

The neural correlates of linguistically evoked pupil light responses

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Abstract

Research shows that the comprehension of words conveying a sense of brightness or darkness constricts or dilates the pupils. This semantic Pupil Light Response (sPLR) is believed to happen as a result of sensory imagery occurring during semantic processing. However, little is known about the cognitive architecture driving such pupil responses. To investigate this, we concurrently recording electrophysiological signals and pupil size while participants heard words inducing a sense of brightness or darkness. We found that pupil size during word comprehension may be correlated with activity over frontal electrodes in a time-window of 300-1200 ms. This broad timing can indicate a range of different types of cognitive processing. Therefore, the present task does not allow us to pinpoint the neural substrates of the sPLR. Nevertheless, the correlation was strongest during the N400 time-window, suggesting that semantic processing may indeed have played a role in modulating pupil size. In general, we show a proof-of-concept that the method of correlating pupil size and electrophysiological signals can be used to learn more about cognition.

Introduction

Imagine you are laying in your bed at night, trying to fall asleep. Suddenly, you get a phone call from your friend. She tells you that tonight there is a full moon, and that it is shining even brighter than usual. The process of understanding what she means requires a distributed network of brain areas to work together and compute what is being said. Listening to her story requires your brain to perform lexical, semantic and syntactic computations in order to analyze and make sense of her utterances, but also to generate sensory imagery related to the objects in her story such as the bright moon, or the dark night sky around it. According to embodied theories of cognition (e.g. Barsalou, 1999; Gallese & Lakoff, 2005), such sensory responses would not be a mere by-product, but rather an essential ingredient of language comprehension.

The involvement of sensory imagery and involuntary movements during language comprehension was recently demonstrated in two experiments by Mathôt, Grainger, and Strijkers (2017). They showed that the act of reading or listening to words conveying either bright or dark meaning (such as “day” or “night”) can respectively trigger constriction or dilation of the pupils.

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This semantic Pupil Light Response (sPLR) occurred while keeping environmental luminance constant, and in response to task-irrelevant stimuli. According to the authors, this effect on pupil size is likely driven by mental simulations of brightness or darkness occurring during word comprehension.

Currently, there is no direct evidence that the sPLR is triggered by sensory imagery. However, research shows that a PLR in the absence of luminance changes can also occur when participants covertly attend (i.e. without eye movements) to a bright or dark surface (e.g. Binda, Pereverzeva, & Murray, 2013; Mathôt & van der Stigchel, 2015), or when keeping bright or dark objects in working memory (e.g. Husta, Belopolski & Mathôt, in prep.). These results suggest that the pupil circuitry is linked with a general attentional network in the brain, and that the currently selected (i.e. most salient) perceptual signals can bias pupil size accordingly. This is supported by neurophysiological evidence showing that the magnitude of PLRs is modulated when directly stimulating neurons in the Frontal Eye Fields (FEF) of monkeys, thereby producing covert shifts of attention towards bright or dark surfaces (Ebitz & Moore, 2017). These findings suggest that pupil light responses are not dependent only on changes in retinal input, but also to the visual information currently selected by attention, suggesting that the sPLR is in part mediated by high-level cortical areas such as the prefrontal cortex.

There are good reasons to believe that the sPLR is triggered during semantic processing, as the visual representation of an object is believed to be part of its semantic representation in the brain. In general, semantic processing is thought to involve a distributed network of brain areas located in temporal, parietal and frontal lobes, which all seem to serve lexical, semantic, and sensory functions in language (Binder, Desai, Graves, & Conant, 2009; Friederici, 2011; Patterson, Nestor, & Rogers, 2007). Electrophysiological (EEG) research shows that semantic processing is generally indexed by a negative effect on amplitude around 400 ms after word onset, regardless of the scalp distribution of the signal (e.g. Federmeier & Kutas, 2000; Trébuchon, Démonet, Chauvel, & Liégeois-Chauvel, 2013; Winsler, Midgley, Grainger, & Holcomb, 2018).

