University of Groningen

Pupillary response indexes the metrical hierarchy of unattended rhythmic violations

Damsma, Atser; van Rijn, Hedderik

Published in:
Brain and Cognition

DOI:
[10.1016/j.bandc.2016.10.004](https://doi.org/10.1016/j.bandc.2016.10.004)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2017

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Damsma, A., & van Rijn, H. (2017). Pupillary response indexes the metrical hierarchy of unattended rhythmic violations. *Brain and Cognition*, 111, 95-103. <https://doi.org/10.1016/j.bandc.2016.10.004>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Pupillary response indexes the metrical hierarchy of unattended rhythmic violations

Atser Damsma*, Hedderik van Rijn

Department of Psychology, University of Groningen, Grote Kruisstraat 2/1, 9712 TS Groningen, The Netherlands

ARTICLE INFO

Article history:

Received 1 February 2016

Revised 28 September 2016

Accepted 11 October 2016

Available online 2 November 2016

Keywords:

Beat perception

Music cognition

Attention

Pupil dilation

ABSTRACT

The perception of music is a complex interaction between what we hear and our interpretation. This is reflected in beat perception, in which a listener infers a regular pulse from a musical rhythm. Although beat perception is a fundamental human ability, it is still unknown whether attention to the music is necessary to establish the perception of stronger and weaker beats, or meter. In addition, to what extent beat perception is dependent on musical expertise is still a matter of debate. Here, we address these questions by measuring the pupillary response to omissions at different metrical positions in drum rhythms, while participants attended to another task. We found that the omission of the salient first beat elicited a larger pupil dilation than the omission of the less-salient second beat. This result shows that participants not only detected the beat without explicit attention to the music, but also perceived a metrical hierarchy of stronger and weaker beats. This suggests that hierarchical beat perception is an automatic process that requires no or minimal attentional resources. In addition, we found no evidence for the hypothesis that hierarchical beat perception is affected by musical expertise, suggesting that elementary beat perception might be independent from musical expertise. Finally, our results show that pupil dilation reflects surprise without explicit attention, demonstrating that the pupil is an accessible index to signatures of unattended processing.

© 2016 Elsevier Inc. All rights reserved.

1. Introduction

1.1. Expectations in music

Fulfilments and violations of expectations are key in our appreciation of music (Huron, 2006). The perception of music is therefore a complex interaction between what we hear and our anticipatory interpretation (Vuust, Gebauer, & Witek, 2014). This is reflected in *beat perception*, in which a listener infers a regular pulse from a musical excerpt that does not necessarily contain this pulse explicitly (Honing, 2012). In addition, people are able to perceive a hierarchy of stronger and weaker beats, known as *meter*. This cognitive ability has an important social function by allowing people to synchronize movements and play music together, a capacity that human infants can utilize from about four years of age (Endedijk et al., 2015). The perceived beat drives our expectations about the timing and salience of the rhythm (Large & Kolen, 1994).

Although beat perception is a fundamental and widespread human capability, two major issues still need to be resolved. First,

it is still unknown how much attention is needed to detect the beat (Bouwer & Honing, 2012). On the one hand, it has been argued that beat perception is pre-attentive (Bouwer, Van Zuijlen, & Honing, 2014; Geiser, Sandmann, Jäncke, & Meyer, 2010; Ladinig, Honing, Håden, & Winkler, 2009; Winkler, Håden, Ladinig, Sziller, & Honing, 2009), while other studies have suggested that attention is necessary to establish a representation of the beat (Chapin et al., 2010; Geiser, Ziegler, Jancke, & Meyer, 2009). Second, to what extent beat perception is open for learning and dependent on expertise is still a matter of debate (Hannon & Trehub, 2005; Honing, 2013). Whereas Geiser et al. (2010) found that musicians were more sensitive to the metrical position of accents than non-musicians, Bouwer et al. (2014) found no difference in ERP response to beat omissions between musicians and non-musicians.

To investigate beat perception and metrical expectancy, recent studies have measured the mismatch negativity (MMN) as a response to expectancy violations (Bouwer et al., 2014; Honing, Bouwer, & Håden, 2014; Ladinig et al., 2009; Winkler et al., 2009). The MMN is a negative event-related potential (ERP) component that is elicited by unexpected stimuli in a sequence (e.g., Näätänen, Gaillard, & Mäntysalo, 1978, who manipulated loudness and pitch, or Kononowicz & van Rijn, 2014, who demonstrated MMN-like responses in a task with temporal violations). The mag-

* Corresponding author.

E-mail address: A.Damsma@rug.nl (A. Damsma).

nitude and latency of these early EEG potentials reflect the magnitude of the violation (Kononowicz & van Rijn, 2014; Näätänen, Paavilainen, Rinne, & Alho, 2007; Schröger & Winkler, 1995), and thus allows for indexing subjective metrical salience. In addition, the MMN is elicited irrespective of attention, which makes it particularly suitable for studying *unattended* beat perception.

In order to test whether people perceive the beat without attention, several studies have investigated the MMN as a response to sound omissions in drum rhythms while the listeners were instructed to focus their attention elsewhere (Bouwer et al., 2014; Ladinig et al., 2009; Winkler et al., 2009). Based on theoretical models of hierarchical beat perception (Lerdahl & Jackendoff, 1983; Longuet-Higgins & Lee, 1984), one would predict that salient omissions are more surprising than less salient omissions. Thus, in a standard Western rock drum rhythm (Fig. 1), in which the first beat of a measure is more salient than later beats, we can expect that the omission of the first beat violates expectations more than the omission of the second beat. In that case, the former omission is expected to elicit a larger MMN than the latter omission. However, empirical work has failed to find univocal evidence for this hypothesis.

To test whether hierarchical beat perception is innate or learned, Winkler et al. (2009) presented sleeping newborns with rock drum rhythms with occasional omissions at different metrical positions. They found that the omission of a bass drum at the first beat (the most salient metrical position) elicited a larger MMN than hi-hat omissions at the lowest level of metrical salience. Although Winkler et al. (2009) concluded that the newborns perceived the beat, the MMN difference might alternatively be due to the nature of the omitted sound instead of the metrical position (Bouwer et al., 2014). Controlling for this alternative explanation, Ladinig et al. (2009) presented adult participants with rock drum rhythms in which the bass drum sound was either omitted at the first or at the second beat while they performed a concurrent task. Whereas Ladinig et al. (2009) found a slightly earlier MMN for the first beat compared to second beat, they did not find a difference in

amplitude (Ladinig, Honing, Hádén, & Winkler, 2011). In a similar, more recent experiment, Bouwer et al. (2014) also reported a lack of significant differences in MMN amplitude elicited by the omission of the first and second beat, and also failed to observe any differences in the latency of the MMN as a function of the hierarchical level of the omitted sound. Thus, while these MMN studies show that participants detect violations of the beat without attention, it remains largely unknown whether people perceive a hierarchy of stronger and weaker beats when attention is focussed on another task.

