained will cause a prediction error at some place in the prediction hierarchy. In higher levels this effect will only change slowly while short-term changes in the statistical context will have rapid effects in the lower levels of the processing hierarchy.

One finding that suggests a link between cognitive control and predictive coding is the fact that the behavioral Stroop incongruity effect diminishes if the previous trial also was an incongruent trial (Gratton, Coles, & Donchin, 1992). Other types of short-term context and contingency effects have been observed for the Stroop task as well (Bugg, 2012; Schmidt & Besner, 2008). Response times have been found to be lower for a given Stroop task color when this color is often presented in the incongruent condition, compared to a color that was most often presented in a congruent condition. This suggests that participants during the time-course of an experiment adapt to the response contingencies of the stimuli and learn to override the incongruity, but do so slower for the less predictable responses.

In the present experiment we investigated the degree to which Broca's region is sensitive to predictability. Within a simplified Stroop paradigm where participants respond to whether the ink of a given word is green or red, regardless of whether the printed word was "GREEN" or "RED", we added a frequency manipulation (see Fig. 1), such that one of the colors

(counterbalanced across participants) would occur more often than the other and thus become more predictable during the course of the experiment. If the response in Broca's region reflects a short-term prediction error signal, then we should expect to see a modulation of it as a function of predictability. In order to keep the Stroop effect orthogonal to the frequency effect, we did not change the response contingencies, i.e., the distribution of congruent and incongruent stimuli was the same for both frequent and infrequent stimuli (50%) – see Fig. 1. We were thus primarily interested in investigating if we could find an overlap in activation between the Stroop effect and the frequency effect in Broca's region. This could be taken as an argument in favor of Broca's area being involved in more general prediction error processing and subsequently that the Stroop effect might also be interpreted as a sort of prediction error. A potential interaction between the Stroop incongruity effect and the frequency effect would further strengthen this hypothesis by demonstrating online context sensitive modulation.

1.4. Primary hypothesis

Our primary hypothesis in this experiment was that Broca's region incongruity activation for Stroop words reflects a prediction error signal. If this is true, then we should expect to see a modulation of the activation in Broca's area as a function of predictability (i.e., frequency) of a given stimulus and potentially an interaction between the effect caused by the incongruity and the effect caused by predictability.

1.5. Visual Word Form Area

The Visual Word Form Area (VWFA) is located in the posterior part of the inferior temporal gyrus (Dehaene & Cohen, 2011; Dehaene, LeClecq, Poline, Le Bihan, & Cohen, 2002; Wallentin et al., 2014). The area has repeatedly been found to be associated with reading words. Furthermore, it has been found to be functionally specific to words relative to objects (Szwed et al., 2011) and relative to mirror images of words (Dehaene et al., 2010). Similar to Broca's region, there are findings that suggest that VWFA may be involved in processing participant's statistical knowledge about words, e.g., it has been found to be sensitive to word frequency (Kronbichler et al., 2004) and bigram frequency, i.e., the statistics of letter pairs in a particular language (Vinckier et al., 2007). Controversies about the alleged specificity of the region also exist (Price & Devlin, 2003) with some studies also highlighting the context dependency of the VWFAs response pattern (Starrfelt & Gerlach, 2007), and some studies finding the VWFA to be involved in the processing of both spoken words and pseudo-words (Orfanidou et al., 2006). The VWFA may thus also be a region relevant for the interface between visual and auditory aspects of word forms. Supporting the latter is our recent one-back word experiment, reporting that VWFA, similar to Broca's region, displays more activity for new words compared to repeat words and for words that are presented in a new perceptual modality, regardless of whether it is in the visual modality or not (Wallentin et al., 2014). These short-term sensitivities to novelty point towards a possible role in attempting to predict the incoming stimuli, and as such it

should also be sensitive to a frequency manipulation beyond the trial-by-trial time interval. Studies of the nearby face sensitive region (Fusiform face area) have also shown that repetition suppression in this area is sensitive to the statistical distribution of face repetitions over the course of an experiment (Summerfield et al., 2008).

Additional to the Stroop manipulation in the visual domain, the present experiment also included an auditory condition where the same words (“red” and “green”) were presented to the participants with no incongruity effects present (see Fig. 1). This allowed us to investigate the extent to which the frequency effects were modality independent or not. Our hypothesis was that the lower levels of the predictive coding hierarchy closest to the perceptual input regions would be sensitive to predictability only within a particular perceptual modality while the higher levels would be modality independent, i.e., representing more abstract predictions. By manipulating frequency across both visual and auditory stimuli, we could thus directly test whether VWFA is responsive to auditory input. If the region is strictly unimodal, then we should not only see a difference in the region between visual and auditory stimuli, but we should also expect to see an interaction between the perceptual modality of the stimulus and the frequency with which it occurs. If the region is unimodal then we would expect it to adapt to visual frequency differences but not to differences in the auditory stimuli.

