



Occipital and orbitofrontal hemodynamics during naturally paced reading: An fNIRS study



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ABSTRACT

Humans typically read at incredibly fast rates, because they predict likely occurring words from a given context. Here, we used functional near-infrared spectroscopy (fNIRS) to track the ultra-rapid hemodynamic responses of words presented every 280 ms in a naturally paced sentence context. We found a lower occipital deoxygenation to unpredictable than to predictable words. The greater hemodynamic responses to unexpected words suggest that the visual features of expected words have been pre-activated previous to stimulus presentation. Second, we tested opposing theoretical proposals about the role of the medial orbitofrontal cortex (OFC): Either OFC may respond to the breach of expectation; or OFC is activated when the present stimulus matches the prediction. A significant interaction between word frequency and predictability indicated OFC responses to breaches of expectation for low- but not for high-frequency words: OFC is sensitive to both, bottom-up processing as mediated by word frequency, as well as top-down predictions. Particularly, when a rare word is unpredictable, OFC becomes active. Finally, we discuss how a high temporal resolution can help future studies to disentangle the hemodynamic responses of single trials in such an ultra-rapid event succession as naturally paced reading.

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Introduction

The cognitive system uses context information to predict upcoming stimuli (Bar et al., 2006; Friston, 2010; Rao and Ballard, 1999; Rauss et al., 2011; Summerfield and Egner, 2009). When a stimulus is presented, it can either match these predictions or not. For instance, a sentence like “The road to hell is paved with good inventions” ends with a prediction error. Most readers would predict this sentence to end with ‘intentions’, as expected by the famous proverb.

The present study targets the function of two different brain regions in making predictions. On the one hand, Rao and Ballard (1999) suggest

that higher-level visual areas generate predictions of lower-level neural activation in the occipital cortex. On the other hand, the medial orbitofrontal cortex (OFC) has been suggested to host the generation of expectations (Bar et al., 2006; Nobre et al., 1999).

When an unexpected word like ‘inventions’ occurs during natural reading, word recognition takes more time and a second look at this word becomes likely (Rayner, 1998). If a second look is impossible because of sequential stimulus presentation, two recent studies show that unpredictable visual events lead to greater activation in the occipital gyrus (Alink et al., 2010; Fischer et al., 2012; cf. Obleser and Kotz, 2010). Such effects are explainable by a predictive coding framework, which suggests that visual representations of expected events can become active previous to stimulus exposure (Rao and Ballard, 1999; Rauss et al., 2011). Similarly, the free energy principle suggests that an iterative search for a plausible ‘cause’ for the unexpected event can explain such a greater occipital activation (Friston, 2010). As long as higher-level information mismatches lower-level information, prediction errors occur. To test whether predictive coding within the free energy principle can also account for primary visual processes during

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reading, we manipulated word predictability. For this purpose, the results of a pre-experimental cloze task were used. High and low predictability words were defined by their respective cloze completion probability (Dambacher et al., 2009).

A critical target region engaged in the generation of such visual expectations is the medial orbitofrontal cortex (OFC). In contrast to the generally accepted role of the occipital cortex in primary visual processes, the role of the OFC is elusive. There are controversial findings how this region responds to stimuli that either match or violate predictions. Nobre et al. (1999) proposed that the breach of expectation engages the OFC (Petrides, 2007; Schoenbaum et al., 2009). If a cueing stimulus predicts the spatial or temporal occurrence of a target stimulus, unexpected events elicit OFC activation (Nobre et al., 1999). The OFC's role in violated predictions was often demonstrated using rewarding stimuli (e.g. Berns et al., 2001; Kringelbach and Rolls, 2004; O'Doherty et al., 2003; Petrides, 2007; Wallis, 2007). For instance, Berns et al. (2001) showed that the OFC responds stronger to mildly pleasurable stimuli such as fruit juice when they are unpredictable.

In contrast to Nobre et al.'s (1999) proposal, Bar et al. (2006) suggest that the OFC becomes active when top-down predictions match rapidly incoming bottom-up information. Therefore, correctly recognized pictures lead to greater OFC activation than incorrect recognition. Moreover, the authors manipulate the spatial frequency of pictures to vary the amount of available bottom-up information. They suggest that low spatial frequency information is submitted fast to the OFC, which in turn generates top-down predictions. These predictions are validated against high spatial frequency information, which becomes available later. When bottom-up and top-down informations match, OFC becomes active at around 130 ms after stimulus exposure (Bar et al., 2006).

Although both of the complementary theoretical proposals – OFC responding either to prediction error or to match – appear to contradict each other, they agree that timing is crucial (e.g., Kiebel et al., 2008). When stimulus presentation is too long in a recognition task, there is no need to rely on top-down predictions and OFC activation diminishes. In this case, bottom-up information is sufficient to recognize the stimulus (Bar et al., 2006).

In visual word recognition, there is an elegant way to manipulate the speed with which bottom-up information is submitted to higher-level processes. Access to a hypothetical mental lexicon is faster to frequent than to rare words (Grainger and Jacobs, 1996; McClelland and Rumelhart, 1981). Therefore, we manipulated the frequency with which a word occurs in the natural language in addition to word predictability.

Word frequency effects are relatively well understood. They can be explained by Hebbian learning: Repeated exposure strengthens the connections of the neurons representing a word (e.g., Hauk and Pulvermüller, 2004; Hebb, 1949; Seidenberg and McClelland, 1989). Therefore, high-frequency words are processed with increased synaptic efficacy (Pulvermüller, 1999). In event-related potentials (ERP), this leads to lower amplitudes to high-frequency words within 200 ms after stimulus exposure, which provides an upper time limit for the access to the mental lexicon (Dambacher et al., 2006; Hauk and Pulvermüller, 2004; Sereno et al., 1998). State-of-the-art models of word recognition suggest that high-frequency word recognition is based on a fast visual-orthographic match, while particularly low-frequency word recognition profits from processing after 250 ms. In this late period, for instance, phonological information contributes to word recognition (Coltheart et al., 2001; Grainger and Holcomb, 2009; Perry et al., 2007; Proverbio et al., 2004). Larger predictability effects for low-frequency words in this time frame support this (Dambacher et al., 2006; Kutas and Federmeier, 2011). During natural reading, single-word fixations take around 250 ms (Rayner, 1998), but particularly low-frequency word processing is still underway when the eyes move to the next word (Kliegl et al., 2006).