Although the study of Winkler et al. (2009) suggests that simple beat detection is already present at birth, the extent to which hierarchical beat perception is open for learning is still a matter of debate (Honing et al., 2014; Nozaradan, 2014). One way to tackle this question is by investigating whether musical training leads to a more pronounced representation of beat and meter. So far, this question has been approached by behavioural, fMRI and ERP experiments, which have resulted in partly ambiguous results. While some studies show that musical training enhances beat processing (Chen, Penhune, & Zatorre, 2008; Vuust et al., 2005), others found no differences between musicians and non-musicians (Bouwer et al., 2014).

Thus, while MMN studies suggest that people perceive the omission of beats without attention, it is still unclear (1) whether they perceive a hierarchy of stronger and weaker beats, and (2) to what extent musical expertise influences beat perception. As the MMN amplitude might not reflect differences in beat salience (Bouwer et al., 2014; Ladinig et al., 2009), we will employ a new approach to investigate these questions: pupil dilation. Several findings suggest that pupil dilation has the potential to be an accessible measure of musical expectation. First, a phasic pupillary response has been found in response to deviant, surprising stimuli (Friedman, Hakerem, Sutton, & Fleiss, 1973; Preuschoff, Marius't Hart, & Einhäuser, 2011; Steinhauer & Zubin, 1982). Second, pupil dilation has been suggested to reflect preconscious processing (Laeng, Sirois, & Gredebäck, 2012). Third, Wierda, van Rijn,

Fig. 1. Graphic depiction of the six different drum patterns, consisting of hi-hat, snare and bass sounds, used in the current study. Metrical salience is denoted by the hierarchical tree-structure at the top, in which the dots represent the first and second beat. Base pattern S1 was a typical rock drum rhythm without any omission. In the three other standard patterns (S2, S3, and S4), a hi-hat sound was omitted at the lowest level of salience. Deviant pattern D1 contained the theoretically most salient omission: the bass sound on position 1. In deviant pattern D2, the bass sound on the second most salient position was omitted (Adapted from Bouwer et al., 2014).

Taatgen, and Martens (2012) have shown that the relatively slow pupillary response accurately indexes processing at a high temporal resolution.

1.2. Pupil dilation reflects surprise

Decades of research have shown that pupil dilation reflects several fundamental cognitive processes. For example, it has been shown that phasic pupil size indicates mental effort (e.g., Ahern & Beatty, 1979; Granholm, Asarnow, Sarkin, & Dykes, 1996; Kahneman, 1973), emotional arousal (e.g., Hamel, 1974; Hess & Polt, 1960), memory strength and encoding (e.g., van Rijn, Dalenberg, Borst, & Sprenger, 2012; Wolff, Scholz, Akyürek, & van Rijn, 2015), language processing (e.g., Vogelzang, Hendriks, & van Rijn, 2016), and dynamical attention (e.g., Verney, Granholm, & Marshall, 2004; Wierda et al., 2012). Although the pupillary response is relatively slow, recent studies have shown that the pupil reflects events with a high temporal resolution (Wierda et al., 2012; see also Willems, Damsma, Wierda, Taatgen, & Martens, 2015; Wolff et al., 2015; Zylberberg, Oliva, & Sigman, 2012). In this way, measuring pupil dilation offers an accessible, non-invasive and relatively inexpensive method to reveal online cognitive processing.

In addition to the cognitive processes listed above, there is increasing evidence that pupil dilation reflects surprise. As a first indication of this relationship, Friedman et al. (1973) found that pupil dilation was negatively correlated with stimulus probability. In line with this finding, Steinhauer and Zubin (1982) found a larger pupil dilation as a response to a rare target stimulus compared to the frequent distractor stimulus in an auditory oddball task. More recently, Preuschoff et al. (2011) found a larger dilation for surprising outcomes in a gambling task. In the experiment of Preuschoff et al. (2011), participants were presented with two sequential playing cards. Before this, they placed an uninformed bet on whether the first or the second card would be higher. The results showed that pupil dilation was higher when the second card resulted in a reward that was unexpected given the first card (e.g., when a 2 was shown after a 3), compared to when the expected reward indeed occurred.

Pupil dilation has been suggested to reflect brain activity in the locus coeruleus (LC; for reviews see Laeng et al., 2012; Sara, 2009). The LC is a nucleus in the brainstem that forms the hub of the noradrenergic (NA) system (Aston-Jones & Cohen, 2005). It has been argued that the LC is an important modulator in the attentional system, by regulating the neural responsivity of brain areas involved in selective attention, such as the frontal and parietal cortex (Coull, Büchel, Friston, & Frith, 1999; Sara, 2009). The LC-NA system is thought to facilitate “attentional and cognitive shifts and behavioural adaptation to changes in environmental imperatives” (Sara, 2009, p. 220), or context-updating in response to unexpected stimuli (Nieuwenhuis, 2011). In line with this proposed role of the LC-NA system and the finding that pupil dilation reflects surprise, Dayan and Yu (2006) showed that the phasic activation of NA neurons in rats and monkeys depends on the prior probability of a target: Infrequent targets elicited a larger phasic NA signal than frequent targets. In accordance with this result, Alexinsky, Aston-Jones, Rajkowski, and Revay (1990) found that an increased target frequency led to a decrease in phasic LC activity.

1.3. Pupil dilation and ERP components

Interestingly, the evidence that pupil dilation signals surprise suggests that it might be an accessible measure of expectation. As such, it might reflect expectancy violations in a similar fashion as ERP components such as the MMN and the P3. Whereas the

MMN has been found to be relatively automatic (Näätänen, Paavilainen, Titinen, Jiang, & Alho, 1993; Otten, Alain, & Picton, 2000), the P3 reflects the evaluation of the stimulus in a given context, which requires active attentional allocation (Polich, 2007). The amplitude of the P3 depends on the amount of attentional resources allocated to the stimuli, so that the P3 is smaller when a secondary task is performed (e.g., Isreal, Chesney, Wickens, & Donchin, 1980) or when the stimuli do not require active processing (Polich, 2007). As a theoretical account, the P3 has been proposed to reflect context-updating: the revision of one's mental representation of the current environment based on the stimuli (Donchin, 1981). In line with this theory, the P3 has been suggested to reflect phasic activity of the LC-NA system (Nieuwenhuis, Aston-Jones, & Cohen, 2005). In this way, the P3 and phasic pupil dilation might be manifestations of the same underlying neural, as well as cognitive, process.

