Trends in Neurosciences

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Forum

The forgotten wave of early pupillometry research

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Changes in pupil size offer a rich, continuous, and integrated neurophysiological readout of attention and cognition. I here briefly reintroduce examples of a vast, forgotten literature, full of inspiring ideas, which described attentional modulations of pupil size decades earlier than often assumed. I outline parallels between these early studies and recent developments in pupillometry.

Pupillometry as a neuroscientific method: a rediscovery

Pupil size is modulated by cognition and attention, including attentional alerting, orienting, and executive functioning. Alerting-linked pupil size changes are commonly thought to have been first scientifically described in the 1960s, whereas attentional modulations of the pupil light response and pupil near response linked to executive functioning are often thought to be a discovery of the past 15 years or so. A closer look at the historical literature, however, reveals that neither is correct. Around 1900, pupillometry was no niche method; it was employed by a large number of early-day psychologists and pioneering neuroscientists, including laboratories such as those of Wilhelm Wundt, Vladimir Bekhterev, Oswald Bumke, and Carl Westphal [1,2] with research groups in Germany, Russia, Switzerland, Poland, France, and other countries.

Here, I highlight examples of this vast and often overlooked body of literature that continues to reveal fascinating insights and provide inspiration for future research, underscoring the longstanding tradition of pupillometry as a neuroscientific method. In the tradition of Irene Loewenfeld's foundational book [1], I connect these early studies to current understanding and recent developments in pupillometry. In the following sections, I introduce these studies in an order that approximately follows the framework proposed in [3], and Table 1 summarizes factors affecting pupil size, progressing from low- to high-level responses (based on [3]). For more in-depth and comprehensive reviews, I recommend Loewenfeld's [1] and Bumke's [2] books, as well as [3] for an overview of more recent studies.

Alerting-linked responses

Many neuroscientists study pupil size due to its covariation with alerting and vigilance states. More specifically, pupil size scales with the changes in alerting that accompany changes in mental or physical effort, with separate effects on baseline and evoked pupil sizes. In his 1911 book, Bumke [2] astutely summarized existing work: 'every vivid mental event, every mental effort, every impulse of the will, whether it results in a muscular action or not, every tensing of attention, every vivid imagination whatever the content, and namely every affect causes a dilation of the pupil just as much as every sensitive stimulus flowing to the brain from the periphery' (pp. 60–61; translated by C. Strauch[i]). In 1875, it was observed that cats and dogs exhibited stronger pupil dilations in response to more intense tactile stimulation, earning the pupil the label of the 'finest physiological aesthesiometer' and an excellent indicator of sensitivity [4]. The remarkable sensitivity of the pupil to even the smallest fluctuations in the alerting system continues to provide important insights in modern research. For instance, alerting-linked transient pupil dilations during encoding of continuous information can signal event boundaries that form the basis for the segmentations between adjacent episodes in later memory [5]. Pupil size can even pick up the subtle effort needed to plan eye movements. These tiny 'cost' differences across different types of eye movements predict saccade preferences, demonstrating that oculomotor selection considers (and minimizes) effort expenditure to select eye movements [6].

Attentional modulations of pupil light response and pupil near response

Executive functions, including the allocation of focal, top-down attention, influence pupil responses. Among the most exciting developments in the use of pupillometry to study attention of the past two decades is the finding that both the pupil light response and the pupil near response are attentionally modulated: responses are stronger the more attention is paid. Higher-level attention hereby affects pupil dilation in a cascading manner by modulating lower-level and intermediate-level circuits and responses (also including attentional orienting responses; see [3]).