1.6. Secondary hypothesis

Our secondary hypothesis was that the VWFA would display the same sort of overlap between frequency based activation and Stroop effect as we hypothesized to be present in Broca's region, potentially with an interaction between perceptual modality and frequency.

1.7. Primary perceptual regions

In order to investigate if the bottom of the putative predictive hierarchy closest to the perceptual input responds in a modality specific fashion and is sensitive to changes in predictability, we investigated if regions showing a main effect of perceptual modality would also display frequency effects. If the hierarchical account of the processing system is correct and if the link between low-level and short-term adaptability is correct, then these regions should display a modality specific frequency modulation of activity.

2. Material and methods

2.1. Participants

The participants in the current study were part of a control group for a patient study (Skakkebæk, Bojesen, et al., 2014; Skakkebæk, Gravholt, et al., 2014 – data from patients not included here). Sixty five male controls were included as controls in this study, recruited through advertisement in local hospitals, in local newspapers, at local work services, among volunteer fire fighters, at citizen service offices and at local libraries. Fifty-three participants out of this group also

completed the fMRI experiment. Four participants had to be excluded. Two participants were excluded due to artifacts in the EPI-images and two due to poor performance in the behavioral task.

All 49 participants were male (median age: 36 years, range: 19–59 years), 44 participants reported being right-handed, five reported left-handedness. The demographics of the patient group were so that the control participants to a large extent were representative of the Danish population, apart from the fact that they were all male. We have, however, little reason to believe that our results would be different with a mixed gender population (Wallentin, 2009; Wallentin et al., 2014). Median length of education was 13 years (range: 8–18 years).

All participants received oral and written information about the study before giving their written consent. The study was approved by the Danish Data Protection Agency and local ethics committee (Region Midtjylland, Denmark number M-20080238) and registered at ClinicalTrials.gov (Clinical trial NCT00999310).

2.2. Stimuli

The experiment consisted of 400 trials mixing 250 visual and 150 auditory single word stimuli. Stimuli consisted of three Danish words: “GRØN” (GREEN), “RØD” (RED) and “GUL” (YELLOW). 300 Trials were either GREEN or RED, 100 trials were YELLOW (see Fig. 1). Participants responded with button presses using their right hand.

2.2.1. Stroop versus Non-Stroop trials

For the visual stimuli, participants were requested to respond with their index finger if the color of the letters were green, and with their middle finger if the color of the letters were red, regardless of the written word. The words GREEN and RED could be written in either green letters or red letters. The RED/GREEN part of the visual stimuli thus made up a simplified Stroop task (MacLeod, 1991; Stroop, 1935).

2.2.2. Frequent versus Infrequent trials

Counterbalanced across participants either GREEN or RED was the more frequent stimulus across both auditory and visual conditions (see Fig. 1). The frequent stimulus appeared three times as often (225 trials) as the infrequent stimulus (75 trials). This meant that for the visual stimuli the frequent color would be displayed 75 times in the incongruent condition and 75 times in the congruent condition. The infrequent color was displayed 25 times in the incongruent condition and 25 times in the congruent. All visual stimuli thus had the same within-color probability of a trial being a Stroop trial (50%).

2.2.3. No response trials

The word YELLOW was always displayed in yellow letters (50 trials). For YELLOW trials, participants were requested not to respond. These stimuli were included as a baseline to which Stroop and Frequency effects could be compared (e.g., see Fig. 6).

2.2.4. Auditory stimuli

For the auditory stimuli, the participants responded to the word itself, i.e., index finger for the word “GREEN” (75 or 25

trials) and middle finger for the word “RED” (75 or 25 trials) and no response for “YELLOW” (50 trials). Again, in concordance with the visual stimuli, either “GREEN” or “RED” would be frequent and thus presented 75 times or infrequent and presented 25 times (see Fig. 1). This allowed an analysis that would indicate whether potential frequency effects were limited to the visual modality or not. Auditory stimuli were recorded in mono in a male neutral voice (sample frequency: 22050 Hz) using a laptop computer.

2.3. Procedure

Stimuli were presented and responses obtained using Cogent 2000 (http://www.vislab.ucl.ac.uk/cogent_2000.php), executed in MATLAB. Visual stimuli were displayed on a black background and projected onto a screen placed at the foot of the scanner bed and participants viewed the stimuli through a mirror mounted on the head coil. Auditory stimuli were delivered through pneumatic headphones from Avotec (Stuart, FL USA). These also helped to attenuate scanner noise.