Recently, Kamp and Donchin (2015) investigated whether pupil dilation and the P3 indeed reflect the same cognitive function in a categorization task. Participants categorized words or pictures in either a frequent (e.g., living) or infrequent category (e.g., non-living), with the frequent words describing both living and non-living entities, and the infrequent pictures only depicting living entities. Kamp and Donchin (2015) found no correlation between the amplitude of the pupil dilation and the P3. In addition, whereas the P3 was higher for pictures than for words, pupil dilation only reflected category frequency. That is, while the P3 was also sensitive to perceptual deviance, the pupil only reflected categorical deviance. Kamp and Donchin therefore argued that response conflict – the need to inhibit a prepotent response tendency and give an alternative, appropriate response – might be crucial for eliciting a pupillary response.

With respect to whether attention is needed for a pupillary response, Laeng et al. (2012) suggested that pupil dilation might offer “a window to the preconscious” by reflecting cognitive processes outside of awareness and without an overt response. Evidence for this view comes from patients with *blindsight* who showed a pupillary response to visual stimuli presented in the blind visual field, that therefore were not consciously seen (Tamietto et al., 2009; Weiskrantz, Cowey, & Barbur, 1999). Similarly, Laeng et al. (2007) found that amnesic patients showed a larger pupil dilation for novel compared to old stimuli, even when the patients had no explicit memory of these stimuli. Also in healthy participants, a small number of studies have found a pupil dilation response to stimuli that are not consciously perceived. For example, Bijleveld, Custers, and Aarts (2009) found that pupil dilation reflected the value of subliminal reward cues. Overall, these findings suggest that pupil dilation may reflect cognitive processes even in the absence of attention.

In summary, both direct and neuroscientific evidence suggests that pupil dilation reflects the violation of expectations. However, it is still unclear whether attention or overt response is crucial for this pupil reaction. Whereas Kamp and Donchin (2015) argued that response conflict is an essential requirement for a pupillary response, others have suggested that the pupil might reflect processes below the threshold of consciousness (Laeng et al., 2012). In the latter case, we might expect that the pupillary response, like the MMN, reflects the violation of expectancy rather automatically. However, the pupillary response to unattended, surprising stimuli has not yet been investigated. Therefore, a secondary aim of the present experiment is to elucidate whether pupil dilation indeed reflects the violation of expectancy in the absence of attention.

1.4. Current study

In the current study, we will assess whether participants perceive beat and the hierarchical aspects of meter while they focus

attention on another task by measuring pupil dilation. In addition, we will investigate whether higher musical expertise entails more pronounced beat perception. Participants are asked to perform a visual target detection task while a continuous stream of Western rock drum patterns is presented. The participants are instructed that the drum rhythms are irrelevant to the task at hand and are instructed to ignore the audio. The drum patterns in the stream contain omissions at different levels of metrical hierarchy, and thus of theoretical salience, as shown in Fig. 1.

We expect that, first, if participants perceive the beat, salient omissions will elicit a pupillary response. Second, if participants perceive meter, we expect that salient omissions will elicit a higher pupillary response than less-salient omissions. Third, if beat perception is enhanced by musical training, we expect that the level of musical expertise as assessed by a validated questionnaire will be a predictor of the pupillary response to the omissions. If, on the other hand, unattended beat perception is a general human ability that is independent of expertise, we expect to find no effect of musical expertise.

2. Methods

2.1. Participants

Twenty participants enrolled in the Bachelor program Psychology at the University of Groningen (10 female, mean age 20.9, range 19–26) participated in the experiment in exchange for course credits. Participants were naive to the purpose of the study. The Psychology Ethical Committee of the University of Groningen approved the experimental protocol (13223-NE) and all participants gave written informed consent prior to the experiment.

2.2. Materials

Stimuli were generated and presented using Matlab 2010 software running under Windows XP. Visual stimuli were presented on a 22-inch computer screen with a 100 Hz refresh rate. The '+' and '-' in the target detection task were presented in black, 22-point Arial on a light grey background. Drum rhythms were presented on a Superlux HD-662 F studio headphone at ~65 dB.

Similar to Ladinig et al. (2009), six different drum patterns were constructed that conform to typical drum patterns found in Western tonal music (Fig. 1). Four patterns were standard patterns (S1–S4) and two were deviant patterns (D1 and D2). Whereas standard patterns contained either no omissions (S1) or an omission at the lowest level of salience (S2–S4), deviant patterns contained a salient omission on the beat.

The base pattern, S1, was a typical rock drum rhythm composed of bass, snare and hi-hat sounds. The bass and hi-hat sound consisted of samples from a Linn LM-1 drum computer, whereas the snare was sampled from a Sequential Circuits DrumTraks drum computer. The S1 pattern consisted of eight consecutive sounds at equidistance intervals (150 ms onset-to-onset) and a total duration of 1200 ms. To collect data that can be used to rule out the alternative explanation that the measured responses to deviating patterns are a result of simple pattern matching (Ladinig et al., 2009), three additional standard patterns (S2–S4) were created that contained an omission of a hi-hat sound at the lowest level of metrical salience. In the deviant patterns D1 and D2, the bass and hi-hat sounds were omitted at the most salient position (position 1) or the second most salient position (position 5), respectively. All sound samples are available at <https://osf.io/ezgup/>.

2.3. Design and procedure

Participants performed a visual target detection task, during which drum rhythms were presented. In the target detection task, a '+' was presented at the middle of the screen. The task of the participant was to press the spacebar as fast as possible whenever the fixation cross was replaced with a '-'. The inter-target onset asynchrony (TOA) of the '-' was determined by a constrained non-aging distribution: Every 10 ms the '-' had a 1/1200 chance of appearing, with a maximum TOA of 20 s. In order to motivate participants to perform well, participants could keep track of their performance using a simple scoring scheme. Responses faster than 400 ms were rewarded with a score increase of 10 points. Participants were told that they would receive a candy bar when they had more than 1000 points at the end of the experiment. They were informed that drum rhythms would be presented during the experiment, which could be ignored.

At the start of the experiment, participants performed a practice block consisting of the target detection task combined with a continuous stream of 50 drum patterns presented without any pauses. Next, participants were presented with 20 blocks, each consisting of 100 drum patterns presented continuously. Eighteen blocks were Deviant blocks, in which standard and deviant patterns were presented. Two blocks served as Control blocks, which consisted of the repeated presentation of a deviant pattern. These blocks served to test whether the pupillary response towards deviants indeed reflects expectation and not a response to the omission itself. The order of the blocks was random.

A Deviant block consisted of 80 standard patterns (20 repetitions $\times$ 4 patterns) and 20 deviants (10 repetitions $\times$ 2 patterns). The order of the patterns within a Deviant block was pseudorandom with the constraint that there were at least three standard patterns between consecutive deviants. In addition, D1 could not follow S4, because that would lead to the presentation of two consecutive omissions. Each Deviant block started with at least two standard patterns. In the Control blocks, participants were presented with a stream of repeated D1, or repeated D2 patterns.