When aiming to investigate occipital and orbitofrontal hemodynamic responses in a naturally paced sentence context, however,

natural reading rates of around three to five words per second pose a problem for the relatively low temporal resolution of fMRI techniques with a typical sampling rate of about 0.5 Hz. Several solutions were proposed to circumvent this limitation while addressing language processing.

The first and most commonly used solution is to present subjects with whole sentences. Though the experimental manipulation in this case is often at the word level, local blood oxygenation is modeled as a response to sentence presentation (e.g., Bohrn et al., 2012). Thus, it is confounded by the hemodynamic responses of the non-target words. A second solution is to present the words at slower-than-natural presentation rates (e.g., Fiebach et al., 2004). This, however, is problematic for the investigation of sentence processing, because slow presentation rates lead to unnatural processing strategies. For instance, an early interaction between predictability and word frequency occurs only at natural, but not at artificially slow reading rates (Dambacher et al., 2012). This is in line with Bar et al.'s (2006) proposal that slow presentation rates engage a largely bottom-up driven processing strategy, which prevents the OFC from becoming active. Third, as several ultra-rapid hemodynamic responses sum up in an approximately linear fashion (Burock et al., 1998; but cf. Boynton et al., 1996), Yarkoni et al. (2008) propose to add the predictor variables of many words to account for hemodynamic responses. A fourth option is to trade off a bit of fMRI's outstanding spatial resolution for sampling frequency (e.g., Sabatinelli et al., 2009). Even with a typical sampling frequency, however, the investigation of the hemodynamic response in the OFC leads to large drop-off rates (e.g., Kringelbach and Rolls, 2004). Thus specialized stimulation sequences were developed for this region (e.g., Schmidt et al., 2005).

Here we pioneer an alternative approach. Functional near-infrared spectroscopy (fNIRS) allows a sufficient sampling frequency for tracking ultra-rapid hemodynamic responses. This method is a reliable tool to investigate visual word recognition (Chen et al., 2011; Hofmann et al., 2008; Noguchi et al., 2002; Plichta et al., 2006), and can sensitively detect deoxyhemoglobin changes in the OFC (Brink et al., 2011). Neural activation is indicated by a decrease of deoxygenated hemoglobin, which indexes neural energy consumption (Buxton et al., 2004; Mandeville et al., 1999; Raichle and Mintun, 2006). Therefore, we used optical imaging to investigate the hemodynamic response, when word recognition is as fast as in natural reading (Devor et al., 2012).

Material and methods

Participants

28 right-handed native German speakers participated in the present study (21 females, mean age: 25.27, SE = 1.34). They had corrected or corrected-to-normal sight, reported no history of neurological or language disorders, and received 12€ for participation. All procedures were in accordance with the 2008 Declaration of Helsinki. Participants gave written informed consent after full explanation of procedures.

Materials

Stimuli were taken from Dambacher et al. (2009, 2012). Each participant read 144 sentence units. Respectively 36 sentence units reflected one experimental condition in the 2×2 experimental design of the factors word frequency (low/high) and predictability (low/high). Each sentence unit is composed of two context sentences and one neutral sentence (cf. Fig. 1 for example). In the neutral sentences, a target word of low frequency was presented to half of the participants, while the other half were exposed to a high frequency word. Low-frequency words occurred rarer than 10 times per million of written text, while high-frequency words occurred at least 100 times per million words (Geyken, 2007). Length and target position in the sentences were carefully matched.

