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Department of Physiology and Pharmacology, Western University, London, ON, Canada.
*E-mail: andrew.pruszynski@uwo.ca

Correspondence

Spontaneous pupillary oscillations increase during mindfulness meditation

Antonella Pomè[1], David C. Burr[1,3], Annalisa Capuozzo[1], and Paola Binda[2]

A significant body of literature has shown that pupil size varies with cognitive and perceptual states [1,2]. Furthermore, the pupil diameter oscillates spontaneously at low frequencies, sometimes referred to as *pupillary hippus* [3,4]. Oscillation amplitude varies with many neural factors, including arousal and cortical excitability. Here we show that pupillary oscillations are modulated by mindfulness meditation, increasing by 53% compared to pre- and post-meditation baselines. The effect occurs only in trained meditators and is specific for low frequencies (below 1 Hz), with delta frequencies (1–5 Hz) unchanged. The study suggests that pupil size may be a useful marker of the altered cortical state during meditation.

We measured pupillary oscillations in a group of trained mindfulness-meditators before, during, and after a short period of meditation, with eyes open (see Supplemental Information for details of methods and example traces). Figure 1A shows the Fourier power of the dynamics of pupil size, averaged over all meditators, during baseline (average of before and after meditation: dark-grey trace) and meditation (red trace). The red trace clearly falls above the grey at low frequencies (<1 Hz, the hippus range), then becomes intertwined with baseline at higher frequencies (delta range).

Figure 1B shows average power in the low-frequency (Hippus) range before, during and after meditation. The meditation-induced effect was large and highly significant (Repeated measures Bayesian ANOVA: $F(2,19) = 7.8$, $p = 0.001$, log-BF = 1.38: strong evidence in favour). Hippus power measured during meditation was significantly higher than both baselines, before and after meditation ($t(23) = -3.57$, $p = 0.002$, log-BF = 1.36; $t(19) = 3.63$, $p = 0.002$, log-BF = 1.34, respectively), whereas there was no significant difference between the two baselines ($t(19) = -0.68$, $p = 0.50$, log-BF = –0.54). Conversely, average power in the adjacent Delta range (Figure 1D) was unaffected by meditation (ANOVA: $F(2,19) = 2.0$, $p = 0.15$, log-BF = –0.22).

To control that the effects were specific for meditation, we repeated the experiment with 20 participants who had never meditated, asking them simply to relax and listen to the meditation track. We found no significant change in Hippus in these participants (Figure 1C: Bayesian ANOVA: $F(2,19) = 0.01$, $p = 0.99$, log-BF = –0.87). Direct between-group comparison shows that the Hippus power change in meditators was significantly higher than in non-meditators (two-sample $t(42) = 2.71$, $p < 0.01$, log-BF = 0.61).

Figures 1E and F show individual results for meditators and non-meditators, plotting meditation-induced Hippus power change against pupil diameter change (both expressed as percentages of baseline values). For 20 of the 24 meditators the change in Hippus was positive. The increase (53%) is highly significant ($t(23) = 4.14$, $p < 0.001$, log-BF = 1.9, clear from the shaded 95% confidence limits shown as shaded blue regions. On the other hand, half of the 20 non-meditators showed a negative effect, and the average change was not significantly different from zero ($t(19) = 1.05$, $p = 0.30$, log-BF = –0.42).

The abscissae of Figures 1E and F show the change of average pupil diameter compared with baseline. For both groups, the pupil constricted during 'meditation' by a similar amount (–7% in meditators: $t(23) = -4.23$, $p = 0.001$, log-BF = 1.98; –4% in controls: $t(19) = -3.42$, $p = 0.003$, log-BF = 1.16; between group comparison: two-sample $t(42) = 1.29$, $p = 0.203$, log-BF = –0.45). Importantly, the pupil constriction did not correlate with the increase in Hippus power, for either group (meditators: $r = -0.17$, $p = 0.4$, log-BF = –0.7; controls: $r = -0.20$, $p = 0.4$, log-BF = –0.62). Furthermore, the constriction effect in meditators was driven only by the difference in the pre-meditation baseline ($t(23) = 5.06$, $p < 0.001$, log-BF = 2.79), probably due to dark-adaptation, with no significant difference between measurements during and after meditation ($t(19) = -1.78$, $p = 0.091$, log-BF = –0.06: Figure S1 in the Supplemental Information). All the evidence suggests that the