After the experiment, the musical expertise of the participants was assessed by completing the self-report inventory from the Goldsmiths Musical Sophistication Index (Gold-MSI; Müllensiefen, Gingras, Musil, & Stewart, 2014). The Gold-MSI combines the scores on multiple subscales (e.g., musical training, active musical engagement) into a General Musical Sophistication factor.

2.4. Pupil dilation

Pupil dilation was recorded using the EyeLink 1000 eyetracker (www.sr-research.com) at a sampling rate of 1000 Hz. Before recording, the eye tracker was calibrated to track the left eye. To minimize head movements, participants were asked to rest their chin on a chin-rest and their forehead against a forehead-bar (SR Research Head Support) that was fixed to the table resulting at a viewing distance of ~50 cm.

2.4.1. Pre-processing

The pupil data were down-sampled to 50 Hz. In every block, blinks and missing data were recovered using spline interpolation, but only when not more than 500 ms of sequential data was contaminated. Epochs were extracted from the continuous data by taking the data in a time window of 600 ms before and 3600 ms after the onset of every pattern. Epochs containing non-interpolated missing data or blinks, and patterns containing more than 200 ms of interpolated data were removed from analysis. Epochs were time-locked to omission onset and baseline corrected by the average pupil size during the 100 ms before the onset of the

omission. The first and last two patterns of each block were not analysed.

To investigate the effect of omissions, the pupil dilation in deviant patterns (D1, D2) and standard patterns (S2, S3, S4) was compared to the dilation in base pattern S1. In order to control for the different location of the omissions within the drum pattern, for each comparison pattern separately, S1 was time-locked and baseline corrected to the onset of the omission in that particular pattern. Thus, for comparison, the onset of S1 was matched to the omission onset of each pattern. To further eliminate differences in acoustic context between deviants and base pattern S1, the dilation in deviant patterns was compared to a subset of S1 patterns with a similar context. As deviants could not be followed by another deviant by design, the same constraint was applied to the selection of S1 patterns for the analysis of the deviant patterns. Thus, deviant patterns were compared to the subset of S1 patterns that did not precede a deviant. Similarly, as S4 patterns could not be followed by a D1 pattern by design, only the subset of S1 patterns that were not followed by D1 were used for the S4 analysis.

For another set of analyses, difference waves were calculated at trial-level by subtracting the participant-average S1 pupil dilation, time-locked and baseline corrected to the relevant omission onset, from the dilation of the different patterns. For these difference waves, we calculated the area under the curve (AUC) in the time window from 400 to 1600 ms after omission onset. Considering that the pupillary response peaks ~ 1 s after a relevant event (e.g., Hoeks & Levelt, 1993), the dilation was expected to be most apparent in this time window.

2.4.2. Statistical analysis

First, we tested whether the dilation of D1, D2, S2, S3 and S4 differed from base pattern S1 by comparing the dilation elicited by these patterns to the aligned S1 dilation. For this analysis, data in a time window from 0 to 2000 ms after omission onset were taken into account. For each comparison against S1, a nonparametric permutation test was performed (Maris & Oostenveld, 2007) in which the condition for each data point and participant was randomly labelled 10000 times. Conditions were compared with a standard t -test. To control for multiple comparisons, a critical t -value (t_{crit}) was calculated with a single threshold test (Nichols & Holmes, 2002). The null hypothesis, stating that there is no difference between two conditions, was rejected if the t -value exceeded the critical t -value.

To test the effect of omission position and musical sophistication on pupil dilation, the AUC of the difference waves was analysed with Linear Mixed Models (LMM) using the *lme4* package (version 1.1-7) in R version 3.1.2 (Bates, Maechler, & Bolker, 2012). Before analysis, the fixed factors Baseline and Trial were centred and scaled to a range of -1 to 1 and the factor Pattern was recoded using effect coding.

Separate LMMs were performed for deviant patterns in the Deviant condition, for deviant patterns in the Control condition, and for standard patterns. A direct comparison of the pupillary response between all deviants and standards would not be informative, as not only their omission position differed, but also the omitted sound and the presentation frequency. That is, in deviant patterns a bass drum and hi-hat were omitted whereas only a hi-hat was omitted in the S2–S4 standard patterns. The LMMs were performed with Pattern, Musical Sophistication, and their two-way interaction term as fixed factors. In addition, the main effect of Trial and the absolute Baseline were entered in the models. In each model, Participant was entered as a random factor.

In addition to the LMMs, we performed Bayesian analyses. These analyses allow for quantifying the statistical evidence in favor of the null hypothesis. For non-significant fixed factors in the LMMs, we compared the Bayes factors of a model without

the particular fixed factor with the original model using the *lmbf* function from the *BayesFactor* package in R (Morey, Rouder, & Jamil, 2014). We will denote the evidence for H_0 over H_1 as BF_{01} .

All materials and analysis scripts are available at <https://osf.io/ezgup/>.

3. Results

3.1. Pupil dilation results

Figs. 2 and 3 show the mean normalized pupil dilation and the difference waves for the deviant and standard patterns, respectively. The permutation test showed that the dilation for D1 was higher than for S1 in the time window of 540–660 ms after omission onset ($t_{\text{crit}} = 3.18$, $ps < 0.027$; Fig. 2A). In contrast, no differences were found between D2 and S1 ($t_{\text{crit}} = 3.18$, $ps > 0.906$; Fig. 2B). Thus, whereas the most salient deviant (D1) elicited an increased pupil dilation, the less salient deviant (D2) did not. Similarly, standard patterns S2, S3 and S4 did not differ from S1 ($t_{\text{crit}} = 3.09$, 3.08 and 3.00 respectively, $ps > 0.210$; Fig. 3), indicating that the omission of a hi-hat sound at the lowest level of salience did not elicit a pupillary response. In addition, no differences were found between both D1 and D2 in the Control blocks and S1 ($t_{\text{crit}} = 2.99$ and 2.95 respectively, $ps > 0.924$; Fig. 2C and D), showing that the deviating pupillary response to D1 and (if an effect would have been found) to D2 are driven by a context that provides a baseline compared to which D1 and D2 deviate.

The AUC of the difference waves of all patterns in the Deviant and Control condition can be found in Table 1. The model for the AUC of the deviants showed a significant negative effect of Trial ($\beta = -3.99$, $t = -3.65$, $p < 0.001$) and Baseline ($\beta = -134.82$, $t = -27.52$, $p < 0.001$), indicating that the pupillary response decreased over the scope of the experiment, and that higher pupillary baselines were associated with lower pupillary responses. The AUC for D1 was higher than for D2 in the Deviant condition ($\beta = -1.29$, $t = -2.14$, $p = 0.032$), showing that D1 elicited a larger pupillary response than the less-salient deviant D2. Post-hoc t -tests indicated that the AUC associated with the difference between D2 and S1 did not significantly differ from 0. When presented with a block consisting of only D1 or D2 patterns (the Control blocks), no difference between D1 and D2 was observed ($\beta = 1.09$, $t = 1.46$, $BF_{01} = 164$).

