Global and selective effects of auditory attention on arousal: insights from pupil dilation

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Abstract

This study investigated the interplay between attention and arousal in humans by measuring pupil dilation as a function of task engagement and stimulus relevance. Arousal in response to task-relevant and unexpected irrelevant sounds was measured in healthy young adults during the performance of an auditory detection task, the Competitive Attention Test, and in sensory matched passive conditions. Attention was manipulated using informative and uninformative visual cues. Both relevant and irrelevant sounds elicited a larger increase in pupil dilation in the active compared to the passive condition, revealing a global effect of task engagement on arousal. Additionally, in the active condition, the pupil dilation amplitude during the anticipation and detection of the task-relevant sound was greater following an informative compared to an uninformative cue, while no cue effect was found on the pupil dilation response to distracting sounds. This finding suggests that arousal can be selectively enhanced by attention for task-relevant, but not -irrelevant, events.

Declarations

Ethics approval statement

The experimental paradigm was approved by a French ethical committee, Comité de Protection des Personnes Sud-Est IV, number 11/90, authorization B11291-10. All participants gave written informed consent (according to the Declaration of Helsinki).

Availability of data and materials

The dataset supporting the conclusions of this article will be available in the OSF repository of the corresponding author.

Competing interests

The authors declare that they have no competing interests.

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Introduction

Efficient attention abilities and optimal level of arousal are critical to adapt to the ever-changing environment (Kahneman, 1973; Howels et al., 2012). Arousal is defined as one's physiological state of alertness or reactivity (Broadbent, 1971; Kahneman, 1973; Coull, 1998; Näätänen, 1992; Sturm & Willmes, 2001), and more recently, has been related to a general state of cortical excitation, considered to be driven by the activity of the locus coeruleus - norepinephrine (LC-NE) system (Aston-Jones & Cohen, 2005; Nieuwenhuis et al., 2011). The LC is a brainstem neuromodulatory nucleus responsible for most of the NE release in the brain through widespread projections to the entire neocortex (Berridge & Waterhouse, 2003). A moderate level of arousal has been shown to result in improved cognitive performance, whilst reduced and enhanced levels of arousal lead to distractibility (Yerkes & Dodson, 1908; Easterbrook, 1959). Attention enables us to prioritize and focus on relevant information, while still processing irrelevant stimuli, allowing us to stay aware of - but yet not distracted by – unexpected events in our environment. Achieving this requires a good balance between mechanisms that facilitate or inhibit the processing of task-relevant and -irrelevant information. Therefore, attention would control the allocation of resources to the processing of specific events (task-relevant rather than -irrelevant); while task engagement is defined as the allocation and focusing of attentional resources to a given task (Tops and Boksem, 2010). Importantly, attention and arousal alterations are strongly associated with numerous neurodevelopmental and neurovegetative disorders, profoundly impacting autonomy and well-being (for examples, Malhotra, 2019; Ohm et al., 2020). Understanding the dynamic interplay between attention and arousal is thus essential to propose robust measurements of these components in clinical settings and develop patient-specific therapeutic solutions.

Most theoretical and physiological models of attention have emphasized an interplay between attention and arousal. Kahneman (1973) proposed a capacity model of attention, including both transient (i.e., phasic) and sustained (i.e., tonic) arousal. This model suggests that available attentional capacities and arousal dynamically influence each other to achieve optimal performance. This model also considers the orienting response toward novel stimuli as resulting from the involuntary allocation of attention to these stimuli and from a transient increase in arousal (see also Näätänen (1992) for a similar proposal). Later, Broadbent (1971) and Eysenck (1982) proposed theories of arousal by distinguishing between two systems: a passive, low-level physiological arousal system, and an active, high-level cognitive arousal system. They proposed that the arousal level of the passive system fluctuates during task performance and can be actively regulated by the cognitive system to achieve and sustain an optimal global arousal level for improving task performance. Importantly, recent theories suggested that arousal could play a more specific role in improving

selective attention (Dahl et al., 2022). Indeed, arousal, through NE release, could *selectively* facilitate the processing of relevant stimuli by suppressing only weak and random neuronal activities and not strong neuronal activities (Mather et al. 2016).

The interplay between attention and arousal is also supported by anatomical brain connections. Experimental studies, mostly in rodents and monkeys, showed widespread projections from the LC-NE system to the cerebral cortex, the cerebellum, and subcortical structures (thalamus, amygdala) (Berridge & Waterhouse, 2003). Conversely, attention control is supported by brain networks, including frontal and parietal regions (Corbetta & Shulman, 2002; Posner & Peterson, 1990), with descending connections toward the locus coeruleus (Corbetta et al., 2008; Schwarz et al., 2015; Breton-Provencher & Sur, 2019; Totah et al., 2021). However, to date, the functional interplay between attention and arousal remains poorly understood as there are only a few non-invasive methods allowing to measure deep brain activity within structures such as the LC in humans.