In 1885, over a century before its present-day (re)discovery, Otto Haab [7] described how covert attention to differently luminant locations in space modulates pupil size: during constant fixation on a spot in an otherwise dark room, directing covert attention to a laterally positioned candle lets the pupil constrict, whereas directing it to a dark part of the visual field lets the pupil redilate. This finding was heavily contested (as discussed in [2,3]) with both unsuccessful and successful independent replication attempts for both dark and bright stimuli [8], a phenomenon referred to as Haab's cortical reflex or the Haab–Piltz effect. Because of these effects, Haab suggested that the cortex must be involved with the pupil light response, despite this response being widely regarded – both before and after Haab's suggestion – as a strictly subcortical reflex. As of 1999, Loewenfeld remained highly skeptical of these reports [1]. Many studies of the past

Table 1. Pupil size is affected by changes in brightness, focal distance, and attention

	Type of pupil response
Low-level responses	• Pupil light response: constrictions in response to increases in brightness, dilations in response to decreases in brightness; stronger and more sustained responses to blue compared with red light • Pupil near response: constrictions for short (near) focal distance, redilations for long (far) focal distance
Intermediate-level responses	• Pupil orienting response: transient fast dilations in response to incoming stimuli. Transient constrictions in response to changes in visual input; the amplitude scales with visual sensitivity and attention paid to the causal event • Alerting/effort response: baseline pupil size adjusts according to alerting/vigilance states. Evoked pupil sizes scale with such changes in the alerting system that accompany changes in effort or the 'intensity of attention'
High-level responses	• Attentional modulation of pupil light response and pupil near response: imagery and perception of brightness and focal distance lead to similar albeit reduced responses as changes in physical stimuli (bright/dark, near/far)

15 years (see [3] for an overview) have since helped to (re)establish this phenomenon. Together, these more recent works demonstrate that Haab was correct: the pupil light response is influenced by covert attention and can therefore be used to measure it.

Attentional modulations of the pupil light response can also be triggered by imagination or perception: imagining bright objects, such as the sun, lets the pupil constrict, whereas imagining dark objects lets the pupil dilate ([3], and see reference [8] from 1899). An impressive example of this effect is a case study from the 1920s of a person who fully lost vision in childhood and could consistently constrict pupils by imagining bright objects, such as snow or the sun more than a decade after losing eyesight. Perhaps due to differences in imagery strength, this effect was not consistently observed in a small number of other blind individuals at the time [9]. Effects of imagery on the pupil light response were described to scale with the vividness of imaginations, in turn providing a measure of the imagery content and strength. Recently, this idea resurfaced, showing tight coupling between the vividness of imaginations and pupillary responses. The absence of such modulations can even provide a physiological readout of aphantasia, the inability to picture things mentally [10]. As illusionary higher brightness or interpreting an equiluminant stimulus as sun over a moon lets the pupil constrict as well (see [3]), the pupil light response must be modulated by attention.

Attention affects the pupil near response in a similar way to the pupil light response [3,11]. Imagining or recalling near objects constricts the pupil, whereas imagining or recalling distant objects dilates the pupil [11]. Such effects, to the author's knowledge, have been (re)discovered only recently ([11]; see [12] for a brief note of the phenomenon in 1849), for both the imagination of near/distant stimuli and illusionary differences in depth. This demonstrates that both types of low-level pupil responses are attentionally modulated, as recognized by Samuel Goldflam in 1922 [9]. Furthermore, these effects critically support the sensory recruitment account that proposes sensory areas specialized in perceiving and encoding to be active when working memory is used [11,12]: the pupil changes size, albeit less so, in a similar way during imagination as during perception.

Concluding remarks

To conclude, pupillometry has been known and well studied as a neuroscientific measure for well over a century, with remarkable parallels between some of the overlooked early studies and current work. With this forum article, I hope to reinvigorate interest in this fascinating historical literature, which may help to foster synergies of past and present-day work to inspire future studies using pupillometry.

Acknowledgments

I thank my colleagues Stefan Van der Stigchel, Leon Kenemans, Chris Paffen, Damian Koevoet, Evi Hendrikx, and Surya Gayet for comments and discussions.

Declaration of interests

The author declares no competing interests.

Resources

[i]https://doi.org/10.17605/OSF.IO/5JFRE

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https://doi.org/10.1016/j.tins.2024.06.002

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