As a post-hoc analysis, suggested during review, we aimed to test whether the difference in AUC between D1 and D2 decreased over the course of a block. To this end, we added a factor corresponding to the trial number within a block and the interaction between this factor and Pattern to the LMM. The model showed that although the dilation decreased over the course of a block ($\beta = -7.60$, $t = -6.92$, $p < 0.001$), the difference between D1 and D2 did not change ($\beta = 0.20$, $t = 0.20$, $BF_{01} = 21$).

Overall, Musical Sophistication was not a significant predictor of the AUC of the deviants ($\beta = 0.18$, $t = 0.42$), nor a predictor of the difference in AUC between D1 and D2 ($\beta = -0.08$, $t = -1.63$). Bayes factor analysis showed that a model excluding the main effect of Musical Sophistication and its interaction with Pattern was preferred over the model including these factors with $BF_{01} = 19$, providing strong evidence (Jeffreys, 1961) for the view that Musical Sophistication does not predict the pupillary response. Thus, participants with a greater musical expertise did not show a larger pupil dilation in response to deviants than participants with a smaller expertise. Furthermore, musical expertise had no influence on the difference in pupillary response to omissions of different salience.

Deviant Condition

Control Condition

Fig. 2. Average dilation and difference waves for deviant patterns D1 and D2 in the Deviant condition (A and B respectively) and the Control condition (C and D). Time point 0 corresponds to the omission onset. The dashed grey line presents the time-locked base pattern S1, the colored dashed lines present the dilation of the patterns and the solid lines present the difference waves of the patterns with S1. Significant differences between the pattern and S1 are denoted by asterisks. For these figures, the signals were smoothed with a 5-point running average filter.

Fig. 3. Average dilation and difference waves for standard pattern S2, S3, and S4 (A, B, and C respectively). Time point 0 corresponds to the onset of the hi-hat omission. The dashed grey line presents the time-locked base pattern S1, the colored dashed lines present the dilation of the patterns and the solid lines present the difference waves of the patterns with S1. For these figures, the signals were smoothed with a 5-point running average filter.

For the standard patterns, we found that Pattern had no effect on the AUC ($\beta = 2.48$, $t = 0.61$). Bayes factor analysis showed that the restricted model excluding Pattern was preferred over the full model with $BF_{01} = 4405$, providing decisive evidence (Jeffreys, 1961) that the position of the hi-hat omission did not influence

the pupillary response. Furthermore, Musical Sophistication was not a significant predictor of the AUC of the standard patterns ($\beta = 0.24$, $t = 0.55$). In addition, the effect of Musical Sophistication did not differ between patterns ($ps > 0.121$). The model without Musical Sophistication was preferred over the model including

Table 1

Average AUC of the difference waves per pattern and condition.

Pattern	AUC	SE
<i>Deviant condition</i>		
D1	3.14	1.31
D2	1.45	1.68
S2	1.16	1.47
S3	−0.37	1.21
S4	−0.53	1.43
<i>Control condition</i>		
D1	1.57	1.52
D2	−0.45	1.31

Musical Sophistication with $BF_{01} = 665$, providing, again, decisive evidence against including Musical Sophistication as a predictor for the pupillary response.

3.2. Behavioural results

The mean response time in the target detection task was 429.65 ms with a standard deviation, calculated over the mean response times per participant, of 72.30. Participants earned points when a response was faster than 400 ms. On average, participants were faster than 400 ms in 51.64% of the trials, showing that the task was considerably difficult to perform. We found no evidence that the auditory stimuli affected the performance on the target detection task. That is, responses to targets that appeared within 1 s after D1 or D2 omissions were not faster or slower than responses to targets outside this range ($t(37.9) = -0.28$, $p = 0.785$ and $t(34.4) = 0.63$, $p = 0.536$ respectively).

The mean Musical Sophistication score was 75.95 with a standard deviation of 12.40 and a range of 58.00–111.00. In a large scale online study ($n = 147,633$) aimed at the general public, the Musical Sophistication score was 81.58 ($SD = 20.62$) (Müllensiefen et al., 2014).

4. Discussion

In this study, we have investigated whether participants perceived beat and the hierarchical aspects of meter found in Western tonal music while paying attention to an alternative task by measuring pupil dilation. On the one hand, it has been argued that hierarchical beat perception is pre-attentive (Bouwer et al., 2014; Ladinig et al., 2009; Winkler et al., 2009), which would predict that salient omissions in rhythms elicit a larger pupillary response than less salient omissions. On the other hand, however, several studies have suggested that attention is necessary to perceive the beat (Chapin et al., 2010; Geiser et al., 2009), predicting no effect of metrical position on pupil dilation. Furthermore, in order to test whether beat perception is open to learning and exposure, we have investigated whether higher musical sophistication entails more pronounced beat perception. As a secondary objective, we have tested whether pupil dilation can index surprise as operationalized by the omission of expected stimuli in the absence of attention.

We found that salient omissions in the rhythm elicited an increased pupil dilation compared to standard rhythms without omission. However, this was only the case in the most salient deviant (D1) and not in the less-salient deviant (D2) or standard patterns in which a hi-hat sound at the lowest level of salience was omitted. In line with these results, we found that D1 elicited a larger pupil dilation than D2. With respect to musical expertise, we did not find an effect of musical sophistication on the pupillary response to omissions at the different metrical positions, nor did

musical sophistication have an effect on the difference in dilation between D1 and D2.

4.1. Unattended beat perception

In line with Ladinig et al. (2009) and Bouwer et al. (2014), our study shows that violations of the beat can be perceived without paying explicit attention to the rhythmic patterns. Furthermore, the absence of an increased pupillary response in the control condition provides evidence against the alternative explanation that the pupillary response to D1 could be caused by an omission of a beat at that particular position in and of itself. Instead, the combination of these results suggests that the pupillary response to omissions depend on the context in which the pattern is presented. Thus, our results show that participants extracted a regular and hierarchical structure from the rhythm while attending to another task.

These conclusions are driven by the observed difference in pupil dilation between D1 and D2, which consisted of the omission of an identical bass drum and hi-hat sound at a different metrical position. This finding suggests that a meter representation was induced. That is, participants did not only perceive a regular beat, but also perceived a hierarchy of stronger and weaker beats. This in line with the theoretical model of beat perception proposed by Longuet-Higgins and Lee (1984), which predicts that the first beat of a measure is more salient than the second beat (Fig. 1). Thus, our findings provide further evidence that hierarchical meter is not merely a theoretical concept, but actually drives our expectations when we listen to music (Ladinig et al., 2009), even while attending something else.

