Pupil dilation patterns reflect the contents of consciousness

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**A B S T R A C T**

The study of human consciousness has historically depended on introspection. However, introspection is constrained by what can be remembered and verbalized. Here, we demonstrate the utility of high temporal resolution pupillometry to track the locus of conscious attention dynamically, over a single trial. While eye-tracked, participants heard several musical clips played diotically (same music in each ear) and, later, dichotically (two clips played simultaneously, one in each ear). During dichotic presentation, participants attended to only one ear. We found that the temporal pattern of pupil dilation dynamics over a single trial discriminated which piece of music was consciously attended on dichotic trials. Deconvolving these pupillary responses further revealed the real-time changes in stimulus salience motivating pupil dilation. Taken together, these results show that pupil dilation patterns during single-exposure to dynamic stimuli can be exploited to discern the contents of conscious attention.

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1. Introduction

Understanding the mind means understanding the ebb and flow of conscious experience. However, objectively measuring the what and when of conscious experience has proven elusive. While various methods discriminate conscious from unconscious states (Seth, Dienes, Cleeremans, Overgaard, & Pessoa, 2008), accessing the contents of conscious experience has historically relied on introspection (Libet, 1993) with its concomitant bottlenecks of memory and language. What can be remembered and reported, although informative, is necessarily a fraction of what was experienced and subject to various distortions (Block, 1995; Schooler & Schreiber, 2004). As James noted, introspective analysis is like “trying to turn up the gas quickly enough to see how the darkness looks” (1890). Here we show that high temporal resolution pupillometry and deconvolution analyses can inform our understanding of conscious experience by affording a direct, temporally-sensitive window onto one of its correlates: the locus of conscious attention. We demonstrate that pupil dilation patterns can reveal what information stream is being attended on a single trial.

Pupil dilation has been used for decades to index mental processing. Hess and Polt found that participants’ peak pupil diameter and latency to peak dilation differed as a function of difficulty during mathematical calculations, leading the authors to conclude that a combination of those pupillary features would comprise a metric of “total mental activity” (1964). Although standard pupillometric analyses extract both amplitude and latency measures as prescribed by Hess and Polt, these analyses typically reduce the data to a single maxima or average dilation diameter within and across trials.

Only recently have studies demonstrated the potential for pupillary time-series data to reflect conscious and preconscious dynamic processing (Einhäuser, Koch, & Carter, 2010; Kang, Huffer, & Wheatley, 2014; Laeng, Sirios, & Gredeback, 2010).
Naber and colleagues, for instance, exploited pupillary sensitivity to light by manipulating stimulus brightness over time. They found that the frequency of this overlaid luminance “flicker” was mirrored in pupil dilations when that stimulus was attended (2013). This finding suggests that information about selective visual attention to static stimuli is objectively measurable in the eyes. However, this method requires overlaying an identifying pulse onto a static visual stimulus, and this pulse relays nothing about the stimulus except its identity. Our conscious experience is shaped by multimodal information that often occurs in streams, relaying meaning dynamically over time (e.g., music, conversation). Here, we extend recent pupillometric efforts by investigating whether natural patterns of pupil dilation – obtained under constant light conditions and in response to common and unmanipulated informational streams – can be used to identify the contents of conscious attention on a single trial. This approach differs from more traditional pupillometric approaches in three key ways: it considers the dynamic pupillary response to dynamic stimuli, it tests the sensitivity of the pupillary response to naturally occurring salience changes in real-world stimuli, and it aims to discriminate this sensitivity on a single trial.

Previous research suggests that the pupils are indeed sensitive to momentary fluctuations in attention. Under conditions of controlled light, pupil diameter exhibits a close positive relationship with exclusive norepinephrine (NE) release by locus coeruleus (LC) neurons (Rajkowski, Kubiak, & Aston-Jones, 1993; see Fig. 1). As NE effects changes in attention and arousal (Berridge & Waterhouse, 2003), the pattern of pupil dilation dynamics (PDy) over time reflects these changes on a sub-second time-scale. This characteristic makes PDy a candidate biomarker for tracking the locus of consciousness. Although “attention” and “consciousness” are not synonymous, they are tightly coupled. As Koch and Tsuchiya (2007) noted: “When we attend to an object, we become conscious of its characteristics; when we shift attention away, the object fades from consciousness.” In the following studies, we tested whether fluctuations in pupil diameter comprise a temporally sensitive readout of conscious attention during single exposure to a dynamic stimulus (music). We predicted that different musical clips would be defined by different patterns of attentional salience, and thus that the pupillary dilation pattern in response to the simultaneous presentation of two clips would discriminate which clip dominated conscious awareness on a trial-by-trial basis.