In the case of semantically driven mental imagery, highly imaginable words have been shown to require the involvement of prefrontal regions around 400 ms (Swaab, Baynes, & Knight, 2002). However, fMRI research shows that sensory imagery accompanying language

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comprehension is stored in corresponding sensory brain areas, such as a ventral occipito-temporal system (e.g. Martin, 2007), which are likely activated during or following semantic processing. It could therefore be argued that the mental imagery that triggers the sPLR must occur only once the visual representation of the corresponding object is activated, which should start developing around 400 ms when semantic processing occurs. In general, both frontal and posterior brain regions have been implicated in semantic imagery.

Although the neural structures regulating task-evoked pupil responses in humans are still under debate, research with monkey suggests a positive correlation with activity in the Locus Coeruleus (LC) (e.g. Aston-Jones & Cohen, 2005; Joshi, Li, Kalwani, & Gold, 2016), and the Superior Colliculus (SC) (e.g. Wang & Munoz, 2015). These anatomical findings suggest that the pupil circuitry is related to structures known to play an important role in goal-directed behavior and attentional control. However, in humans direct neurophysiological evidence linking LC or SC activity and pupil dilation has so far been difficult to establish due to the fact that these areas cannot be accessed without intrusion. The finding that PLR amplitude is modulated by areas such as FEF (Ebitz & Moore, 2017) shows that EEG may be useful in finding the cortical substrates of pupil responses such as the sPLR. However, as the pupils respond to many different types of cognitive processing (Mathôt, 2018), the sPLR would account for only a slight proportion of variance in the amplitude of general pupil dilation responses, and might rely upon specific neural substrates beyond LC, SC and FEF.

To our knowledge, the combination of pupillometry and EEG is relatively novel. Some studies have correlated the two signals before, for example to study the effects of semantic incongruity (e.g., Kuipers & Thierry, 2011; 2013). Kuipers and Thierry report that after the onset of images preceded by either a semantically congruous or incongruous word, there was a positive correlation between pupil dilation and ERP amplitude around 300-400 ms (e.g. N400), and at a later period around 600 ms (e.g. P600). These results suggest that pupil dilation during word comprehension is modulated by cognitive processing regardless of the semantic congruity of eliciting stimuli.

In summary, the neural substrates of lexically-driven PLRs are still unknown. PLRs in the absence of luminance changes have been causally linked to activity in the prefrontal cortex (e.g. FEF), but the activation of visual representations of objects during lexical tasks is believed to be

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mediated by a posterior system involving the ventral temporal cortex and the parietal cortex. We investigated the neural mechanisms underlying the semantic PLR by attempting to: (1) replicate the semantic PLR effect; and (2) correlate pupil size with Event-Related Potentials (ERPs).

Our first hypothesis was that the average amplitude of pupil responses will be smaller when presented with words conveying a sense of brightness (e.g. “white”, “day”, “lamp”, etc.) compared to words conveying a sense of darkness (e.g. “black”, “night”, “shadow”, etc.) - a replication of the semantic pupil light response (sPLR) effect.

Our second hypothesis was that pupil size in response to the comprehension of words conveying a sense of brightness or darkness will correlate with cortical activity around 400 ms after word onset, indexing semantic processing.

Methods

Participants

27 participants (age range: 20-37 years; 11 female) took part in the experiment and received 20 euro as compensation. Participants were recruited via advertisements on social media, and from the Aix-Marseille University campus area. All participants reported being native French speakers. All but three participants reported having normal uncorrected vision. Data from three participants was excluded due to poor data quality (e.g. excessive movements, or distorted signals from several electrodes). Therefore, our analyses include data from 24 subjects.

Design

The experiment was designed using OpenSesame v.3.2.7 (Mathot, Schreij & Theeuwes, 2012), and displayed on a 24 inch flat screen monitor with a resolution of 1920x1080 px, placed approximately 85 cm away from participants. The display consisted of a gray central fixation dot (0.3° ; 3.6 cd/m^2), presented on a grey background (35.5° , 3.8 cd/m^2) (Figure 1).

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Auditory stimuli were generated using the Google Text-to-Speech Python module, based on the stimulus set used in the original study (Mathôt et al., 2017). The stimulus set contained French words ($N=122$), separated into three categories: animals ($N=20$), words conveying a sense of brightness or darkness ($N=67$), and control words ($N=35$). Crucially, we were only interested in conditions with bright or dark words, the rest of the stimuli being used to keep participants engaged in the task. Silence in the beginning and end portions of the generated .OGG files was manually trimmed using Audacity, in order to improve the relative timing of EEG triggers and sound onset. All sound files were leveled at a maximum amplitude of -12 dB FS.