The fMRI part of the experiment lasted approximately 20 min. Before entering the scanner, participants were given a short trial run of the task in order to get accustomed to the study design and response procedure. After positioning in the scanner, the participant was randomly attributed to one of the two groups that would get a particular stimulus type more often (Fig. 1). Participants were not informed beforehand that one of the trial types would be more frequent than the other.

2.4. fMRI acquisition

A 3T General Electrics Medical Systems (Milwaukee, WI USA) MR system with a standard head coil was used to acquire both T²-weighted gradient echo, echo-planar images (EPI) with Blood Oxygenation Level-Dependent (BOLD) contrast and T₁-weighted structural images. 570 EPI volumes were acquired per participant, not including the first 5 volumes that were discarded to allow for effects of T₁ equilibrium. Whole brain coverage was achieved using 36 axial slices of 3.5 mm thickness with an in-plane resolution of 3.33 × 3.33 mm in a 64 × 64 voxel matrix (FOV 213.3 mm). Images were obtained with a TR of 2200 ms, a 30 ms TE and a 90° flip angle. A high-resolution 3D GR T₁ anatomical scan was acquired for an additional voxel-based morphometry study (Skakkebæk, Bojesen, et al., 2014;

Skakkebæk, et al., 2014b). It consisted of 256 × 256 × 134 voxels with a .94 × 0.94 × 1.2 mm³ voxel size, obtained with a TR of 6.552 ms, a 2.824 ms TE and a 14° flip angle.

2.5. Data analysis

2.5.1. Pre-processing of fMRI data

All fMRI image pre-processing and data analyses were performed using Statistical Parametric Mapping software (SPM8; Wellcome Department of Imaging Neuroscience, www.fil.ion.ucl.ac.uk/spm), implemented in MATLAB. Functional images were motion corrected and registered to the first EPI image and normalized to the EPI template in SPM8. Finally, data were spatially smoothed with an isotropic 8 mm full width at half maximum (FWHM) Gaussian kernel to account for differences between participants.

2.5.2. Statistical analyses of fMRI data

Statistical analyses of fMRI data were performed using a two-level general linear model approach (Penny & Holmes, 2007; Worsley & Friston, 1995). Eight regressors of interest were included at the first level (see Fig. 1): Visual Stroop/Low Frequency (VS/LF); Visual Stroop/High Frequency (VS/HF); Visual Non-Stroop/Low Frequency (VNS/LF); Visual Non-Stroop/High Frequency (VNS/HF); Visual Non-Stroop/No Response (VNS/NR); Auditory Non-Stroop/Low Frequency (ANS/LF); Auditory Non-Stroop/High Frequency (ANS/HF); Auditory Non-Stroop/No Response (ANS/NR). Onset for each trial was defined as the onset of the stimulus. Duration was set to .5 sec for all trials and conditions. The model was convolved with the standard hemodynamic response function in SPM8 to account for the delay in the BOLD signal. Additional nuisance regressors included error trials and six regressors modeling head motion. Six contrast measures were sent to the 2nd level analysis: Main effect of Stroop ([1 1 −1 −1 0 0 0 0]), main effect of Frequency (visual) ([1 −1 1 −1 0 0 0 0]), Stroop × Frequency interaction ([1 −1 −1 1 0 0 0 0]), effect of Frequency (auditory) ([0 0 0 0 1 −1 0]), main effect of perceptual modality for non-stroop trials ([0 0 1 1 0 −1 −1 0]) and an interaction between modality and frequency ([0 0 1 −1 0 −1 1 0]). In order to control for false positives, we thresholded results at $p < .05$ and family-wise error corrected for multiple comparisons. Putative anatomical regions of peak activation sites were defined using the Wake Forest University Pickatlas (Tzourio-Mazoyer

	VS/LF	VS/HF	VNS/LF	VNS/HF	VNS/NR	ANS/LF	ANS/HF	ANS/NR	N (GROUP)
N (STIM)	25	75	25	75	50	25	75	50	
GROUP 1	RED	GREEN	GREEN	RED	YELLOW	"GREEN"	"RED"	"YELLOW"	26
GROUP 2	GREEN	RED	RED	GREEN	YELLOW	"RED"	"GREEN"	"YELLOW"	24

Fig. 1 – Experimental setup. Participants received eight types of stimuli. Visual Stroop/Low Frequency (VS/LF); Visual Stroop/High Frequency (VS/HF); Visual Non-Stroop/Low Frequency (VNS/LF); Visual Non-Stroop/High Frequency (VNS/HF); Visual Non-Stroop/No Response; Auditory Non-Stroop/Low Frequency (ANS/LF); Auditory Non-Stroop/High Frequency (ANS/HF); Auditory Non-Stroop/No Response (ANS/NR). Participants responded with a button press using their index finger if the color of the letters (for visual stimuli) were green and if a voice said “green” (auditory stimuli) and responded with their middle finger if the color was red or if a voice said “red”. In the case of a yellow or “yellow” stimulus, the participants were instructed not to respond. Stimuli could be highly frequent or less frequent. Participants were randomly attributed to two groups that counterbalanced color and frequency.