At first sight, the different pupillary response to D1 and D2 could be seen as being in contrast to the results of Bouwer et al. (2014) and Ladinig et al. (2009), who did not find a difference in MMN amplitude in response to D1 and D2. Although this latter finding might mean that no metrical hierarchy was induced, other explanations have to be considered. First, the MMN response to D1 and D2 might have been near ceiling level (Bouwer et al., 2014). Second, the drum rhythms did not contain explicit cues that indicate a hierarchy between the first beat and the second beat, other than the onset of the audio stream. It thus might be possible that participants perceived the second beat (position 5) as the first beat (position 1), and vice versa. These two alternatives potentially explain the discrepancy between our findings and both Ladinig et al. (2009) and Bouwer et al. (2014). First, as we measured pupil dilation instead of the MMN, we presumably did not encounter the ceiling effects present in ERPs. Second, we presented shorter blocks of continuous drum patterns than Ladinig et al. (2009) and Bouwer et al. (2014), which might make it more probable that participants used stream onset for the representation of meter during the whole block. If that is the case, we might expect that the difference in pupillary response to the different levels of salience decreases over the course of the continuous stream. However, we found no evidence that the difference in dilation between D1 and D2 decreased in an experimental block.

If participants indeed perceive meter in accordance with Longuet-Higgins and Lee (1984), we can expect that omissions on-the-beat are more salient than omissions off-the-beat. As a drawback of the current experimental paradigm, irrespective of whether EEG or pupillary measures are assessed, we cannot validly compare psychophysiological response to omissions in deviant patterns with the response in standard patterns: Not only their metrical position differs, but also both the sound that is omitted and the presentation frequency are different (Bouwer & Honing, 2012). Future studies could take this limitation into account, for example by presenting a bass drum omission off the beat (see also Bouwer et al., 2014).

Investigating the effect of musical expertise on beat perception, we found no evidence that higher musically sophistication leads to a more pronounced beat representation. This result suggests that beat perception is independent of musical expertise. This is in line with Bouwer et al. (2014), who found no difference in the MMN response to omissions between musicians and non-musicians. In contrast, Geiser et al. (2010) found that musicians were more sensitive to the metrical position of perceptual accents than non-musicians. However, the stimuli of Geiser et al. (2010) consisted of snare drum rhythms, whereas the stimuli in the current study consist of acoustically richer drum rhythms. The additional intensity and timbre information might make it easier to perceive the beat (Bouwer et al., 2014). In addition, it might be that musical expertise needs to be better specified. For example, Cicchini, Arrighi, Cecchetti, Giusti, and Burr (2012) demonstrated that percussionists show superior interval timing compared to non-percussionist musicians, indicating that the type of instrument played by the participant might play a role in rhythm perception. Finally, an effect of musical expertise might only be observed when participants are sampled from a broader range of expertise than the range present in a typical Psychology student population.

In summary, our results show that participants detected the beat while they attended to another task. In addition, we found that participants perceived a metrical hierarchy, in which the first beat is more salient than the second. Finally, we found that this unattended beat perception was independent of musical expertise.

4.2. Pupil reflects unattended surprise

To our knowledge, we are the first to show that pupil dilation is elicited by *unattended* surprising events. This finding suggests that the pupil dilation response is elicited by surprising stimuli relatively automatically. In addition, the different pupillary response to D1 and D2 shows that pupil dilation is modulated by the level of salience of an event.

The current finding that the pupil reflects the processing of stimuli that are not attended and not relevant to the task at hand provides further evidence for the role of the pupil as “a window to the preconscious” (Laeng et al., 2012). This is in contrast to Kamp and Donchin (2015), who suggested that detection of response conflict is crucial for eliciting a phasic pupillary response. Importantly, however, our finding that the pupil reflects the processing of unattended and irrelevant stimuli does not rule out that the pupil dilation magnitude is modulated by task-relevance as well as the need for a motor response. As one indication for the enhancing role of motor response on pupil dilation, Privitera, Renninger, Carney, Klein, and Aguilar (2010) found a larger pupil dilation when a button press was required when a visual target was detected, compared to the same detection task without a motor response. However, future studies are needed to further reveal the effect of both attention and response on pupil dilation.

Considering the hypothesis that the pupil is an indicator of activity in the locus coeruleus (LC), our findings are in line with studies showing that unexpected stimuli elicit larger phasic noradrenergic activity than frequent stimuli (Alexinsky, Aston-Jones, Rajkowski, & Revay, 1990; Dayan & Yu, 2006). In this way, the current study delivers further support for the proposed role of the LC-NA system as a signaller of the need for adapting the mental model of the environment (Nieuwenhuis, 2011). In addition, however, the current findings suggest that the LC-NA system also plays a role in signalling unattended expectancy violations.

Our results suggest that pupil dilation might reflect surprise in a similar way as the MMN: it is sensitive to different levels of salience without attention. However, two differences with previous MMN studies have to be considered. First, in contrast to Ladinig et al. (2009) and Bouwer et al. (2014), we found a difference in

response to different levels of salient beat omissions (D1 and D2). This finding suggests that pupil dilation might be more sensitive to different levels of expectancy violation than the MMN. An alternative explanation is that, as mentioned above, the shorter lengths of the presented audio stream in the current experiment might have made it easier to distinguish between the first and the second beat.

Second, whereas Ladinig et al. (2009) and Bouwer et al. (2014) found a MMN in response to both D1 and D2, we only found an increased pupillary response for D1. This finding suggests that, in contrast to the MMN, only highly salient violations elicit a pupillary response in the absence of attention. However, the lack of a pupillary response to D2 might also be due to a slightly different experimental setup: Whereas Ladinig et al. (2009) and Bouwer et al. (2014) used a deviant probability of 5% and 3.3% respectively, we employed a deviant probability of 10%. The higher deviant probability might decrease the salience of the deviant. As a second alternative explanation, the absence of a significant pupil dilation to D2 might be due to interfering pupillary responses to the visual detection task. That is, the dilated pupil as a response to a visual target might have decreased the overall responsiveness of the pupil to the auditory stimuli, preventing the weaker response to D2 from reaching significance. In support of this hypothesis, we found that a larger absolute pupil size at the onset of an omission (i.e., the baseline) resulted in a smaller pupillary response.

In summary, we found that pupil dilation reflects surprise in the absence of attention. This is in line with the hypothesis that the pupillary response can be driven by subconscious processing (Laeng et al., 2012). In comparison with earlier MMN studies, we found that the pupil might be more sensitive to different levels of salience as we found that the pupil only responded to the most salient expectancy violation and not to weaker violations.

5. Conclusions

In this study, we observed that participants were able to perceive beat and hierarchical meter while paying attention to another task. This indicates that beat perception is an automatic process that requires minimal attentional resources. In addition, we found that hierarchical beat perception is independent of musical expertise, providing further evidence that beat perception is a general, widespread cognitive ability. Finally, our results show that pupil dilation reflects surprising events in the absence of attention, indicating that pupil size is an accessible index of subconscious processing.