2. Methods

2.1. General descriptions

2.1.1. Participants

All participants were recruited from Dartmouth College and compensated for their participation monetarily (in accordance with standard rates) or with course credit. All participants were over 18 years of age, with normal or corrected-to-normal vision and audition. Written informed consent was obtained prior to the start of the study.

2.1.2. Materials

Eight 30-second clips were taken from well-known classical instrumental pieces. In order to control for potential salience differences associated with valence (Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006), we used equal numbers of negatively- and positively-valenced music clips, and dichotic pairs were always comprised of same valence clips. Music clips

![Fig. 1. Pupil dilation dynamics and locus coeruleus activity are tightly coupled. Using single-unit recording, Rajkowski and colleagues demonstrated the existence of a close positive relationship between norepinephrine release by the locus coeruleus neurons in the monkey and pupil diameter (1993). This figure is adapted from Rajkowski et al. (1993).](image-url)
were categorized as “positive” or “negative” on the basis of subjective binary ratings made by a set of independent raters (all comparisons significant using binomial tests at \( p < .05 \), Bonferroni-adjusted). Positive clips were taken from Pachelbel’s *Canon in D*, Tchaikovsky’s *Love Theme* from *Romeo and Juliet*, Beethoven’s *Ode to Joy* from *Symphony No. 9*, and Liszt’s *Hungarian Rhapsody*. Negative clips were taken from Holst’s *Mars: Bringer of War*, Mussorgsky’s *Night on Bare Mountain*, Mozart’s *Symphony No. 40*, and Beethoven’s *Symphony No. 7*.

Each clip was paired with the same partner clip throughout the course of the experiment, resulting in the following four paired stimuli: Positive – *Canon in D/Love Theme; Ode to Joy/Hungarian Rhapsody*; Negative – *Mars: Bringer of War/Symphony No. 40; Night on Bare Mountain/Symphony No. 7*.

Music clips were presented on over-ear headphones using E-Prime 2.0 Professional software. The Applied Science Laboratories (ASL) Eye-Trac D6 eye-tracker was used to measure pupil dilation (Applied Science Laboratories, Bedford, MA). Data preprocessing and analyses were conducted in Matlab (Mathworks, Nattick, MA, USA) and R (R Core Team, 2014: http://www.R-project.org/).

2.1.3. Eye-tracking and quality control

Pupil diameter was collected from the left eye at 120 Hz using the ASL Eye-Trac 6 eye-tracker. Missing values were linearly interpolated. Trials requiring over 25% of the pupil dilation data to be interpolated were discarded. If the number of discarded familiarization trials (see Sections 2.1.4 and 2.1.5) for a participant precluded analysis, that participant was removed from analysis. Following standard procedures (Smallwood et al., 2011; Wierda, van Rijn, Taatgen, & Martens, 2012), resultant pupil data was median filtered (order 5) and low-pass filtered (cutoff frequency 10 Hz) to remove spikes from the data, averaged into 100 ms bins, z-scored to account for individual differences in pupil size, and detrended to correct for slow drift.

2.1.4. Design and procedure

Participants were seated in front of an LCD monitor, and placed their heads in a chin rest affixed 30 inches away from the eye-tracker. Light levels remained constant for the duration of the 30-min study. The experiment was divided into two parts: Familiarization and Dichotic Listening (see Fig. 2).

In the Familiarization portion of the study, participants were eye-tracked while they heard each musical clip diotically (same clip in both ears). Each clip was presented twice throughout the course of the familiarization trials, and the order of presentation was randomized using E-Prime’s ‘Randomize’ feature. Participants were told to attend carefully to each clip “as though you were trying to memorize it”. After each clip, participants reported how much their mind wandered on a 1–5 Likert scale (“1” – not at all, “3” – half the time, “5” – the entire time). Mind-wandering was defined as “actively thinking unrelated thoughts, passively ‘zoning out’, and/or drowsiness” but “mental imagery evoked by the music [was] not considered mind-wandering.”

In the Dichotic Listening portion of the study, participants heard these same music clips presented in dichotic pairs (a different music clip in each ear). Before each trial, the computer directed participants to attend to either their left or right ear. The order of this direction was randomized by E-Prime, under the condition that participants attend each clip four times over the course of the experiment. Each of the eight clips was presented twice in each ear, resulting in a total of 32 experimental trials. Participants were told, “Try your best to attend *only* to the clip playing in the directed ear, and block out the other song as much as possible. If you notice your attention being drawn to the song playing in the other ear, actively bring...”