et al., 2002). Only peaks >10 mm apart are reported. In order to inspect putative regional overlaps between the Stroop effect and the Frequency effects, we created two conjunction maps: Conjunction 1 displays the overlap between Stroop and the Frequency effect for the visual stimuli (Fig. 5 top), and Conjunction 2 displays the overlap between the Stroop effect and the Frequency effects for both visual and auditory stimuli (Fig. 5 bottom). To further estimate and visualize effects in particular voxels, we extracted beta-estimates from all participants for all eight conditions. The extracted single voxel data within Broca's region and primary perceptual regions were submitted to 2×2 repeated measures ANOVA analyses in order to investigate the extent to which lack of significant frequency and interaction effects might be due to our stringent multiple comparison correction.

3. Results

3.1. Behavioral results

3.1.1. Stroop $\times$ frequency (visual): response time

A 2×2 factorial repeated-measures ANOVA was conducted on each participant's median response time. Only correct responses were analyzed. A main effect of the Stroop task was found [$F(1,48) = 49.23$, $p < .001$, Bonferroni corrected], and a main effect of frequency [$F(1,48) = 19.78$, $p < .001$, Bonferroni corrected]. The low frequency color yielded longer response latency. A borderline significant interaction between Stroop and frequency was seen [$F(1,48) = 6.064$, $p = .051$, Bonferroni corrected], indicating that the frequency effect is greater for congruent trials than for incongruent trials (Fig. 2A, columns 1–4).

3.1.2. Stroop $\times$ frequency (visual): accuracy

A 2×2 factorial repeated-measures ANOVA revealed a main effect of the Stroop task [$F(1,48) = 10.03$, $p < .01$, Bonferroni corrected], a borderline significant main effect of frequency [$F(1,48) = 5.99$, $p < .054$, Bonferroni corrected]. No interaction was observed for accuracy [$F(1,48) = .18$, $p = .6$] (Fig. 2B, columns 1–4).

3.1.3. Perceptual modality $\times$ frequency: response time

A new 2×2 factorial repeated-measures ANOVA was conducted using only the non-Stroop visual trials, but including the auditory trials as well on response time for perceptual modality versus frequency. Only correct responses were analyzed. A main effect of perceptual modality was found [$F(1,48) = 11.90$, $p < .01$, Bonferroni corrected], with RT for visual stimuli being shorter than for auditory. A main effect of frequency was also observed [$F(1,48) = 85.35$, $p < .001$, Bonferroni corrected]. The low frequency color yielded longer response latencies. No interaction was observed for response time [$F(1,48) = .29$, $p = .6$] (Fig. 2A, columns 3–6).

3.1.4. Perceptual modality $\times$ frequency: accuracy

A 2×2 factorial repeated-measures ANOVA on accuracy was also conducted contrasting perceptual modality and frequency, again only including non-Stroop trials. No main effect of perceptual modality was found [$F(1,48) = .001$, $p > .5$], while

a main effect of frequency was observed [$F(1,48) = 11.96$, $p < .01$, Bonferroni corrected]. The low frequency color yielded more errors. No interaction was observed [$F(1,48) = .08$, $p = .8$] (Fig. 2B, columns 3–6).

3.2. fMRI results

3.2.1. Stroop $\times$ frequency (visual) analysis

3.2.1.1. STROOP EFFECT. The main effect of Stroop was found in a number of regions, including inferior frontal gyrus (Broca's region), bilaterally, premotor regions in the left hemisphere, posterior parietal cortex, bilaterally, extending to both the inferior and the superior parietal lobule. Activation in the VWFA in the inferior part of the left temporal lobe was also observed (Fig. 3 top panel, Table 1). There were no significant decreases in activation as a function of the Stroop task.

3.2.1.2. FREQUENCY EFFECT (VISUAL). The main effect of frequency revealed a number of regions that were more active for the

Fig. 2 – Behavioral effects. A 2×2 ANOVA on the visual data revealed both a response time effect (A – four leftmost bars) and an effect on accuracy (B – four leftmost bars) as a function of stroop (VS vs VNS) and frequency (LF vs HF). No interactions were observed. When the visual non-stroop data (VNS) were compared to the auditory data (ANS), we again observed a significant effect of frequency on both response time (A – four rightmost bars) and accuracy (B – four rightmost bars). No interactions were observed, suggesting that the frequency effects are not strongly affected by perceptual modality. Error bars reflect the standard error of the mean, but note that this describes between-participant variability while the data are all within-participant comparisons.

Table 1 – fMRI-effects of the Visual Stroop (VS) versus Visual NonStroop (VNS) contrast, regardless of frequency.