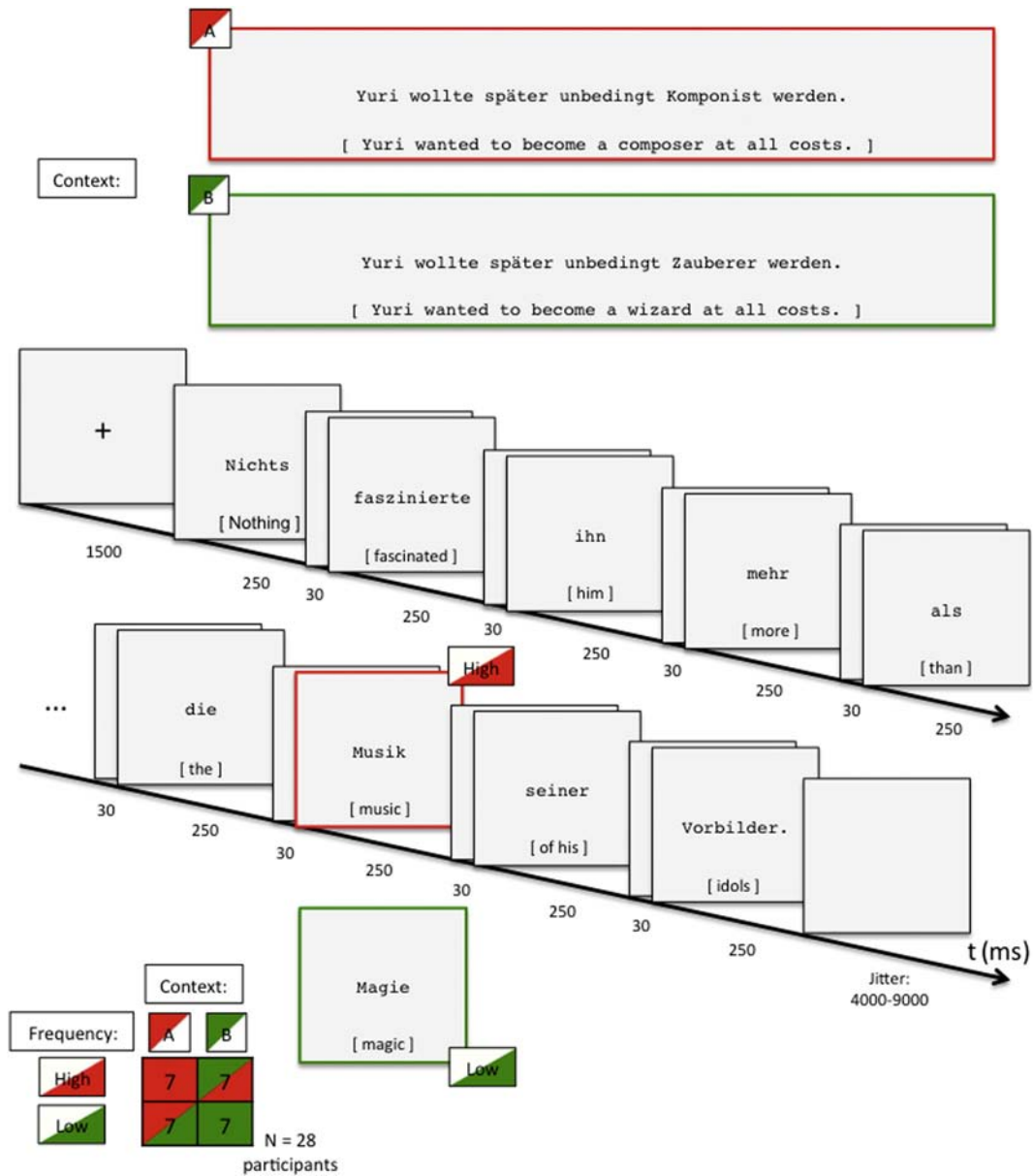


Fig. 1. Experimental design and procedure are exemplified on one sentence unit. Half of the participants were exposed to context sentence A (upper-red), and the other half to context B (upper-green). Context sentence presentation was terminated by a button press. The fixation cross was exposed for 1500 ms. Then a neutral sentence frame was shown word-by-word. Words were presented for 250 ms and followed by a 30 ms blank screen. Target stimuli were embedded into this neutral sentence. They were of either high (lower-red) or low frequency (lower-green). Each participant saw 36 of the 144 sentence units in one of the conditions. Sentence conditions were balanced across participants according to Latin Square, such that one sentence unit was presented a quarter of the participants in one condition, respectively (N = 7 of a total of 28 participants). Congruent colors code for high predictability, while incongruent colors index low predictability.

High predictability of a target word was induced by a prior context sentence that triggered the expectancy of either the high- or the low-frequency target word. Predictability norms of targets were assessed from 151 subjects in an independent cloze study. High predictability was defined by a cloze-completion probability greater than 0.5 (mean = .8), and low predictability by a probability lower than 0.1 (mean = .01). None of the cloze-test subjects participated in the present experiment (see Dambacher et al., 2012, for further details about the material).

Each participant saw only one version of a sentence unit, that is, target-word frequency and predictability were counterbalanced across subjects. For a given target word, low- and high-predictability conditions differ only in the preceding context sentence. Thus, effects of predictability were measured on physically identical target words embedded in the same neutral sentences (cf. Fig. 1).

Procedure

Stimuli were exposed on a 17 in. monitor (70 Hz screen refresh rate) using Presentation Software on a Windows XP computer. Cerebral oxygenation changes were recorded by a Hitachi optical topograph (ETG-4000, Hitachi Medical Co., Kashiwa, Japan), which allowed for a sampling frequency of 10 Hz. This continuous wave device measures changes in light attenuation at 2 wavelengths (695 and 830 nm, ± 20 nm) and hence allows for the differentiation of two dynamic absorbers (oxygenated and deoxygenated hemoglobin). Concentration changes of [deoxy-Hb] are obtained from a modified Beer–Lambert approach (Cope and Delpy, 1988). The probe set contained 16 light emitters and 17 detectors, which results in 52 channels. These optodes were attached on a plastic shell with an inter-optode distance of 3 cm. Using this array, we covered an area of ~6 × 30 cm. The probe array was positioned on

the subject's head with the medial detector of the lowest optode row corresponding to T3 of the 10–20 system. The lower edge of the probe set was defined to be 1 cm above the nasion. In sum, the present probeset definition allowed for investigating the largest part of the left hemisphere, as well as the frontal and occipital poles (cf. Fig. 2 below; Hofmann et al., 2008).

After eight practice trials, subjects read 144 experimental sentence pairs. There was also a short break after half of the experimental trials, terminated by the subject's keypress. All words were presented in black letters on a light gray screen in courier font (size 18). Each trial started with the presentation of a context sentence that was entirely displayed on the screen. Participants pressed a button after they had read and understood the context sentences. Following a blank screen of 500 ms, a fixation cross was presented for 1000 ms, followed by another blank screen of 500 ms. Then, the neutral sentence (including the target word) was presented word-by-word at the screen center. Each word was displayed for 250 ms and followed by a blank screen of 30 ms. Following the last word of the neutral sentence, presentation of a blank screen randomly varied between 4500 and 12,500 ms. After another blank of 500 ms, either the next trial started (67% of the trials), or a three-alternative multiple choice question (33% of the trials) tested sentence comprehension. An overall error percentage of 1.49% suggests that the participants generally read and understood the sentences.

Data analysis

Event-related oxygenation changes were analyzed by a 2-staged GLM (Plichta et al., 2006; Schroeter et al., 2004). As oxygenated hemoglobin is prone to be contaminated by extracerebral artifacts due to skin oxygenation in the OFC (Haeussinger et al., 2011; Kirilina et al., 2012), the present study focused on deoxyhemoglobin, which is the major constituent of the BOLD response (Steinbrink et al., 2006). To correct for artifacts due to heartbeat, data were band-pass filtered to include signals between 0.02 and 0.7 Hz.