![Fig. 2](image-url)  
**Fig. 2.** A schematic of “Familiarization” and “Dichotic Listening” tasks. Participants first completed a “Familiarization” task (left), during which they heard each of the eight music clips presented twice diotically. In the “Dichotic Listening” task (right), they were presented with dichotic pairs of music, and instructed to attend to only one clip to the exclusion of the other. Participants were eye-tracked in both tasks, and pupillary response patterns were compared using dynamic time warping algorithms.
your attention back to the directed ear." After each trial, participants reported the percentage of time they attended to the clip playing in the directed ear, and how much of the time they "consciously heard" the other song (each on a 0–100% scale). They were told, "These ratings do not have to add up to 100%, as you can experience periods of mind-wandering (during which neither ear is consciously attended) and periods where you listen to both clips simultaneously." Participants again reported how much they mind-wandered on a 1–5 Likert scale.

2.1.5. Trial selection
The three experiments reported here investigate whether PDy sensitively indexes attentional dynamics over time and on a single trial. To test this hypothesis, we selected the best-attended diotic and dichotic trial for each music clip for each participant. Trial selection occurred in the following manner:

1. Diotic trials were the first diotic presentation of each music clip, for each participant. If this first trial required in excess of 25% interpolation, we used data from the second diotic presentation of that clip for that individual (this occurred for 13.2% of trials in Experiment 1, 5.7% of trials in Experiment 2).

2. We calculated "perceived conscious attention scores" by subtracting participants' rating for how much they attended the undirected song from their rating for how well they attended the directed song. This constituted a subjective estimate of the percentage of time participants spent attending only to the directed ear. Possible scores ranged from –100% (complete attention to the undirected ear) to 100% (complete attention to the directed ear), with 0% indicating equal attention to both ears. We discarded dichotic trials for which participants reported being incapable of any preferential attention to the directed ear (≤0), or reported mind-wandering half or more of the time (3+). From the remaining trials, the dichotic trial for each song for which participants reported being most successful at attending exclusively to the clip playing in the directed ear was chosen for analysis (as determined by their perceived conscious attention scores). In cases in which multiple trials shared the highest perceived attention score for a given song (Experiment 1: 18.1%, Experiment 2: 16.7% of all trials), the trial with the lowest mind-wandering score was selected. These were often identical, so in remaining ties (Experiment 1: 16.2%, Experiment 2: 16.7% of all trials), the trial with the most data (lowest interpolation percentage) was selected. Although trial selection thus relied upon introspection, it relied on a rating of overall trial performance assumed to be "reliably introspectible" (Goldman, 2004).

2.2. Experiment 1

2.2.1. Participants
28 Participants (22 females) participated in this study. Four participants failed to meet acceptable data standards (see Section 2.1.3). Data from 24 participants (18 females) were analyzed.

2.2.2. Dynamic time warping
Dynamic time warping (DTW) was used to compare the morphological similarity between pupillary time-courses. DTW is a standard method for comparing signals that can stretch and compress in time (e.g., in speech and motion recognition – Kuzmanic & Zanchi, 2007; Sakoe & Chiba, 1978; space telemetry – Senin, 2008; signal processing – Müller, Mattes, & Kurth, 2006; protein sequence alignment and chemical engineering – Aach & Church, 2001; Vial et al., 2009) because, unlike linear methods of comparison, it is insensitive to small temporal differences between otherwise similar signals (Berndt & Clifford, 1994). DTW shows better performance at clustering similar signals when they are offset in time and equivalent performance when signals are temporally aligned (Berndt & Clifford, 1994; Keogh & Ratanamahatana, 2004).

The DTW algorithm (adapted from Ellis, 2003) fixes the start and endpoints of two signals (e.g., Signals A and B). These signals are then parsed into a user-defined number of segments, each representing some window of time. We defined 3 s windows with 1.5 s overlap to ensure that each "chunk" was local, but large enough to encapsulate meaningful musical change. The algorithm calculates the vector associated with these segments, and compares them across signals. Specifically, DTW calculates the cosine similarity of these vectors, i.e., the degree to which they are similarly oriented. Unlike correlation, which makes single comparisons of values at specific time-points across signals, DTW makes three comparisons for each segment: the same segment (e.g., segment 1) on both signals (A1:B1), and that segment on one signal with the following segment on the other (A1:B2 and B1:A2). Critically, the temporal progression of events is conserved: once a point on signal A has been aligned with a point on signal B, the next point on A cannot be aligned with an earlier point on B.