Stimuli were presented using two desktop speakers, placed approximately 95 cm away from participants. Sound volume levels were kept constant between participants. The average sound intensity was -36.6 dB FS as recorded through a Philips active microphone.

Procedure

Participants were seated in a dimly lit room. Their head was rested in a chin-rest (average height from the desk ~40 cm). While performing the experiment, participants kept their eye gaze fixated in a central fixation dot, and were asked to minimize movements and blinks.

Participants performed an auditory go/no-go categorization task in which they had to press one of the two upper trigger buttons of a joystick in response to nouns representing animals (e.g. “dog”, “rabbit”, “tiger”, etc.), and to avoid responding to other words (Figure 1). Crucially, participants sometimes heard words conveying a sense of brightness or darkness, or unrelated control words. Every trial started with a 3000 ms silent period, after which an auditory stimulus was played. The duration of the stimulus varied ($M_{duration} = 743$ ms; $SD=173$ ms). The end of each stimulus was followed by 3000 ms of silence during which participants had to either respond or simply wait. Afterwards, the fixation dot changed its color to green or red for 500 ms in order to provide feedback (correct/incorrect).

The experiment consisted of 10 practice trials, followed by 250 experimental trials. The order of stimuli was randomly generated. All stimuli were repeated twice throughout the

experiment, in order to ensure that enough within-subject data was acquired. Participants had to take a 2 minute break after every 50 trials.

EEG recording and preprocessing

EEG was recorded from 64 electrodes using a BioSemi ActiveTwo system at a rate of 1024 Hz. Offline signal pre-processing was done using the mne-python module (Gramfort et al., 2013). All electrode signals were re-referenced to the average of both mastoid references, and then band-pass filtered between 0.3-40 Hz with a finite impulse response (FIR) filter. ERP epochs were defined as the time period between 0-1200 ms after stimulus onset, and baseline-corrected based on the average signal amplitude in a time window 250 ms before stimulus onset. Eye blinks were detected using either the two vertical EOG channels, or in some cases the “Fpz” channel (with a threshold of 55-75 uV depending on the subject). Epochs with detected blinks were excluded from the dataset. The epoched signals were resampled to 100 Hz.

Artifact correction was performed using Independent Components Analysis (ICA) for each participant separately. The epoched EEG signal was decomposed into 30 components. Bad components were subjectively identified by a combination of their scalp distribution, their waveform, and their frequency power spectrum. A bad component was therefore identified by: a limited scalp distribution that does not resemble a typical dipole generator; a waveform which does not resemble a typical ERP response; and deviations from the typical frequency spectrum of an ERP response (i.e. peaking around 10 Hz and progressively losing power as frequencies increase). The original EEG signal was afterwards reconstructed excluding the identified bad components.

Pupil size recording and preprocessing

Pupil size was recorded from the right eye at 1000 Hz using an EyeLink 1000 eye-tracker (SR Research), after performing a 3-point calibration. Every trial started with a drift-correction procedure, ensuring that participants are fixating in the center of the display. Preprocessing and analyses were done using the python-eyelinkparser and python-datamatrix modules. The signal was first downsampled to 100 Hz. Pupil epochs were defined as the time period between 0-2000

ms after stimulus onset. Trials with blinks during the ERP epoch were excluded based on detection via the ocular electrodes, and blinks detected later were linearly interpolated. The signal was baseline corrected based on the average pupil size in a time period of 0-20 ms after stimulus onset.

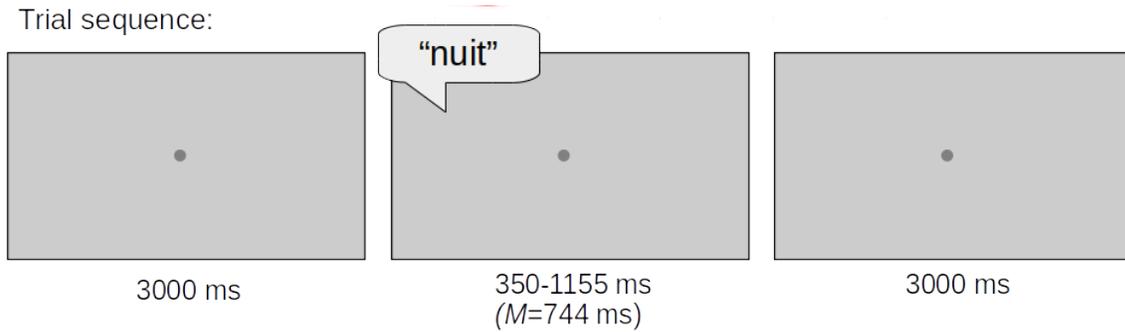


Figure 1: Schematic example of a single trial from the “Dark” semantic category.