The first-level analysis comprised 9 predictors. Four predictors coded the experimental conditions, that is, the 2×2 design with the experimental factors of frequency (low/high) and predictability (low/high). Additional five predictors coded the fixation cross, the presentation of the context sentence, the question, a button press, as well as a single predictor for non-target words in the neutral sentences. These five predictors were excluded from second-level analyses. We generated the GLM-predictors by convolving a Gaussian function with each event (duration = 15 s; SD = 2.5 s; Plichta et al., 2007). To absorb variance resulting from interindividual differences in the onset and the dispersion of the hemodynamic response, first and second derivatives of each prediction term were included. Beta values for each predictor were determined by optimizing the model-to-data fit by a least-squared error

procedure (Bullmore et al., 1996). Finally, we fitted a first-order auto-regressive model to the resulting residuals and removed serial autocorrelated error variance from the final model re-estimation (Cochrane and Orcutt, 1949; Plichta et al., 2007).

In the second-level analysis, the four first-level beta values of the experimental conditions obtained for each subject were submitted to a 2×2 repeated measures ANOVA. To correct for false positives due to alpha inflation, partial Bonferroni correction was applied (Sankoh et al., 1997). The Dubey/Armitage-Parmer alpha boundary considers the mean intercorrelation of 0.41 between the channels. Therefore, the channels are not treated as fully independent samples. As the mean intercorrelation of the channels was 0.41, the Bonferroni-corrected alpha of $P < 0.05$ (0.01) corresponds to an uncorrected significance threshold of $P < 0.0049$ (0.00097).

To obtain an estimate of the empirical hemodynamic responses of the target events, we purged the critical hemodynamic responses from the non-target responses in a deconvolution analysis (Koch et al., 2009). For each of the four target conditions, we subtracted the eight remaining predictors from the empirical hemodynamic responses. Averages time-locked to the event of the respective critical stimulus presentation were generated for each participant and experimental condition relative to the mean of a 1-second pre-stimulus epoch. Finally, we averaged these time courses across participants for each experimental condition, and calculated the difference waves for low minus high predictability (see Figs. 6 and 7).

To allow for anatomic inference of the channel positions, we applied a virtual optode registration technique (Tsuzuki et al., 2007), which was documented in Hofmann et al. (2008). The general rationale is to attach a virtual probe set by the same anatomic definition points on 1000 simulated heads. Standard deviations of registration accuracy are indicated by the size of the channel positions, and given in Table 1. x/y/z-coordinates are given in MNI space, and anatomically labeled by Tzourio-Mazoyer et al.'s (2002) brain atlas.

Results

The 2×2 repeated-measures ANOVA at the second level revealed a significant main effect of predictability in an occipital channel (Fig. 2; Table 1). This channel has been termed OCC. Fig. 3 shows the beta-value differences of low–high predictability, separately for low- and high-frequency words. Planned comparisons revealed an effect of predictability for low- ($t(27) = -3.24$, $P < 0.01$, uncorrected), and for high-frequency words ($t(27) = -2.01$; $P < 0.05$), respectively.

Moreover, we obtained significant interactions between frequency and predictability in two channels located in the OFC (Fig. 4). These channels were termed OFC-1 and OFC-2. The estimated beta value differences can be examined in Fig. 5. While planned comparisons for

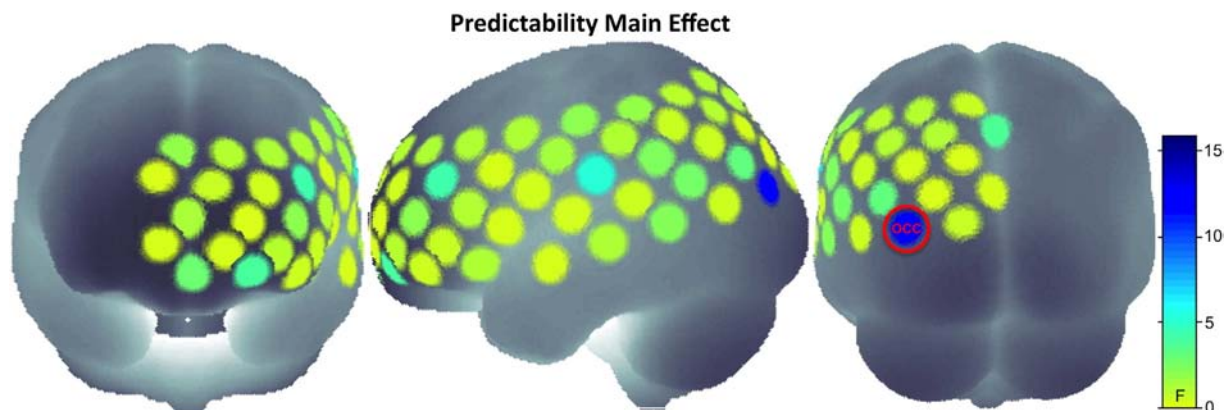


Fig. 2. The figure shows the results of the repeated measures ANOVAs for the main effect of predictability. Resulting F-values are color-coded. The only channel that surpassed a Bonferroni-corrected threshold is hence termed OCC (cf. Fig. 3 and 6).

Table 1

Results of the 2×2 rmANOVA. The first column indexes the effect, and the second column the channel label (cf. Figs. 2–5). We found one channel reaching the Bonferroni-corrected significance threshold for the main effect of predictability (Figs. 2 and 3). Two channels revealed a reliable interaction between word frequency and predictability (Figs. 4 and 5). The next columns show the most likely MNI-x/y/z coordinates and the localization due to Tzourio-Mazoyer et al.'s (2002) brain atlas. Anatomical standard deviation of the localization approach is given in brackets (mm).