The cosine similarity values associated with these three segment pairs are compared. The pair that yields the smallest cosine similarity value is deemed to be the time at which the content of the two signals best align, and the temporal axes of both signals are adjusted accordingly. Each adjustment (i.e., stretching or compressing of the time axis) incurs a penalty: a "cost" of realignment. The sum of these penalties yields an overall cost value, which represents the overall effort involved in warping one signal to another. Thus, higher cost values will indicate greater dissimilarity between two patterns. It is important to note that these cost values are relative and parameter-free. DTW costs can only be compared across signals of equal length, as longer signals require more warping windows and have an inherent disadvantage for accruing warping costs.
2.3. Experiment 2

In order to test the reliability of PDy to track the locus of conscious attention on a single trial, we directly replicated the materials, design, procedure, and analysis used in Study 1.

2.3.1. Participants

24 Dartmouth students (14 females) participated in this study. Sample size was determined by an a priori power analysis based on the results of Experiment 1 for obtaining a .6 effect at power = .8. Two participants were excluded from analysis for failing to adhere to experiment instructions.

2.3.2. Dynamic time warping

Data was analyzed using dynamic time warping algorithms described in Section 2.2.2.

2.4. Experiment 3

Experiments 1 and 2 tested whether patterns of pupillary responses were conserved as a function of attention to specific stimuli. Experiment 3 used automatic pupil dilation deconvolution (Wierda et al., 2012) to investigate whether this conserved pupillary morphology was due to the unique pattern of salience associated with each music clip, which was attended during diotic and dichotic trials.

2.4.1. Participants

Given the concordance between the results of Experiments 1 and 2 (see Sections 3.1 and 3.2 below), the selected diotic and dichotic trials for the 46 participants (32 females) across both experiments were used as the data for Experiment 3.

2.4.2. Pupil dilation deconvolution

Although it is well established that the pupil dilates to salient stimuli, this dilation response can be difficult to decipher in the face of rapid presentation of salient stimuli (Wierda et al., 2012). When stimuli are presented in quick succession (e.g., during an attentional blink paradigm) the pupillary response becomes convolved: the response to the second stimulus will merge with the response to the first. Deconvolution separates this convolved signal into its constituent responses. Extending the approach of Hoeks and Levelt (1993), Wierda and colleagues’ deconvolution algorithm models the pupillary response as a response to a series of events (“attentional pulses”) that are free to vary in salience (“pulse strength”). Given information about the timing of these events, the algorithm creates a model pupillary response that can be compared against the observed pupillary response pattern. This process is iterated with adjustments to the weights of each pulse until the fit is optimized. The result is a “temporal salience map” that reveals the timing and attentional salience of attended events, and achieves a similar fine-grained contour to that observed in the pupillary data on a trial.

To adapt the deconvolution algorithm to investigate attention to continuous stimuli, we set the attentional pulse to occur at a constant rate of once per second. The algorithm calculated the strength of each of these pulses, generating a readout of changing salience throughout the duration of the stimulus. The pattern similarity of these deconvolved attentional pulse patterns was determined using dynamic time warping algorithms.

3. Results

3.1. Experiment 1

We hypothesized that if conscious attention biased processing of the attended clip during dichotic presentation, then the pupillary data recorded during dichotic presentation (PDyDichotic) should resemble the pupillary data recorded when hearing the attended clip alone (PDyAttend) relative to the pupillary data recorded when hearing the ignored clip alone (PDyIgnore). Higher similarity between dichotic and diotic data would be reflected in lower DTW costs (i.e., less of a cost to align one time series to another).

For each participant, PDyDichotic was dynamically time-warped to the time series data collected during each of the component clips when they were presented diotically (see Fig. 2). DTW cost values were averaged across all songs for each participant, and submitted to a paired samples t-test. PDyDichotic was significantly more morphologically similar to PDyAttend ($M = 12.05, SD = 2.03$) than to PDyIgnore ($M = 12.67, SD = 1.83, t(23) = 3.144, p < .005, 95% CI [−1.03, −0.21], d = .64$; see Fig. 3). The power to detect an effect of this size was .854.

3.2. Experiment 2

Following the same procedure as Study 1, we calculated DTW costs from warping PDyDichotic to PDyAttend and PDyDichotic to PDyIgnore, averaged these cost values across all songs for each participant, and submitted the averaged values to a paired
samples $t$-test. We replicated the results of Study 1: PDy\textsubscript{Dichotic} was significantly more morphologically similar to PDy\textsubscript{Attend} ($M = 11.72, \text{SD} = 1.46$) than to PDy\textsubscript{Ignore} ($M = 12.21, \text{SD} = 1.13$, $t(21) = 3.128$, $p = .005$, 95% CI $[.83, .17]$, $d = .67$).