Results

Effects of semantic brightness on evoked pupil dilation

We investigated the within-subject relationship between pupil size amplitude and the comprehension of words conveying a sense of darkness or brightness. To do this, we constructed a series of Linear Mixed Models (LMMs) analyzing each 10 ms time-point of the pupil signal using the lme4 R library (Bates et al., 2014), resulting in 200 individual models. As a predictor of pupil amplitude we used a Fixed Factor of Semantic category (“Dark” vs. “Bright”, excluding “Control” trials) with Subject as a Random Factor, and with random by-subject intercepts and slopes¹. Effects were deemed reliable if they persisted for at least 200 ms (i.e. 20 consecutive models where $|t| > 2$).

We successfully replicated the semantic PLR effect. Pupil dilation responses to “Bright” stimuli had significantly smaller amplitudes than responses to “Dark” stimuli in a window of 1250-1470 ms after stimulus onset ($t_{max}(1,629.89) = -2.161$), with “Bright” conditions associated

¹ R formula: “*Pupil Size* ~ *Semantic category* + (1 + *Semantic category* | *Subject nr*)”

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with a decrease in amplitude of about 14.056 ± 6.503 (SE) at the most significant time-point (Figure 2).

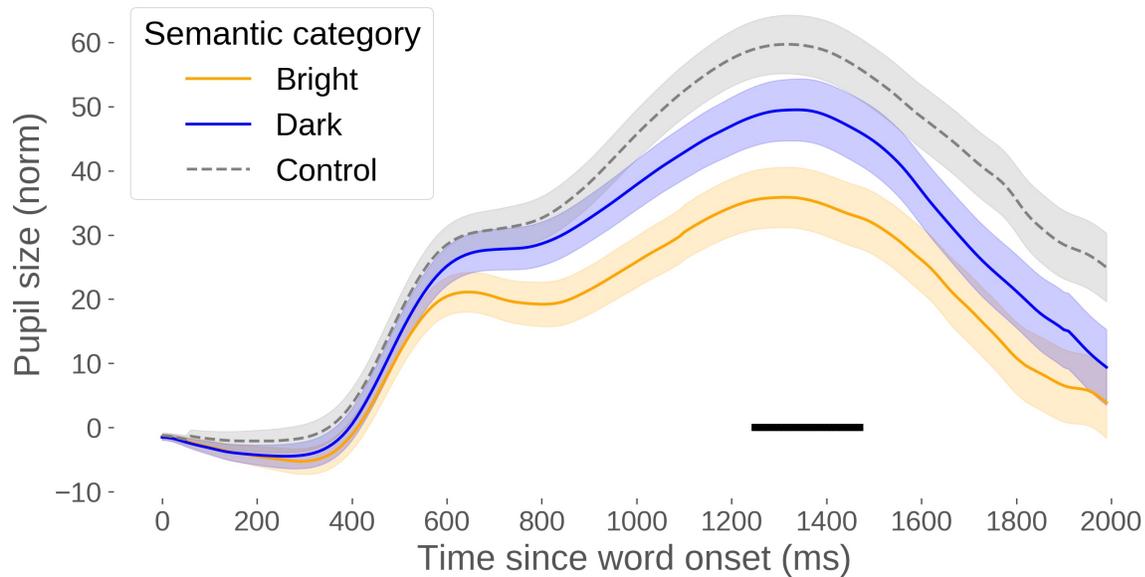


Figure 2: Pupil size differences between the three semantic categories in our task. LMM analyses were carried out with only Bright and Dark trials. Black line shows where $|t|>2$.