Effect	Channel	Localization	x/y/z (SD)	F	P
Predictability	OCC	Occipital, middle, left	−37/−91/20 (12)	11.7	<0.05
Frequency × predictability	OFC-1	Frontal, superior/medial, orbital, right	13/71/−1 (10)	9.6	<0.05
	OFC-2	Frontal, medial, orbital, left	−1/68/−13 (9)	15.5	<0.01

OFC-1 revealed only nonsignificant trends towards a predictability effects in low- ($t(27) = -1.51$; $P = 0.14$), and in high-frequency words ($t(27) = 1.67$; $P = 0.09$), the opposite signs of the t-values account for the interaction. For low-frequency words, planned comparisons revealed a reliable deoxygenation decrease to low predictability in channel OFC-2 ($t(27) = -2.14$, $P < 0.05$).

Discussion

The present study demonstrated that humans can read at incredibly fast rates, because they have concrete hypotheses about which words are likely to occur in a given context. First, low-predictability words elicited a [deoxy-Hb] decrease in the occipital gyrus relative to high-predictability words. This results from a greater wash-out of consumed oxygen (Buxton et al., 2004; Mandeville et al., 1999), which suggests that neural activation is greater to low-predictability words. The effect can be explained by the top-down activation of visual features of expected words prior to target presentation. Second, predictability interacted with word frequency in the OFC. We propose that the speed of bottom-up processing – as manipulated by word frequency – modulates OFC-predictability responses. Therefore, breaches of expectation activate the OFC particularly in low frequency words. Finally, the present study shows that the high sampling frequency of NIRS makes it an excellent method for the ecologically valid investigation of the hemodynamic responses in the ultra-rapid event succession of words during naturally paced reading.

Occipital predictability effect

A significant deoxygenation main effect was observed in a channel likely localized in the left middle occipital cortex. The planned comparison showed that low-predictability words led to a greater [deoxy-Hb]

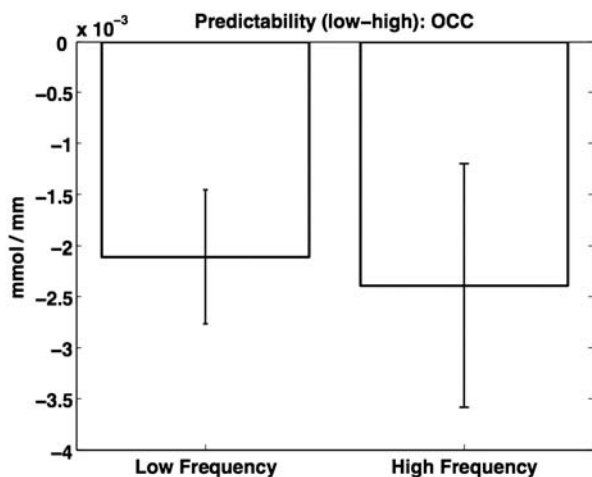


Fig. 3. The beta-value differences index a [deoxy-Hb] decrease for low- relative to high-predictability words. This suggests greater OCC activation to low-predictability words. This decrease is apparent in low- and in high-frequency words. Error bars index (cross-subject) standard errors of this difference.

decrease in comparison to high-predictability words (cf. Alink et al., 2010).

To examine the empirical hemodynamic responses, we conducted a deconvolution analysis (Koch et al., 2009). Therefore, we subtracted the model-based estimates of the non-target events from the empirical time course, averaged these time courses relative to the mean of a 1-s pre-stimulus epoch, and generated a low-high predictability contrast. Fig. 6 shows that [deoxy-Hb] decreases due to low predictability as compared to high-predictability words in channel OCC. Thus the time course of the hemodynamic response provides converging evidence that low predictability engages greater occipital activation than high predictability in words (Buxton et al., 2004).

These findings confirm a previous suggestion by Dambacher et al. (2009). Using the same experimental design, they found an early predictability effect in an ERP time frame between 50 and 90 ms. A relatively posterior ERP distribution made the authors suggest that this follows from activation in visual cortex (e.g., Rauss et al., 2011). The present results agree with this hypothesis. We suggest that, before stimulus presentation, visual-feature templates of expected words are pre-activated in the occipital cortex. Therefore, less novel neural energy must be recruited at the time of stimulus presentation to represent these visual features. In contrast, activating the visual features of an unexpected word is driven by poststimulus bottom-up processing, entailing greater neural energy demands.

The occipital prediction error effect during reading poses clear constraints on connectionist models of associations between words. The activation of visual feature representations in an interactive activation model is associated with neural activation in the occipital cortex (Grainger and Jacobs, 1996; McClelland and Rumelhart, 1981; Schurz et al., 2010; Vinckier et al., 2007). In bottom-up processing, visual features activate letters, which in turn activate word representations. These letter and word layers can be associated with more anterior regions in the ventral visual stream (Schurz et al., 2010; Vinckier et al., 2007). The scientific community seems to converge on the opinion, however, that these representations interface to higher order processes such as semantic associations between words (Dehaene and Cohen, 2011; Price and Devlin, 2011). McClelland and Rogers (2003) reviewed evidence on how such associations are generated. To define an established knowledge system of outlearned long-term representations, an interactive activation model was extended by an associative layer (Hofmann et al., 2011). It is based on a symbolic version of Hebbian learning: Associations between words are defined by the likelihood of words occurring together in the sentences of a large corpus (Quasthoff et al., 2006). Following this rationale, each associated word in a sentence context can be seen as a contextual cue associated with the word expected to occur (Bar et al., 2007). The evidence that predictive associations affect occipital activations suggests an inclusion of top-down connections from higher layers down to the lowest levels of visual feature representations (Hofmann et al., 2011). Therefore, the visual features of expected words become active. This provides empirical evidence for the principle of interactivity, which suggests that lower-level representations are activated by higher levels (McClelland, 1993). For example, because the most strongly associated word to 'composer' is 'music', its visual features are pre-activated in the occipital cortex (cf. Fig. 1; Hofmann et al., 2011;