Physiological markers such as heart rate, skin conductance, and pupil dilation are considered as indirect measures of arousal level (Berntson, 2007; Wang et al., 2018). Among them, pupil dilation can be considered the most sensitive method to investigate the relationship between arousal and attention during task performance, as pupil dilation has previously been related to the LC-NE activity in animal models (Aston-Jones & Cohen, 2005; Gilzenrat et al., 2010; Joshi et al., 2016). Particularly, baseline changes in pupil size would be related to tonic activity in the LC, associated with tonic arousal, which has extensively been associated with sustained alertness and task engagement (Aston-Jones & Cohen, 2005; Gilzenrat et al., 2010; Jepma & Nieuwenhuis, 2011; Murphy et al., 2014; Unsworth & Robison, 2016, 2018; Konishi et al., 2017). Furthermore, the stimulus-related pupil dilation response (PDR) would be related to the LC phasic activity and phasic arousal (Murphy et al., 2011; Wetzel et al., 2016). An increasing number of studies have investigated the relationship between attention and arousal using pupil dilation in the auditory modality (for review Zekveld 2018). Several studies showed that the PDR is larger to deviant or novel sounds compared to standard sounds in passive oddball paradigms (Friedman et al., 1973; Steiner & Barry, 2011; Hong et al., 2014; Korn & Bach, 2016; Wetzel et al., 2016; Marois et al., 2018; Marois & Vachon, 2018; Widmann et al., 2018; Bonmassar et al., 2020; Liao et al., 2016), in line with an increase in phasic arousal.

Hence, to study the interplay between arousal and attention, measuring pupil dilation during auditory attention tasks appears a promising avenue. In a first body of experiments, the effects of auditory attention on the PDR have been investigated by manipulating task demand, from passive to the most complex tasks. Asking participants to actively perform a task (by focusing and providing a motor response) or to passively follow the presentation of the same stimuli can be considered as the

experimental paradigm allowing the maximum contrast in terms of amount of attention required. The mean PDR to novel stimuli seemed to be larger in active than passive oddball conditions (though not statistically tested, Liao et al., 2016). By manipulating the task difficulty, some studies showed that the pupil dilation was larger for the most complex tasks (increased difficulty of tone discrimination: Kahneman and Beatty, 1967; words-in-noise identification task: Kramer et al., 2012). By manipulating attentional load, Lisi et al. (2015) showed a larger pupil dilation during multitasking than in a single task condition. Moreover, in several experiments using Posner visual cueing tasks to manipulate voluntary attention orienting, the amplitude of PDR toward targets increased (Dragone et al. 2018) or remained unchanged (Aminihajibashi et al. 2020) with increasing cue predictiveness. These studies, which vary the overall amount of attentional resources required for task performance, suggest that enhancing task engagement results in increased arousal.

Effects of auditory attention on the PDR could also be investigated by manipulating specifically stimulus relevance, i.e., exploring how attention facilitates or inhibits the PDR to task-relevant and -irrelevant stimuli. To date, only Liao et al. (2016) have investigated this question by manipulating attention during an audio-visual oddball paradigm: no difference in PDR amplitude was found in response to deviant sounds, regardless of whether they were task-relevant (attention directed to the auditory modality) or -irrelevant (attention directed to the visual modality). These limited findings raise questions about how the interplay between attention and arousal is mediated.

The present study is thus aimed at investigating the effect of attention on arousal, using pupillometry in Humans, as a function of both task engagement and stimulus relevance. The Competitive Attention Task (CAT), developed by Bidet-Caulet and collaborators (2015), is an auditory detection test, which allows to study arousal responses to both relevant and unexpected irrelevant events (Figure 1). In the CAT, voluntary attention orienting is modulated by manipulating the predictive value of the visual cue (informative vs. uninformative) preceding a target sound to be detected. Auditory distraction and phasic arousal are triggered by unpredictable task-irrelevant sounds (distracting sounds) presented at random times between the cue and the target. Here, the level of task engagement of participants was also manipulated by asking them to perform actively vs. being passively exposed to the same events of the task. The arousal level was indirectly assessed by measuring pupil dilation (Gilzenrat et al., 2010; Nieuwenhuis et al., 2011; Joshi et al., 2016). We hypothesized that increasing task engagement would result in larger PDR to all events. Furthermore, if the LC/NE does play a role in selective attention as previously suggested (for review see Dahl et al., 2022), increasing voluntary attention orienting should result in differential modulation of the PDR to task-relevant and -irrelevant events.