Putative anatomical region	Peak MNI	Z-score
Effects of Stroop task (Stroop > NonStroop)		
Insula L	–30, 22, 4	4.89
Frontal Inf Oper L – BA 44	–46, 16, 14	5.14
Frontal Inf Orb L – BA 47	–48, 18, –6	5.29
Frontal Inf Tri R – BA 45	56, 32, 24	5.07
Frontal Precentral/Inf Tri L – BA 6/44	–46, 12, 30	6.42
Frontal Precentral L – BA 6	–46, 6, 50	5.45
Frontal Sup L – BA 6	–32, –4, 68	5.14
Parietal Inf L – BA 40	–42, –46, 42	4.99
Parietal Angular/Inf R – BA 39/40	36, –58, 40	5.73
Parietal Sup L – BA 7/40	–32, –64, 48	6.23
Temporal Mid L – BA 21	–58, –38, 0	4.85
Temporal Fusiform/Inf L – BA 37 (VWFA)	–42, –52, –16	5.11
Effects of Stroop task (NonStroop > Stroop)		
No significant effects	–	–
P-FWE < .05.		

low frequency trial type, regardless of whether it was a Stroop task or not. These regions included premotor regions, sensorimotor, and parietal regions, including both superior and inferior lobule. Many effects were bilateral, but stronger in the left than in the right hemisphere. Activations were also observed in the visual word form area (VWFA) in the inferior part of the temporal lobe as well as in the cerebellum (Fig. 3, bottom panel, Table 2). No significant frequency effect was found in primary visual cortex and there were no regions where the high frequency stimuli showed greater activation than the low frequency stimuli.

3.2.1.3. INTERACTION EFFECT (STROOP $\times$ FREQUENCY). No significant interactions were observed.

3.2.1.4. CONJUNCTION 1 (STROOP AND VISUAL FREQUENCY). Fig. 5 (TOP panel) shows the regions that were activated in both the Stroop and in the Frequency contrasts. This overlap included four regions, all in the left hemisphere (circled in yellow and green on Fig. 5). One pre-motor region was found, one in the superior frontal gyrus [–30, –4, 68], two regions in the parietal lobe, one in the inferior parietal lobule [–44, –44, 44] and one in the superior parietal lobule [–30, –64, 50]. Lastly an overlap was found in the VWFA [–44, –54, –18]. Notably, no overlap was observed in Broca's region. As can be seen from the barplot in Fig. 5 (circled in red), this lack of overlap seems not to be caused by our conservative thresholding procedure. There seems to be no effect of visual frequency whatsoever in the coordinate [–46, 16, 14] found to be most responsive to the Stroop manipulation. On conducting a 2 $\times$ 2 ANOVA on the Stroop $\times$ Visual Frequency on this voxel alone, no significant frequency effect is observed [$F(1,48) = 1.934$, $p > .05$, uncorrected for multiple comparisons]. See discussion section and Fig. 6 for further elaboration of this issue.

3.2.2. Auditory frequency analysis

3.2.2.1. FREQUENCY EFFECT (AUDITORY). An analysis of the frequency effects based on the auditory data revealed an activation pattern very similar to that observed for the visual data.

Again activations were found as an effect of the low frequency stimuli yielding greater responses than the high frequency stimuli. These effects were observed in the sensorimotor regions and in the parietal cortex, in the left hemisphere. No significant frequency effects were found in primary auditory regions and no regions displayed greater activation for the high frequency stimuli than for the low frequency (Fig. 5, Table 2).

3.2.2.2. CONJUNCTION 2 (STROOP AND VISUAL FREQUENCY AND AUDITORY FREQUENCY). Only one region in the left inferior parietal lobule [–44, –44, 44] was found to overlap between all three contrasts. As can be seen from Fig. 5 (bottom panel), this region does not discriminate between visual and auditory input in terms of the frequency effect. It does, however, have greater responses to trials with a behavioral response compared to no-response trials, regardless of whether these are visual or auditory. It is also noteworthy that all stimuli generate a positive response in this region compared to the un-modeled baseline.

3.2.3. Perceptual modality $\times$ frequency (Non-Stroop data)

3.2.3.1. MAIN EFFECT OF PERCEPTUAL MODALITY (NON-STROOP ONLY). The contrast between the two perceptual modalities revealed bilateral effects in primary and secondary perceptual cortices (see Fig. 6). The two most significant peaks (see Fig. 6) were used in the analysis of interaction effects between perceptual modality and frequency.

3.2.3.2. INTERACTION EFFECT (MODALITY $\times$ FREQUENCY). No significant interactions were observed between perceptual modality and frequency at the whole-brain corrected threshold level. In order to investigate possible interactions in primary

Table 2 – fMRI-effects of the Low Frequency (LF) versus High Frequency (HF) contrast in visual and auditory conditions separately.