Predictability X Frequency Interaction

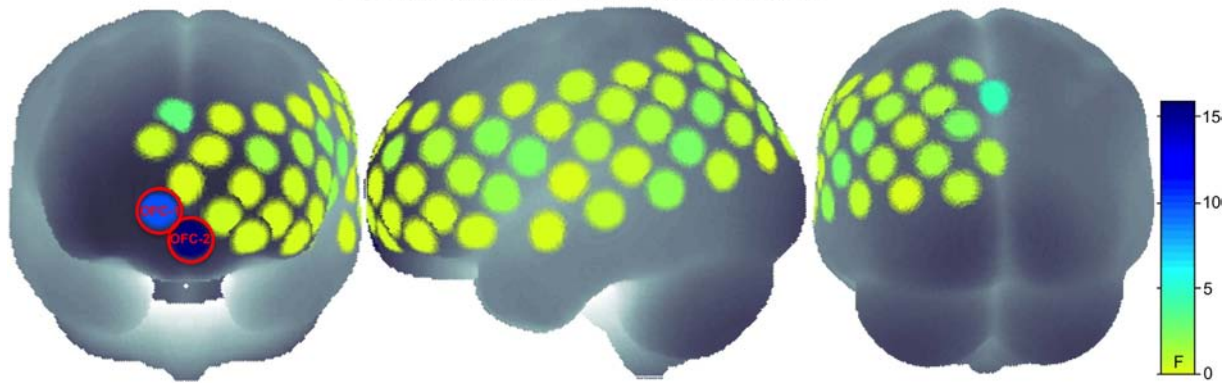


Fig. 4. The figure shows the results of the repeated measures ANOVAs for the interaction of word frequency and predictability. The channels termed OFC-1 and OFC-2 surpassed the Bonferroni-corrected alpha threshold (cf. Fig. 5 and 7).

Quasthoff et al., 2006; <http://corpora.uni-leipzig.de/>). When the critical word is presented, such predictions are validated within 100 ms after stimulus exposure (Dambacher et al., 2009).

Orbitofrontal interaction of word frequency and predictability

Previous proposals that OFC responds either to unexpected or to expected events were controversial (Bar et al., 2006; Nobre et al., 1999). They did not yet identify a factor that determines whether OFC responds to prediction errors or matches. We observed an interaction of word frequency with predictability in two channels that were most likely localized in the OFC (Tsuzuki et al., 2007).

In channel OFC-1, the low–high predictability contrast was positive for high- and negative for low-frequency words. This is also reflected in the deconvolution analysis. The left panel of Fig. 7 shows that the low–high predictability deoxygenation in OFC-1 increases for high-frequency words, while it decreases for low-frequency words. The [deoxy-Hb] increase suggests greater neural activation to high- than to low-predictability words of high frequency, as compared to low-frequency words. In this case, low predictability elicits greater neural activation than high predictability.

In channel OFC-2, low predictability engaged greater neural activation in low-frequency words, which is confirmed by a [deoxy-Hb] decrease of the empirical time course (Fig. 7, right panel). As previous ERP studies proposed that bottom-up processing is faster for high- than for low- frequency words (Dambacher et al., 2006; Hauk and

Pulvermüller, 2004), we suggest that the speed of incoming bottom-up information modulates OFC-function: In slow bottom-up signals, as in low frequency words, greater hemodynamic responses to non-predictable words index a failure to predict a target word.

When a word occurs rarely in natural language, its bottom-up processing is relatively slow. For example, response times can be more than 100 ms slower for low- than for high-frequency words (Hofmann et al., 2008). Moreover, low-frequency words display a greater ERP-amplitude within 200 ms after stimulus exposure (Dambacher et al., 2006; Hauk and Pulvermüller, 2004). Low-frequency words also show greater predictability effects after 300 ms (Dambacher et al., 2006). This suggests that processing of low-frequency words was still underway after the stimulus-exposure time of 250 ms. Contemporary models of visual word recognition would suggest that phonological processing contributes to the visual recognition of low-frequency words in this time frame (Coltheart et al., 2001; Grainger and Holcomb, 2009; Perry et al., 2007; Proverbio et al., 2004). This incomplete processing of low-frequency words may elicit OFC activation as a warning signal when the top-down prediction does not match the presented stimulus. We propose that such a signal triggers a top-down driven search process, initiated by the OFC as a ‘monitor’ of prediction success (Barbey et al., 2011; Nobre et al., 1999).

As opposed to a [deoxy-Hb] decrease to low vs. high predictability in low-frequency words, OFC-1 revealed an increase in high-frequency words (Fig. 5). This interaction indicates greater neural activation to high than to low predictability in high frequency words. In particular,