Acknowledgements

We thank Mathanja Verkaik for her help in conducting the experiment and Florian Sense for his assistance with the Bayesian analyses. This research has been partially supported by EU FET Proactive grant TIMESTORM - Mind and Time: Investigation of the Temporal Traits of Human-Machine Convergence. This sponsors of this study had no influence on the design of the study, nor on the interpretation or dissemination of the results.

References

- Ahern, S., & Beatty, J. (1979). Pupillary responses during information processing vary with Scholastic Aptitude Test scores. *Science*, 205(4412), 1289–1292.
- Alexinsky, T., Aston-Jones, G., Rajkowski, J., & Revay, R. S. (1990). Physiological correlates of adaptive behavior in a visual discrimination task in monkeys. *Society for Neuroscience Abstracts*, 16, 164.
- Aston-Jones, G., & Cohen, J. D. (2005). An integrative theory of locus coeruleus-norepinephrine function: Adaptive gain and optimal performance. *Annual Review of Neuroscience*, 28, 403–450.
- Bates, D., Maechler, M., & Bolker, B. (2012). lme4: Linear mixed-effects models using Eigen and Eigen. *Journal of Statistical Software*, 65, 1–68.

- Bijleveld, E., Custers, R., & Aarts, H. (2009). The unconscious eye opener pupil dilation reveals strategic recruitment of resources upon presentation of subliminal reward cues. *Psychological Science*, 20(11), 1313–1315.
- Bouwer, F., & Honing, H. (2012). Rhythmic regularity revisited: Is beat induction indeed pre-attentive? In *Proceedings of the 12th international conference on music perception and cognition and the 8th triennial conference of the European Society for the cognitive sciences of music* (pp. 122–127).
- Bouwer, F. L., Van Zuijlen, T. L., & Honing, H. (2014). Beat processing is pre-attentive for metrically simple rhythms with clear accents: An ERP study. *PLoS One*, 9(5), e97467.
- Chapin, H. L., Zanto, T., Jantzen, K. J., Kelso, S., Steinberg, F., & Large, E. W. (2010). Neural responses to complex auditory rhythms: The role of attending. *Frontiers in Psychology*, 1, 224.
- Chen, J. L., Penhune, V. B., & Zatorre, R. J. (2008). Moving on time: Brain network for auditory-motor synchronization is modulated by rhythm complexity and musical training. *Journal of Cognitive Neuroscience*, 20(2), 226–239.
- Cicchini, G. M., Arrighi, R., Cecchetti, L., Giusti, M., & Burr, D. C. (2012). Optimal encoding of interval timing in expert percussionists. *The Journal of Neuroscience*, 32(3), 1056–1060.
- Coull, J. T., Büchel, C., Friston, K. J., & Frith, C. D. (1999). Noradrenergically mediated plasticity in a human attentional neuronal network. *NeuroImage*, 10(6), 705–715.
- Dayan, P., & Yu, A. J. (2006). Phasic norepinephrine: A neural interrupt signal for unexpected events. *Network: Computation in Neural Systems*, 17(4), 335–350.
- Donchin, E. (1981). Surprise! ... surprise? *Psychophysiology*, 18(5), 493–513.
- Endedijk, H. M., Ramenzoni, V. C., Cox, R. F., Cillessen, A. H., Bekkering, H., & Hunnius, S. (2015). Development of interpersonal coordination between peers during a drumming task. *Developmental Psychology*, 51(5), 714.
- Friedman, D., Hakerem, G., Sutton, S., & Fleiss, J. L. (1973). Effect of stimulus uncertainty on the pupillary dilation response and the vertex evoked potential. *Electroencephalography and Clinical Neurophysiology*, 34(5), 475–484.
- Geiser, E., Sandmann, P., Jäncke, L., & Meyer, M. (2010). Refinement of metre perception–training increases hierarchical metre processing. *European Journal of Neuroscience*, 32(11), 1979–1985.
- Geiser, E., Ziegler, E., Jancke, L., & Meyer, M. (2009). Early electrophysiological correlates of meter and rhythm processing in music perception. *Cortex*, 45(1), 93–102.
- Granholm, E., Asarnow, R. F., Sarkin, A. J., & Dykes, K. L. (1996). Pupillary responses index cognitive resource limitations. *Psychophysiology*, 33(4), 457–461.
- Hamel, R. F. (1974). Female subjective and pupillary reaction to nude male and female figures. *The Journal of Psychology*, 87(2), 171–175.
- Hannon, E. E., & Trehub, S. E. (2005). Metrical categories in infancy and adulthood. *Psychological Science*, 16(1), 48–55.
- Hess, E. H., & Polt, J. M. (1960). Pupil size as related to interest value of visual stimuli. *Science*, 132(3423), 349–350.
- Hoeks, B., & Levelt, W. J. (1993). Pupillary dilation as a measure of attention: A quantitative system analysis. *Behavior Research Methods, Instruments, & Computers*, 25(1), 16–26.
- Honing, H. (2012). Without it no music: Beat induction as a fundamental musical trait. *Annals of the New York Academy of Sciences*, 1252(1), 85–91.
- Honing, H., Bouwer, F. L., & Håden, G. P. (2014). Perceiving temporal regularity in music: The role of auditory event-related potentials (ERPs) in probing beat perception. In *Neurobiology of interval timing* (pp. 305–323). New York: Springer.
- Honing, H. (2013). Structure and interpretation of rhythm in music. In D. Deutsch (Ed.), *Psychology of music* (3rd ed., pp. 369–404). London: Academic Press/Elsevier.
- Huron, D. (2006). *Sweet anticipation: Music and the psychology of expectation*. Cambridge, MA: MIT Press.
- Isreal, J. B., Chesney, G. L., Wickens, C. D., & Donchin, E. (1980). P300 and tracking difficulty: Evidence for multiple resources in dual-task performance. *Psychophysiology*, 17(3), 259–273.
- Jeffreys, H. (1961). *The theory of probability* (3rd ed.). Oxford, U.K.: Oxford University Press.
- Kahneman, D. (1973). *Attention and effort*. Englewood Cliffs, NJ: Prentice-Hall.
- Kamp, S. M., & Donchin, E. (2015). ERP and pupil responses to deviance in an oddball paradigm. *Psychophysiology*, 52(4), 460–471.
- Kononowicz, T. W., & van Rijn, H. (2014). Decoupling interval timing and climbing neural activity: A dissociation between CNV and N1P2 amplitudes. *The Journal of Neuroscience*, 34(8), 2931–2939.
- Ladinig, O., Honing, H., Håden, G., & Winkler, I. (2009). Probing attentive and pre-attentive emergent meter in adult listeners without extensive music training. *Music Perception*, 26(4), 377–386.