Putative anatomical region	Peak MNI	Z-score
Effects of frequency (low > high)		
Visual stimuli		
Frontal Precentral L – BA 6	–44, 2, 28	4.57
Frontal Sup L – BA 6	–30, –10, 66	5.82
Frontal Sup R – BA 6	32, –8, 62	5.46
Parietal Inf L – BA 40	–54, –26, 40	5.97
Parietal Postcentral L – BA 2/4/40	–46, –36, 50	7.08
Parietal Inf R – BA 40	38, –42, 44	5.97
Parietal Sup L – BA 7/40	–28, –68, 50	5.65
Precuneus – BA 7	–2, –74, 42	4.68
Temporal Fusiform/Inf L – BA 37 (VWFA)	–46, –54, –16	5.01
Temporal Fusiform L	–38, –58, –22	5.32
Temporal Fusiform/Cerebellum R	34, –58, –26	4.85
Auditory stimuli		
Parietal Postcentral L – BA 2/4/40	–60, –18, 26	4.70
Parietal Postcentral L – BA 2/4/40	–46, –30, 46	6.67
Parietal Postcentral L – BA 2/4/40	–48, –30, 56	6.53
Parietal Sup L – BA 5/7/40	–34, –50, 64	6.53
Effects of frequency (high > low)		
No significant effects	–	–
P-FWE < .05.

Fig. 3 – Main effects of Stroop versus non-Stroop (top panel) and Frequency (low > high) for the visual stimuli (bottom panel) at $p < .05$ FWE corrected for multiple comparisons. No regions depicted more activation during non-Stroop than during Stroop and no regions were more active for the high > low frequency contrast, and no interactions between effects were observed.

perceptual areas, we extracted beta-estimates from the peak voxels in the auditory > visual contrast $[-64, -30, 4]$ and visual > auditory contrast $[-30, -98, -8]$ (see Fig. 6). These two data sets were submitted to two repeated measures

ANOVA analyses. For the peak voxel in auditory cortex, we found a significant interaction between perceptual modality and frequency $[F(1,48) = 12.22, p = .001]$. A paired t -test revealed that the interaction effect reflects that low

Fig. 4 – Main effects of frequency (low > high) for the auditory stimuli at $p < .05$ FWE corrected for multiple comparisons. No regions depicted more activation high > low frequency contrast.

Fig. 5 – Conjunction effects. TOP: Rendering showing overlap between activation maps for Stroop and visual frequency effects at $p < .05$ FWE. BOTTOM: Rendering showing overlap between activation maps for Stroop and visual and auditory frequency effects at $p < .05$ FWE. A: No overlap is observed in Broca's region. Bar plot displays peak MNI coordinate for the Stroop condition [-46, 16, 14]. Regions of overlap with peak MNI coordinates are B: Superior frontal gyrus [-30, -4, 68], C: Superior parietal lobule [-30, -64, 50], D: Visual Word Form Area [-46, -54, -18] and E: Inferior parietal lobule [-44, -44, 44]. The latter region is the only region found in all three contrasts, however some indications point towards this being related to thresholding, i.e., the pattern with low frequencies yielding greater activity than high frequencies is apparent across the board. The bar plots show the effect of all 8 conditions in the respective area. Visual Stroop/Low Frequency (VS/LF); Visual Stroop/High Frequency (VS/HF); Visual Non-Stroop/Low Frequency (VNS/LF); Visual Non-Stroop/High Frequency (VNS/HF); Visual Non-Stroop/No Response; Auditory Non-Stroop/Low Frequency (ANS/LF); Auditory Non-Stroop/High Frequency (ANS/HF); Auditory Non-Stroop/No Response (ANS/NR). Error bars reflect the standard error of the mean, but note that this describes between-participant variability while the data are all within-participant comparisons.

frequency auditory stimuli yields a greater response in auditory cortex than high frequency auditory stimuli [$t(48) = 3.67, p < .001$], while there was no significant difference between low-frequency and high frequency congruent stimuli in the visual modality [$t(48) = -1.01, p = .31$]. For the peak in visual cortex, we found no significant interaction effect between modality and frequency [$F(1,48) = .05, p = .8$] (see Fig. 6). Lastly, we tested for interaction effects between modality and frequency in the peak region in VWFA (see Fig. 5). No interaction was found here either [$F(1,48) = .01, p = .9$]. A post-hoc t -test between low frequency and high frequency auditory data indicated that this is due to the fact

that the VWFA to some extent is sensitive to frequencies in auditory stimuli [$t(48) = 2.09, p < .05$].