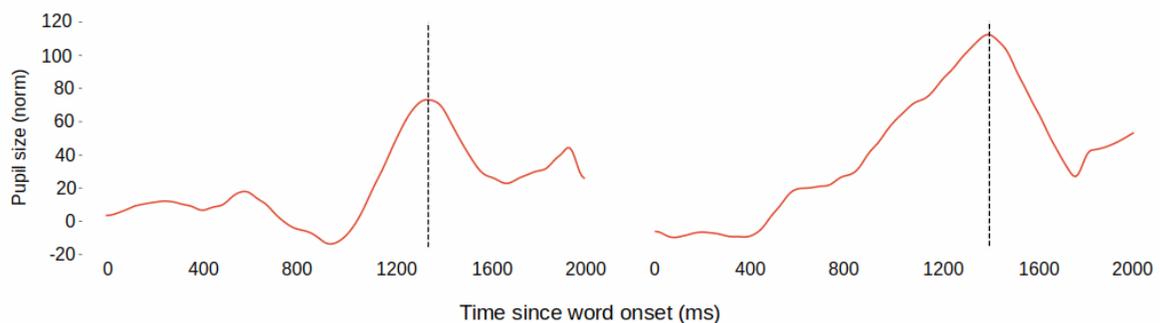


Figure 3: Schematic examples of pupil dilation peak values, taken from two consecutive trials of one participant. These values were afterwards binned in two categories: “Small” and “Large”, based on a within-participant median split. This “Pupi dilation category” variable was used as an Independent Variable in subsequent LMM analyses predicting ERP amplitude.

Relationship between pupil dilation and ERP amplitude

In order to model the within-subject relationship between pupil size amplitude and ERP amplitude, the continuous pupil signal was reduced to a single value for each trial: i.e. the maximum pupil size in a time window of 500-2000 ms after stimulus onset (i.e. maximum amplitude of the pupil dilation response) (Figure 2). This new variable was binned in two categories (Pupil dilation category: “Small” vs. “Large”) based on a within-subject median split. We expected that pupil responses in the “Small” pupil category occurred more often in semantic “Light” trials ($N = 556$) than in semantic “Dark” trials ($N = 519$). However, a Logistic Regression showed that this difference is not statistically significant ($Z=-0.031$, $p=0.975$). Thus, we can conclude that the variable we constructed is not related to semantic brightness, and may mostly reflect the amplitude of general pupil dilation responses. We used both LMMs and permutation t-tests to analyze the data.

We constructed a series of LMMs over each time-point of the ERP epoch, with ERP amplitude as a Dependent Variable. This was done separately for each electrode. We used Pupil dilation category as a Fixed Factor with two levels : “Small” and “Large” (Reference level: “Large”), with Subject as Random Factor, and with random by-subject intercepts². The analysis was done only with semantic brightness or darkness trials (hence excluding the neutral control trials). We restrict our interpretations only to effects that persist for at least 200 ms (i.e. 20 consecutive models where $|t|>2$).

LMMs suggest that there is a significant negative relationship between “Small” pupil responses and ERP amplitude approximately 300-1200 ms after stimulus onset (Figure 4). This relationship was significant only at anterior electrodes, with “F2” having the longest cluster (280-1200 ms) of significant time-points ($t_{max}(2,055.913)=-4.286$), where amplitude in the “Small” pupil category was lower than in the “Large” category with about $2.144 \mu\text{V} \pm 0.5$ (SE) at the most significant time-point. The strongest t-values across anterior electrodes were obtained over the time period between 300-500 ms.

A positive trend can be observed over posterior electrodes at about 500-900 ms, however the longest cluster there (at “PO3”) was only 60 ms long ($t_{max}(2,055.913)=2.439$).

² R formula: “*ERP amplitude* ~ *Pupil dilation category* + (1 | *Subject Nr*)”

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Furthermore, there was a succession of positive and negative effects in the 0-200 ms time window, however due to the occasional time-points of non-significance these effects will not be