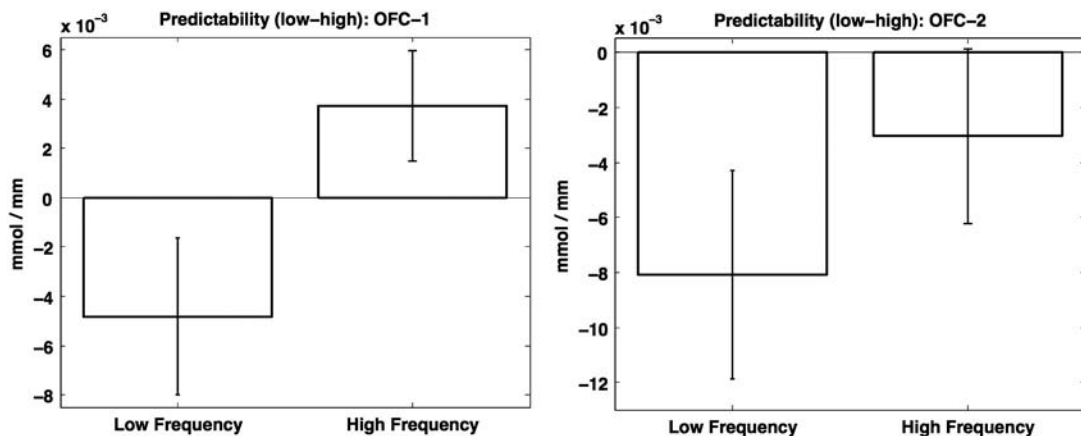


Fig. 5. Beta-value differences for low–high predictability illustrate the Bonferroni-corrected significant interactions. In channel OFC-1, the [deoxy-Hb] difference for low-frequency words became negative, while it became positive for high-frequency words. In channel OFC-2, the deoxygenation decrease was greater for low than for high-frequency words. Error bars indicate the standard errors of the low–high predictability differences across subjects.

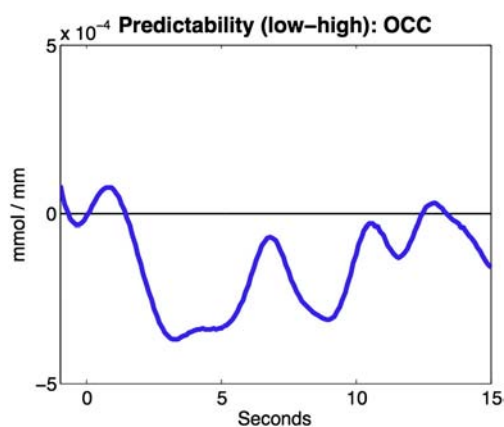


Fig. 6. Empirical time courses of the low–high predictability responses in channel OCC (cf. Fig. 2). The model-based estimates of the non-target events were subtracted in a deconvolution analysis. The figure shows that [deoxy-Hb] to low predictability decreases relative to high predictability. This indexes greater occipital activation for low-predictability words.

as there is faster bottom-up evidence for high- compared to low-frequency words, associative top-down predictions encounter a greater amount of bottom-up evidence within the same amount of time (Hofmann et al., 2011; Jacobs et al., 2003; Kveraga et al., 2007; Ullmann, 1995). For words that are both of high frequency and high predictability, OFC activation might reflect a confirmatory ‘aha’ signal, indexing a match between the predicted and the presented word (Bar et al., 2006).

There are Positron Emission Tomography findings that suggest the OFC’s role in matching top-down predictions in the broader context of language processing. Nathaniel-James and Frith (2002) showed that neural activation is greater, when participants complete a cloze test by naming a matching word, as compared to a completion that does not fit into this sentence. Buckner et al. (1995) showed that OFC regions are activated when participants generate a semantically matching verb to a noun stimulus (cf. Price, 2012). Further, Maguire et al. (1999) found a significant correlation between story comprehension and OFC activation, which indicates that the words matched better with prior expectations. Therefore, novel information can be integrated more seamlessly into an existing knowledge structure.

We suggest that complementary roles in matching and violated predictions could be reconciled within the theoretical framework of Schoenbaum et al. (2009). They suggest that the OFC’s primary function

lies in providing a signal that changes associative representations. This occurs by signaling prediction errors that function as a teaching signal for other brain regions (Friston, 2010). While they emphasized the role of the OFC as one of the brain regions that index such prediction errors, the present study provides evidence that this prediction error effect is modulated by the amount of bottom-up information during reading, as manipulated by word frequency. If matching predictions engage the OFC (Bar et al., 2007), existing associative connections between neurons could be strengthened, when the association predicted the future event. This would also support the Bayesian brain hypothesis (Friston, 2010), which proposes that the brain uses internal probabilistic models to update posterior beliefs, which optimizes future predictions (Duarte et al., 2009; Kiebel et al., 2008). Thus, OFC lesions to disrupt social behavior might actually result from the failure to anticipate the consequences of the patient’s actions, and thus the failure to apply and update such conditional probabilities (Bechara et al., 2000). However, it requires further research to determine whether OFC signals in such a rapid recognition situation as reading lead to an update of the associative connections, i.e. whether OFC activation stimulates learning (Kuchinke et al., 2013). During reading, however, we conclude that the OFC supervises the short-term spreading of associative activation in a long-term memory structure (Anderson, 1983; Bar et al., 2007; Collins and Loftus, 1975; Hofmann et al., 2011), given a particular amount of available bottom-up information. Therefore, OFC allows humans to flexibly adapt to environmental demands.

Fast sampling and ultra-rapid event succession during reading

As recent fMRI studies started to approach the goal of addressing hemodynamic responses during natural reading (Marsman et al., 2011; Richlan et al., 2013), we think that fNIRS and fMRI as methods providing either superior temporal or superior spatial resolution favorably complement one another (Devor et al., 2012).

The present study took one important step towards addressing the hemodynamic response during natural reading, by demonstrating straightforward occipital predictability effects using rapid serial visual presentation with inter-stimulus-intervals of less than 300 ms (Alink et al., 2010; Fischer et al., 2012). While a superior temporal resolution has previously been discussed as a promising potential of the NIRS (Devor et al., 2012), the present study takes full advantage of the rapid sampling frequency.