4. Discussion

Behaviorally, we found both a strong Stroop incongruity effect and a clear frequency effect, thus replicating previous findings. Interestingly, we also observed a marginally significant interaction between incongruity and frequency, indicating that the frequency effect was diminished in the incongruent condition compared to the congruent condition.

Fig. 6 – In peak regions from the main effects of perceptual modality analysis we found an interaction between perceptual modality and frequency in auditory cortex, but not in visual cortex. Primary visual regions did not show any sign of frequency dependence. The bar plots show the effect of all 8 conditions in the respective area. Visual Stroop/Low Frequency (VS/LF); Visual Stroop/High Frequency (VS/HF); Visual Non-Stroop/Low Frequency (VNS/LF); Visual Non-Stroop/High Frequency (VNS/HF); Visual Non-Stroop/No Response; Auditory Non-Stroop/Low Frequency (ANS/LF); Auditory Non-Stroop/High Frequency (ANS/HF); Auditory Non-Stroop/No Response (ANS/NR). Error bars reflect the standard error of the mean, but note that this describes between-participant variability while the data are all within-participant comparisons.

Interpreted within a hierarchical framework this may be taken to suggest that the prediction error related to Stroop incongruity originates at a higher level in the hierarchy and as such adapts at a lower pace, thus partly overriding the effect of frequency.

4.1. Broca's region (LIFG)

We replicated the finding that Stroop incongruity yields increased activation in Broca's region. We found no evidence for our primary hypothesis, that the region should be sensitive to within-experiment frequency effects, neither in the visual nor in the auditory domain. This suggests that if Broca's region activation reflects prediction error based on statistical sampling of the environment, then it does not work on the short-/medium-term time frame within which the present experiment unfolds. The lack of frequency effects in Broca's region is not due to a lack of power since the experiment with its large number of participants ($n = 49$) is well-powered. This is also reflected in the behavioral data where clear frequency effects are seen. The frequency effects observed elsewhere in the brain, including in the VWFA and the parietal lobe also suggest that the lack of Broca's region activation is not due to lack of power. When looking at the coordinate found to be most responsive to the Stroop task in LIFG, we see no indication

whatsoever of a frequency effect (see results section and Fig. 5A). Lowering the significance threshold for the visual frequency contrast to $p < .001$, uncorrected for multiple comparisons, post hoc within a region of interest comprising Broca's region (defined as the left inferior operculum and triangularis by the AAL atlas) to account for possible false negatives, revealed that two small clusters with a total of 175 voxels out of 3563 voxels in the ROI survived this threshold. This number is somewhat higher than what would be expected by chance (1/1000 voxels), but visual inspection indicates that these voxels predominantly reflect spill-over effects from outside the region, i.e., premotor or middle frontal cortex (see Fig. 7 top). A similar ROI procedure for the auditory frequency contrast only yields one voxel $[-34, 14, 16]$ within the ROI which exceeds the cutoff at the $p < .001$ uncorrected level. One activated voxel is well within what would be expected by chance alone (see Fig. 7 bottom). Based on this we conclude that the lack of a frequency effect in Broca's region is not due to a thresholding issue. At first glance this finding is difficult to reconcile with the literature. Previous experiments have indicated that Broca's region is indeed sensitive to certain types of frequency effects in linguistic experiments, such as word frequency (Fiebach et al., 2002; Kronbichler et al., 2004), sentence cloze probability (Obleser & Kotz, 2010) and contextual constraints on sentence

FREQUENCY (VIS)

FREQUENCY (AUD)

$P < .001$, uncorrected

Fig. 7 – In order to rule out false negatives for the frequency effects in Broca's region, we lowered the significance threshold to $p < .001$, uncorrected for multiple comparisons (marked in cyan for visual condition and red for the auditory condition). When compared against a region of interest comprising Broca's region (marked in yellow), we find that voxels that survive this threshold seem to predominantly originate in clusters that have their center of mass in other brain areas, i.e., premotor cortex and middle frontal gyrus.

structure (Kristensen et al., 2014). But these prediction violations all hinge on long-term exposure to linguistic material. Similarly, the Stroop interference effect is built on long-term habituation to word reading. It might thus be the case that Broca's region plays a specific role in the interplay between predictions based on experiences stored in long-term memory and the stimulus at hand. This would be in line with an interpretation where Broca's area is placed at a high level in a prediction hierarchy, where height is at least partly defined in terms of latency of adaptation. It may also be the case that Broca's region is involved in other parts of the cognitive control process, such as attention maintenance or response inhibition (Swick, Ashley, & Turken, 2008). Recent developments suggest that such effects may also be modeled within the

predictive coding framework (Jiang, Heller, & Egner, 2014), but this is beyond the scope of the present paper. Further studies are needed to elucidate these putative other (e.g., long-term memory based) types of prediction error processes in Broca's region.