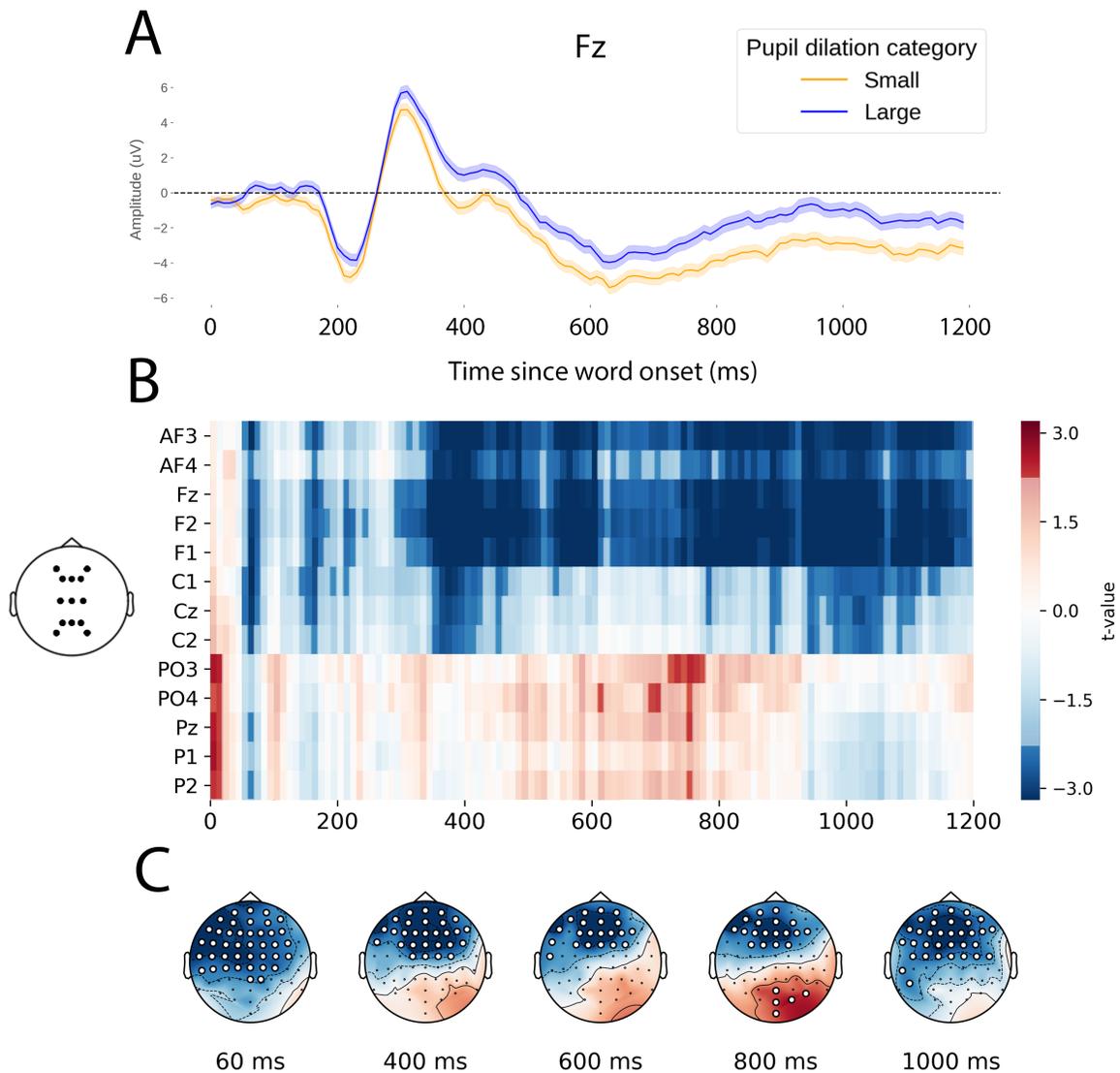


Figure 4: Relationship between pupil dilation category and ERP amplitude:

A: Average difference between the two pupil dilation categories at electrode "Fz".

B: Heatmap representing LMM t-values with time (x-axis), obtained from 13 electrodes at anterior, central, and posterior electrodes on the (y-axis). Reference level is "Large". Highlighted areas show where $|t| > 2$. There is a clear negative effect, over a very long time-window particularly over frontal electrode sites.

C: Topographic map of t-values shown in B. Highlighted electrodes have $|t| > 2$.

discussed further.