3.3. Experiment 3

Pupil dilation deconvolution revealed the attended salience changes underlying each of the selected diotic and dichotic pupillary responses for Experiments 1 and 2. The similarity of these salience patterns was then compared using dynamic time warping. We calculated DTW costs of comparing the attentional pulse strength pattern associated with dichotic trials (AttPulse\textsubscript{Dichotic}) to the pulse strengths calculated for each of the component songs when presented alone (AttPulse\textsubscript{Attend} and AttPulse\textsubscript{Dichotic} to AttPulse\textsubscript{Ignore}). These cost values were averaged across music clips per participants, and submitted to a paired samples $t$-test. AttPulse\textsubscript{Dichotic} was significantly more similar to AttPulse\textsubscript{Attend} ($M = 3.71, \text{SD} = .44$) than AttPulse\textsubscript{Ignore} ($M = 3.81, \text{SD} = .42$, $t(45) = 2.203$, $p = .03$, 95% CI $[-.20, -.09]$, $d = .33$; see Fig. 4). We note again that effect sizes, but not raw DTW costs, can be compared across studies, due to differences in signal length in Experiment 3 versus Experiments 1 and 2.

4. Discussion

Here, we found that PDy during dichotic music presentation discriminated which of two competing music clips dominated conscious awareness. Deconvolving these pupillary responses further revealed the underlying temporal salience maps

![Fig. 3. Pupil dilation patterns discriminate which of two music clips was attended during dichotic listening. (a) A representative participant’s PDy during song A, song B, and the Dichotic AB pair (where song A was attended). (b) Participants’ pupillary time-courses during dichotic presentation were significantly more similar to their PDy during isolated presentation of the attended song versus the unattended song, $t(23) = 3.144$, $p < .005$. Within-subject error bars represent 95% confidence intervals.]

![Fig. 4. Pupil dilation deconvolution reveals the temporal salience maps associated with attended stimuli. This figure shows a representative subject’s pupillary responses during an experimental trial (a,b), and the stimulus salience pattern underlying each pupillary response (c and d, respectively). Salience patterns during dichotic presentation were significantly more similar to the salience pattern associated with the attended versus unattended song, $t(45) = 2.203$, $p = .03$.]

associated with the stimuli driving attention. These results demonstrate that an analysis of fit between PDy time-series can be used to gauge the locus of conscious attention. It further suggests that automatic pupil dilation deconvolution can be used to assess the information considered salient by an individual during presentation of that information. These findings demonstrate the utility of PDy in the study of moment-by-moment conscious attention.

Finally, our results suggest that PDy provides information about both exogenous and endogenous attention. Pupil dilation has long been thought to reflect exogenous attention modulated by LC–NE activity (Aston-Jones, Rajkowski, & Cohen, 1999). In contrast, endogenous attention has been associated with the basal forebrain and cholinergic control (Rokem, Landau, Garg, Prinzmetal, & Silver, 2010). Others suggest a hybrid model, such that endogenous attention can enhance the salience of external cues within the bounds of attentional focus (Mesulaum, 1996; Noudoost, Chang, Steinmetz, & Moore, 2010). Consistent with this hybrid view, it is possible that intentional allocation of attention to one ear in the present study amplified the sensory inputs presented in that ear relative to information presented to the undirected ear. It is also possible that this allocation of attention enabled higher-level information processing of these inputs. The present study reveals that high temporal resolution fluctuations of pupil size reflect what is being attended. Whether those fluctuations are better characterized as amplifications of sensory processing or higher-level information processing or both is an important topic for future research.

From these findings, we infer that PDy, as an index of LC–NE activity, is a biological marker that reflects the locus of conscious attention. As such, high temporal resolution pupillometry combined with dynamic time warping and deconvolution techniques provide a new tool in our quest to track and understand the contents of conscious experience.

5. Conclusions

In three studies, we used computational techniques (DTW, deconvolution) to reveal the temporal dynamics of conscious attention as indexed by pupil dilation patterns. James once said, “My experience is what I agree to attend to” (1890). By identifying the locus of conscious attention, pupillometry may advance our knowledge about the contours and contents of conscious experience. In addition, tracking conscious attention via pupillary changes may afford novel interventions that direct re-directive attention in real-time, with important applications for increased vigilance and learning.

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References