However, Marsman et al. (2011) suggested that undersampling – i.e. a lower sampling than event frequency – is not a problem for condition-wise analyses (Richlan et al., 2013). This is because samples

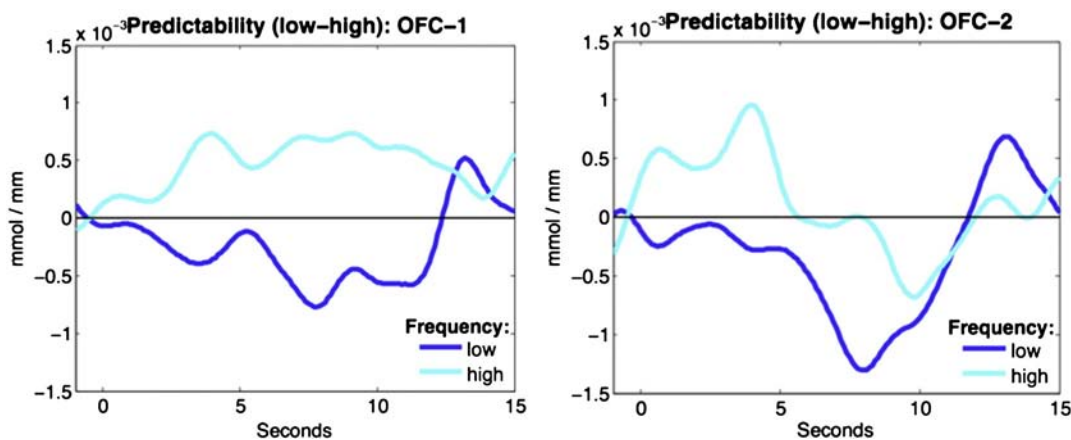


Fig. 7. Empirical time courses of the low–high predictability responses for low- and high-frequency words. The left panel shows that a decrease of [deoxy-Hb] is obtained for low-frequency words (dark blue) in channel OFC-1 (cf. Fig. 4). This suggests greater orbitofrontal activation in low-predictability words of low frequency. In contrast, [deoxy-Hb] increased due to low-predictability in high-frequency words (light blue): This suggests greater neural activation to high- than to low-predictability words. In the right panel, OFC-2 showed a [deoxy-Hb] decrease due to low predictability in low-frequency words.

collected at a different latency from event onset do effectively increase the sampling of the condition over actual recording sampling frequency. Undersampling is equally sufficient when several trials in an experiment contribute to an item-level regressor (Yarkoni et al., 2008). The critical level at which undersampling would not work anymore is the single-trial level: When six to ten words are perceived within a period of 2 s, a subsequent single data point can hardly inform about which of the events caused the deoxygenation to what degree. Deconvolution at the single-trial level will particularly aid multivariate data fusion, when each fixation time is compared to the hemodynamic response it elicited (cf. Ritter and Villringer, 2006, for a similar discussion about EEG and fMRI). These are challenges, however, for future studies, which should use either non-standard fMRI scanning parameters (Sabatinelli et al., 2009), or a NIRS sampling frequency of up to 300 Hz.¹

Speed is crucially important, because we know from ERP studies that an unnaturally slow reading pace can dramatically change the strategy with which readers recognize words in sentences (Dambacher et al., 2012). Dambacher et al. (2012) showed that an early ERP interaction between frequency and predictability occurs only at near-natural reading rates. If we assume that the OFC interaction between predictability and frequency reflects the ERP-interaction starting previous to 150 ms after stimulus exposure (Dambacher et al., 2012), we would expect also the OFC interaction to vanish with greater inter-stimulus intervals during unnaturally slow word recognition. This hypothesis would be fully compatible with Bar et al.'s (2006) proposal that the predictive function of the OFC is engaged around 130 ms after stimulus exposure, when stimulus presentation rate is fast enough such that top-down predictions are required.

Though fNIRS will never reach the spatial resolution of magnetic resonance imaging, this speed adds to the list of advantages that make fNIRS extremely attractive for the ecologically valid study of reading: It is also a silent method that allows undisturbed reading while sitting at a table.

Finally, we propose that a rapid pace circumvents a 'default mode' of brain function (Gusnard and Raichle, 2001). During long inter-stimulus intervals, participants display brain activation that is not under experimental control; rather, brain activation is generated intrinsically. Some have called the cognitive counterpart of the default-mode activation 'mindwandering' (Bar et al., 2007), while others propose that this network directly reflects the semantic processes during verbal thinking (Binder et al., 2009). To our knowledge, there is no language task that successfully defined a resting condition without any language processing (e.g. Price, 2012; Rossi et al., 2012). Such a baseline could be compared to a language-processing condition, as this is possible for motor- vs. non-motor activation (e.g. Boden et al., 2007). This is not possible, because thoughts are language-based in the so-called resting periods (Binder et al., 2009), which can lead to relative deactivation in the non-resting condition (e.g., Brink et al., 2011; Gusnard and Raichle, 2001). Therefore, it may be better to compare language stimuli to similar non-language stimuli (Price, 2012). We suggest that slowly paced word-recognition tasks lead to language-related cognitive processes that are not under experimental control. In contrast, keeping the participants busy with a rapid event succession may lead to a model that more successfully captures all cognitive processes in an experiment.

In conclusion, our data demonstrate that fNIRS provides sufficient temporal resolution for investigating OFC activity, while this region supervises associative processes during reading (Anderson, 1983; Bar et al., 2007; Collins and Loftus, 1975; Hofmann et al., 2011). Induced by a suitable context sentence, the expectation of a word pre-activates its visual features. Therefore, less occipital neural energy is consumed than during the presentation of an unexpected word, in which visual

features must be exclusively activated post-stimulus. We interpret the interaction between word frequency and predictability in terms of a dynamic interplay between top-down and bottom-up processes. OFC function is modulated by the amount of available bottom-up information: With a low amount of bottom-up information in low-frequency words, stimulus processing will take time. If additionally top-down predictions do not match the stimulus, the OFC response may initiate a search process to attribute meaning to the word. In contrast, when a greater amount of bottom-up information is available in high-frequency words, the OFC response is less likely to index a prediction error. Future studies will have to evaluate whether a sufficient amount of bottom-up information will cause an OFC-signal indexing a successful match. In sum, we conclude that it depends on the amount of available bottom-up information, whether the OFC responds to breaches of expectation during reading.

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¹ http://www.shimadzu.com/an/lifescience/imaging/nirs/nirs_top.html.

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