To ensure the reliability of our LMM results, we conducted a temporal cluster-based permutation test with null-distributed data from electrode “F2”. ERP data was first averaged per condition per participant. Then, an independent-samples t-test was performed on each of the 120 time-points. Crucially, before running each t-test, a null-distribution of the data had to be generated. This was done by combining data from the two pupil conditions into one set, randomly shuffling it, and splitting it into two new subsets with the same length as the original conditions (Maris & Oostenveld, 2007). This procedure was repeated 10000 times. Permutation testing revealed no significant ($|t| > 2$) clusters longer than 50 ms, whereas LMMs suggest that the longest cluster of significant timepoints was 920 ms. This suggests that under a null-distribution, the probability of finding significant clusters longer than what we observed is virtually zero.

In summary, smaller pupil dilation responses to words conveying a sense of brightness or darkness were negatively related with ERP amplitude over anterior electrodes. Significant differences in ERP amplitude between small and large pupil trials were observed most reliably in time intervals of 300-500 ms (e.g. N400); and 660-1200 ms (e.g. P600-800).

Discussion

We investigated the neural substrates of lexically-driven pupil light responses, characterized by smaller pupil dilation following the perception of words conveying a sense of brightness relative to words conveying a sense of darkness (e.g., Mathôt et al., 2017). To do this, we tested for a relationship between the amplitude of pupil dilation responses, and the amplitude and time-course of ERPs. The theory put to test was that the sPLR effect occurs due to mental imagery triggered in the process of word comprehension, specifically during semantic processing.

Semantic pupil light response

We managed to successfully replicate the semantic PLR effect in a different sample and using slightly different stimuli than the original study. Our results confirmed that pupil dilation in response to words conveying brightness were smaller than those caused by words conveying darkness (Figure 2). We can also see that dark and control words did not elicit pupil responses of

different amplitudes, suggesting that the auditory sPLR may be only defined by a constriction to brightness-related words. In our study, the sPLR occurred later than in the original study, and pupil responses on average were characterized by two peaks – an early, rapidly developing peak around 600 ms, and a later, larger peak at around 1300 ms after stimulus onset. The earlier peak, which did not differ in amplitude between conditions, is likely elicited as part of an orienting response to stimulus onset/offset (e.g. Wang and Munoz, 2015). The presence of an orienting response in our data may be due to the fact that our task required manual responses and incoming words were scanned for behavioral significance. This has been previously shown to correlate with rapid firing in LC neurons (e.g. Aston-Jones & Cohen, 2005), and thus likely to also lead to rapid pupil dilation. In our data, faster pupil responses were on average smaller in amplitude than slower pupil responses³, suggesting that our ERP correlations may also partly reflect cognitive processing that has impact on peak latency.

Relationship between sPLR and the amplitude and time-course of ERPs

Our main aim was to investigate the neural substrates of lexically-induced PLRs. The pupil size variable we used in our analyses was found to not be reliably correlated with the semantic brightness condition, but rather to reflect pupil dilation in a more aspecific manner. However, it is still possible that the activity underlying pupil dilation responses in our task was related to the generation of sPLRs, but this is difficult to conclude with the present methods.

We found that conditions of small pupil dilation were associated with more negative ERP amplitude at ~330-500 ms (e.g. N400, strongest over anterior electrodes), which was also the time period where the strongest effects were observed. There was also a negative effect around 660-1200 ms (e.g. P600-800, strongest over left anterior electrodes). This later time period was also when a trend towards positivity at posterior electrodes emerged, however, the clusters of significant time-points there were much more sporadic (Figure 4).

Frontal negativity in the broad time window we observed is associated with a wide range of cognitive processing such as: syntactic processing (e.g. Angrilli et al., 2002), visual and lexical semantic processing (e.g. Barrett & Rugg, 1990; Holcomb & Warren, 1994), working memory and attention (e.g. Penney, Mecklinger, & Nessler, 2001), and emotional intensity (e.g. Schindler & Kissler, 2016). There is evidence that frontal brain regions such as the anterior

³ One-way ANOVA: $F(1,3155)=446.822$; $p<.001$

cingulate cortex may have connections with the pupil circuitry (e.g. Joshi, Li, Kalwani, & Gold, 2016), and that stimulation of FEF neurons can increase the amplitude of PLRs (Ebitz & Moore, 2017).