4.2. Visual Word Form Area

While we saw no effect of frequency in Broca's region, such an effect was found to be present in VWFA. Here we observed both a main effect of Stroop and a main effect of frequency in the visual conditions. Using the stringent family-wise error correction threshold, we found no effect of auditory frequency in this region, however, we were also unable to find any interaction between perceptual modality and frequency. Comparing low frequency and high frequency auditory data actually indicates that the region to some extent is sensitive to auditory stimuli (see Fig. 5D). Earlier studies have shown that VWFA is sensitive to long-term visual frequency effects, such as word frequency and bigram frequency in a given language (Kronbichler et al., 2004; Vinckier et al., 2007) and trial-by-trial effects such as those evoked by repetition or priming (Dehaene et al., 2001; Kherif, Josse, & Price, 2011). Previously, we have shown that VWFA is also sensitive to perceptual modality changes (Wallentin et al., 2014), but this might have been caused by the visual part of the switch. The present study adds to these findings by demonstrating sensitivity to frequency in the intermediate time domain (min). VWFA is thought to be a region that during reading acquisition partially recycles a cortical territory evolved for object and face recognition (Dehaene & Cohen, 2011). Consistent with our findings, the anatomically overlapping Fusiform Face Area, has also been found to be sensitive to stimulus frequencies in the intermediate time domain (Summerfield et al., 2008). Our findings thus also extend this line of research into the domain of words. Thirdly, the results indicate that the region plays a role both in auditory and visual word processing. This may be due to the inherent link between sound and orthography in word recognition, but due to the weak statistical evidence, this latter point needs to be further investigated before strong conclusions can be drawn. Interpreted within a hierarchical predictive framework, these findings suggest that the VWFA is placed at a level within the predictive hierarchy where it is neither strictly perceptual nor completely amodal as it is definitely more sensitive to visual than auditory input. This is consistent with the interactive perspective put forward by Price (2012), where VWFA is thought to contribute to written word recognition by integrating feed forward visual processing with top-down influences from phonological, and semantic areas.

4.3. Inferior parietal lobule

Although not predicted in this study, we found evidence for the left inferior parietal lobule playing a role in the putative predictive processes shared between the Stroop task and the frequency manipulation. This region [MNI peak coordinate: $-44, -44, 44$] was the only one found to be activated both by the Stroop task and as a function of frequency differences both in the visual and in the auditory modality (see Fig. 5E).

As a part of the dorsal route for visual processing (Ungerleider & Mishkin, 1982), this region is known to be involved in the processing of spatial attention and spatial working memory (Wallentin, Roepstorff, et al., 2008; Wallentin et al., 2006; Wallentin, Weed, et al., 2008), but given that there is not spatial component to this experiment this line of research cannot explain the results. However, the findings are in concordance with other results reported in the literature, suggesting that the inferior parietal lobule does play a role in predictive coding. The region has been linked to decision making under uncertainty, showing higher activity when the decision was uncertain compared to certain both in monkeys (Kiani & Shadlen, 2009) and in humans (Huettel, Song, & McCarthy, 2005; Vickery & Jiang, 2009). The region has also been found to be activated in a two-choice categorization task in the face of noisy visual categories, i.e., increased Shannon entropy (Daniel et al., 2011). At a certain level, our Stroop task mirrors a two-choice categorization task with the two colors representing the categories and the presence of the Stroop interference representing the noise. In that respect, our findings may be said to be in line with this categorization study as well. Lastly, we note that the parietal effects seem to be tied to the presence of a motor output. This is based on the fact that the effects are larger for both low- and high frequency stimuli with a response, compared to stimuli without a response (see Fig. 5), although these in frequency are comparable to low frequency stimuli (50 visual trials are VNS/NR while the low frequency response is 2×25 trials). The dorsal route is also thought to comprise a link between perception and action, and the parietal activity may thus reflect the predictability of the response rather than the input.

4.4. Primary perceptual regions

We found only quite weak evidence for the hypothesis that primary perceptual regions should display modality dependent predictability effects. In primary visual cortex we found absolutely no indication of a frequency effect, whereas the left auditory cortex displayed an effect, but only at the uncorrected level. This is at odds with a hierarchical model where perceptual input regions are thought to be placed at the bottom of the hierarchy and as such should be responsive to short-term modulations of input frequencies. One explanation might be that the lower levels may be modulated at an even faster rate than what can be modeled in this experiment. Further experiments are needed to investigate the differential effects of different rates of change.

5. Conclusion

We conclude that while both VWFA and left inferior parietal lobule was found to be involved in processing common to both the Stroop tasks and frequency modulation, and as such confirm our hypothesis that these regions play a role in short-term predictability monitoring, this was not the case for LIFG (Broca's region). This speaks against our primary hypothesis that the activation found in this region during the Stroop task reflects a simple prediction error signal.

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