- Ladinig, O., Honing, H., Håden, G., & Winkler, I. (2011). Erratum to Probing attentive and pre-attentive emergent meter in adult listeners with no extensive music training. *Music Perception*, 28(4), 444.
- Laeng, B., Sirois, S., & Gredebäck, G. (2012). Pupillometry a window to the preconscious? *Perspectives on Psychological Science*, 7(1), 18–27.
- Laeng, B., Waterloo, K., Johnsen, S. H., Bakke, S. J., Låg, T., Simonsen, S. S., & Høgsæt, J. (2007). The eyes remember it: Oculography and pupillometry during recollection in three amnesic patients. *Journal of Cognitive Neuroscience*, 19(11), 1888–1904.
- Large, E. W., & Kolen, J. F. (1994). Resonance and the perception of musical meter. *Connection Science*, 6(2–3), 177–208.
- Lerdahl, F., & Jackendoff, R. (1983). *A generative theory of tonal music*. Cambridge, MA: MIT Press.
- Longuet-Higgins, H. C., & Lee, C. S. (1984). The rhythmic interpretation of monophonic music. *Music Perception: An Interdisciplinary Journal*, 1(4), 424–441.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG data. *Journal of Neuroscience Methods*, 164(1), 177–190.
- Morey, D., Rouder, J. N., & Jamil, T. (2014). BayesFactor: Computation of Bayes factors for common designs (R package version 0.9.8). Retrieved from <http://CRAN.R-project.org/package=BayesFactor>.
- Müllensiefen, D., Gingras, B., Musil, J., & Stewart, L. (2014). The musicality of non-musicians: An index for assessing musical sophistication in the general population. *PLoS One*, 9(2), e89642.
- Näätänen, R., Gaillard, A. W., & Mäntysalo, S. (1978). Early selective-attention effect on evoked potential reinterpreted. *Acta Psychologica*, 42(4), 313–329.
- Näätänen, R., Paavilainen, P., Rinne, T., & Alho, K. (2007). The mismatch negativity (MMN) in basic research of central auditory processing: A review. *Clinical Neurophysiology*, 118(12), 2544–2590.
- Näätänen, R., Paavilainen, P., Titinen, H., Jiang, D., & Alho, K. (1993). Attention and mismatch negativity. *Psychophysiology*, 30(5), 436–450.
- Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, 15(1), 1–25.
- Nieuwenhuis, S. (2011). Learning, the P3, and the locus coeruleus-norepinephrine system. In *Neural basis of motivational and cognitive control* (pp. 209–222). Cambridge, Mass: MIT Press.
- Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3, and the locus coeruleus–norepinephrine system. *Psychological Bulletin*, 131(4), 510–532.
- Nozaradan, S. (2014). Exploring how musical rhythm entrains brain activity with electroencephalogram frequency-tagging. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 369(1658), 20130393.
- Otten, L. J., Alain, C., & Picton, T. W. (2000). Effects of visual attentional load on auditory processing. *NeuroReport*, 11(4), 875–880.
- Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, 118(10), 2128–2148.
- Preusschoff, K., Marius't Hart, B., & Einhäuser, W. (2011). Pupil dilation signals surprise: Evidence for noradrenaline's role in decision making. *Frontiers in Neuroscience*, 5(115), 1–12.
- Privitera, C. M., Renninger, L. W., Carney, T., Klein, S., & Aguilar, M. (2010). Pupil dilation during visual target detection. *Journal of Vision*, 10(10), 3.
- Sara, S. J. (2009). The locus coeruleus and noradrenergic modulation of cognition. *Nature Reviews Neuroscience*, 10(3), 211–223.
- Schröger, E., & Winkler, I. (1995). Presentation rate and magnitude of stimulus deviance effects on human pre-attentive change detection. *Neuroscience Letters*, 193(3), 185–188.
- Steinhauer, S. R., & Zubin, J. (1982). Vulnerability to schizophrenia: Information processing in the pupil and event-related potential. In *Biological markers in psychiatry and neurology* (pp. 371–385). Pergamon Press Inc.
- Tamietto, M., Castelli, L., Vighetti, S., Perozzo, P., Geminiani, G., Weiskrantz, L., & Gelder, B. (2009). Unseen facial and bodily expressions trigger fast emotional reactions. *Proceedings of the National Academy of Sciences*, 106(42), 17661–17666.
- van Rijn, H., Dalenberg, J. R., Borst, J. P., & Sprenger, S. A. (2012). Pupil dilation covaries with memory strength of individual traces in a delayed response paired-associate task. *PLoS One*, 7(12), e51134.
- Verney, S. P., Granholm, E., & Marshall, S. P. (2004). Pupillary responses on the visual backward masking task reflect general cognitive ability. *International Journal of Psychophysiology*, 52(1), 23–36.
- Vogelzang, M., Hendriks, P., & van Rijn, H. (2016). Pupillary responses reflect ambiguity resolution in pronoun processing. *Language, Cognition and Neuroscience*, 31(7), 876–885.
- Vuust, P., Gebauer, L. K., & Witek, M. A. (2014). Neural underpinnings of music: The polyrhythmic brain. In *Neurobiology of interval timing* (pp. 339–356). New York: Springer.
- Vuust, P., Pallesen, K. J., Bailey, C., Van Zuijlen, T. L., Gjedde, A., Roepstorf, A., & Østergaard, L. (2005). To musicians, the message is in the meter. Pre-attentive neuronal responses to incongruent rhythm are left-lateralized in musicians. *NeuroImage*, 24, 560–564.
- Weiskrantz, L., Cowey, A., & Barbur, J. L. (1999). Differential pupillary constriction and awareness in the absence of striate cortex. *Brain*, 122(8), 1533–1538.
- Wierda, S. M., van Rijn, H., Taatgen, N. A., & Martens, S. (2012). Pupil dilation deconvolution reveals the dynamics of attention at high temporal resolution. *Proceedings of the National Academy of Sciences*, 109(22), 8456–8460.
- Willems, C., Damsma, A., Wierda, S. M., Taatgen, N., & Martens, S. (2015). Training-induced changes in the dynamics of attention as reflected in pupil dilation. *Journal of Cognitive Neuroscience*, 27(6), 1161–1171.
- Winkler, I., Håden, G. P., Ladinig, O., Sziller, I., & Honing, H. (2009). Newborn infants detect the beat in music. *Proceedings of the National Academy of Sciences*, 106(7), 2468–2471.
- Wolff, M. J., Scholz, S., Akyürek, E. G., & van Rijn, H. (2015). Two visual targets for the price of one? Pupil dilation shows reduced mental effort through temporal integration. *Psychonomic Bulletin & Review*, 22, 251–257.
- Zylberberg, A., Oliva, M., & Sigman, M. (2012). Pupil dilation: A fingerprint of temporal selection during the “Attentional Blink”. *Frontiers in Psychology*, 3, 1–6.