In the case of semantics, EEG research suggests that negativity in frontal electrodes seems to be related to the formation and analysis of object properties for both lexical and visual stimuli. Left frontal negativity around 300-500 ms was found in response to semantically incongruent objects (Barrett & Rugg, 1990; Holcomb & Warren, 1994), suggesting an early role of the PFC in visual semantic categorization. Frontal negative effects in the N400 window can also be modulated by word concreteness and imageability (Kounios & Holcomb, 1994; Swaab, Baynes, & Knight, 2002), meaning that words that are easier to conceptualize and visualize elicit a stronger frontal N400. Furthermore, frontal negativity ~600-800 ms has been shown to index property-based violations (e.g. “barking” – “cat”) versus category-based violations (e.g. “reptile” - “cat”) (Long et al., 2015). This pattern of results suggests that pupil size in our task may have been related to high-level aspects of semantic processing, such as analyzing and sustaining object representations.

However, it is still unclear whether this frontal negativity directly reflects semantic imagery. Research shows that sensory imagery accompanying semantic processing is typically related to the involvement of anterior brain regions, such as posterior parietal cortex and ventral temporal lobes (e.g. Binder et al, 2009). Frontal areas, on the other hand, are believed to control access to information stored in more anterior areas (Martin, 2007). This is supported by ERP research showing that frontal negativity was enhanced when a visual object was first encountered (e.g. during initial memory encoding), and that this effect preceded a much larger positive-going deflection over parietal sites (Penney, Mecklinger, & Nessler, 2001). With stimulus repetition, this effect was diminished, suggesting that this response was indicative of visual memory processing. A similar pattern was observed in our study: the negative correlation between small pupil responses and frontal activity started relatively early (~300 ms), followed by a positive effect around 600-900 ms at posterior electrode sites (although this latter trend reached only marginal significance). The similar pattern of results between our study and the one by Penney and colleagues suggests that pupil responses in our task may be driven by an earlier-acting frontal system that helps initiate a process of memory encoding and storage of object

features (e.g. Mendoza-Halliday & Martinez-Trujillo, 2017), but that activity over posterior regions may more directly reflect the strength of visual imagery.

In summary, we found reliable correlations between pupil size and ERPs in a very broad time-window of 300-1200 ms. This was found over anterior but not posterior electrodes, suggesting that sPLRs were likely associated with attentional and working memory processes accompanying the activation of sensory imagery. However, our results did suggest that pupil size may be related to brain activity indexing semantic categorization and object recognition. Our analysis could not link the amplitude of lexically-driven PLRs directly with activity related to visual representations, which likely appears over occipital, parietal and ventral temporal regions of the brain (e.g. Farah, 1989; Binder et al, 2009; Friederici, 2011; Patterson, Nestor, & Rogers, 2007; Albers, Kok, Toni, Dijkerman, & De Lange, 2013), although an insignificant trend could be observed.

Further research should investigate the correlation between pupil size and ERP activity in response to actual changes in luminance. In that case, pupil size will likely correlate with earlier and more posterior activity than in the present study, reflecting sensory rather than semantic processes. It is also important to further assess the relationship between mental imagery, pupil size, and ERP activity. For example, future studies may ask participants to read and explicitly visualize bright or dark objects, or to retain such objects in working memory while their pupil size and EEG activity are recorded. For example, asking participants to memorize either object color (white/black), or shape, may also show what brain activity is associated with PLRs in the absence of retinal input. In general, the present study demonstrated that EEG can be successfully used to discern the neural substrates of pupillary responses.

Conclusion

In summary, we replicated the semantic pupil light response effect, showing that the processing of words that convey a sense of brightness or darkness is associated with constriction or dilation of the pupils. When relating pupil dilation amplitude with ERPs, our results suggest that pupillary deflections in response to bright or dark words were associated with long-lasting frontal activity from 300-1200 ms after stimulus onset. The involvement of frontal regions

suggests that lexically-induced PLRs may be related to attentional and executive processes implicated in semantic categorization and imagery, but not directly with processing in sensory brain areas. With the present method it is difficult to determine the anatomical substrates of sPLRs, and the degree to which they are related to activity in anterior versus posterior brain regions. Furthermore, we cannot rule out the possibility that pupil responses were also partly driven by other processes related to semantic categorization, executive functions, and working memory. However, our results suggest that the method of correlating pupil size and EEG may be successfully used in the investigation of many other cognitive phenomena.

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