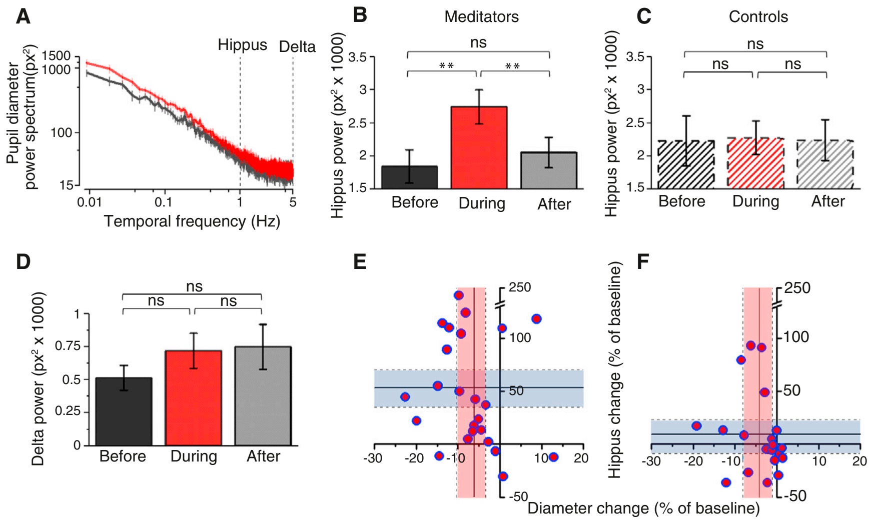

Figure 1. Pupillary oscillations in the hippus and delta ranges.
(A) Mean power spectrum of pupil oscillations, averaged over all 24 meditators. Red shows recordings during meditation, dark grey during baseline (average of before and after). (B) Average Fourier power in the Hippus range (0–1 Hz) for meditation group, before (black), during (red) and after meditation (grey). Significance values refer to paired t-tests (*$p < 0.05$; **$p < 0.01$, ns $p > 0.5$). (C) Average Fourier power in the Hippus range in a group of non-meditators following the same procedure. (D) Average Fourier power in the Delta range (1–5 Hz) for the meditation group. (E) Scatter plot of normalized change in hippus power against normalized change in pupil diameter for the meditators. The shaded areas show 95% confidence limits. (F) Same as E for the non-meditators.

meditation-induced changes in Hippus are independent of, and therefore not driven by, changes in average pupil diameter.

Lastly, we looked for correlations between the increase in Hippus power during meditation and several self-reported indices of meditative practice, including weekly hours of meditation, years of meditative practice and MAAS score: none of the correlations were significant (hours/week: $r = 0.30$, $p = 0.16$, log-BF = –0.38; years: $r = -0.12$, $p = 0.56$, log-BF = –0.73; MAAS: $r = -0.26$, $p = 0.29$, log-BF = –0.50).

Meditation can change several physiological variables (see Supplemental Information), as well as cognitive [5] and perceptual dynamics [6]. The current research shows that spontaneous low-frequency oscillations of pupil size also increase. It is generally assumed that pupil oscillations are driven by the dynamic balance between sympathetic and parasympathetic activity [7]. Many studies suggest that a key link between the autonomic nervous system and pupil diameter is the Locus Coeruleus, the activity of which has been shown to correlate with pupil dilations [8], as well as with several indices of autonomic activity. It is possible that meditation induces a generalized change of autonomic activity, and pupillometry can serve as a reliable and accessible index for measuring the change.

Recent studies are beginning to unravel a link between spontaneous pupil oscillations and cortical activity. In mice, where neural activity can be recorded directly, the changes in pupil diameter have been associated with changes in the excitability of sensory cortical areas [9], broadly consistent with the concept that slow pupil oscillations may be accompanied by increased receptivity towards sensory stimuli. In turn, this is consistent with studies showing that increases in slow pupillary oscillations in humans are associated with cortical plasticity [10], known to be tightly linked with cortical excitability. This could be linked to the positive effects of meditation on learning and attention management [5] — but such links remain speculative at this point.

Given the simplicity, non-invasiveness (light-weight glasses) and low-cost of the apparatus, pupillometry could become a useful tool to non-invasively monitor internal cortical states and validate subjective reports. It may also serve as a learning tool for meditation, providing novices with objective feedback. Conversely, meditation may serve as a useful experimental procedure to manipulate cortical states in order to study the neural mechanisms driving spontaneous pupillary oscillations, and investigate how these relate to EEG, heart-rate, breathing and other major physiological parameters.

SUPPLEMENTAL INFORMATION

Supplemental Information includes experimental procedures, supplemental results, supplemental discussion, one figure and one table and can be found with this article online at https://doi.org/10.1016/j.cub.2020.07.064.

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[1]Department of Nerofarba, University of Florence, Firenze, Italy. [2]Department of Translational Research, University of Pisa, Pisa, Italy. [3]Lead contact.
E-mail: Antonella.pome@unifi.it (A.P.); davidcharles.burr@unifi.it (D.C.B.); annaclisa@gmail.com (A.C.); paola.binda@unipi.it (P.B.)