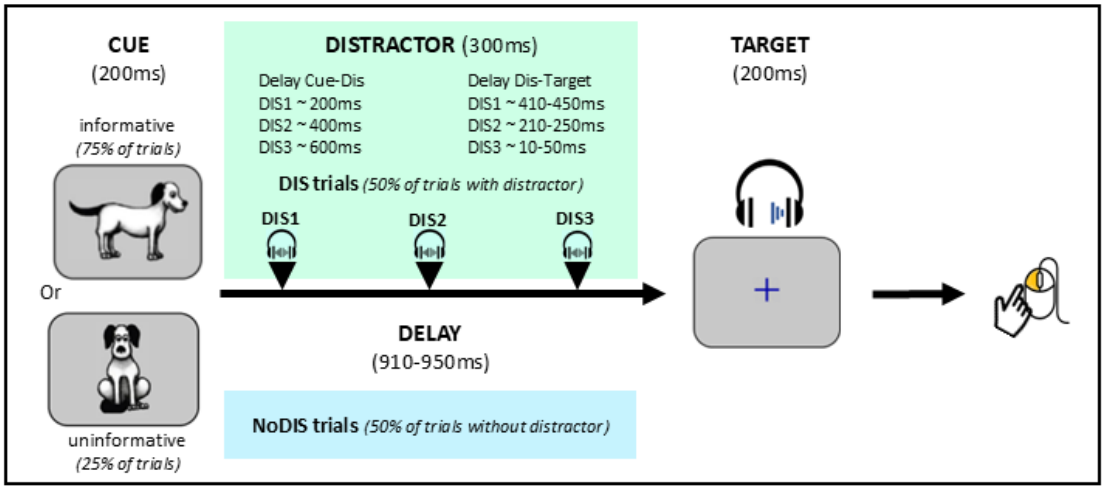

Figure 1. Protocol for active trials. All trials started with a visual cue (200ms duration) and contained a monaural target sound presented 910-950ms after cue offset. Subjects were asked to press the mouse button as fast as possible when they heard the target sound (a dog bark). In trials without distractor (NoDIS trials, 50%, blue box), only the cue and the target were presented. In trials with distractors (DIS trials, 50%, green box), a binaural distracting sound (300ms duration, symbolized by black triangles) was presented during the delay. The distracting sound could equiprobably pop up in three different time periods before the target onset: 410-450ms (DIS1), 210-250ms (DIS2), and 10-50 ms (DIS3) (see corresponding cue-distractor delays in the figure). In 75% of the (noDIS and DIS) trials, a dog facing left or right indicated in which ear (left or right) the target sound would be played (informative cue). In the other 25% of the trials, a dog facing front did not provide any indication in which ear the target sound would be played (uninformative cue).

Method

Participants

Twenty-three paid healthy adults participated in the experiment. Three participants were excluded because of poor data quality. Therefore, 20 participants (mean age ± standard deviation: 23.3 ± 3.8 years old; 12 female, 17 right-handed) were included in the analyses. All participants were free from any neurological or psychiatric disorder, had normal hearing and normal or corrected-to-normal vision, and did not take any substance (alcohol, drug, or medication) affecting the central nervous system during the 24 hours preceding the testing session. Finally, participants were instructed not to consume coffee or energy drinks for at least three hours before the testing session. All participants gave written informed consent. This study was conducted according to the Helsinki Declaration, Convention of the Council of Europe on Human Rights and Biomedicine, and the experimental paradigm was approved by a French ethics committee (Comité de Protection des Personnes Sud-Est IV, number 11/90, authorization B11291-10).

Stimuli

Here we used the same stimuli and trial structure than in previous study employing the CAT (Hoyer et al., 2021 & 2023a). All trials started with a visual cue (200ms duration) depicting a dog facing left, right or front, centrally presented on a grey background screen. Each trial also included a monaural target sound (200ms duration, 5ms rise-time and 5ms fall-time, 15 dB SL) corresponding to a dog bark played 910-950ms after cue offset. In trials without distractor (NoDIS trials, 50%), only the cue and the target were presented. In trials with distractor (DIS trials, 50%), a binaural distracting sound (300ms duration, 35 dB SL) was played during the cue-target delay. The distracting sound could equiprobably pop up in three different time periods before the target onset: 410-450ms (DIS1), 210-250ms (DIS2), and 10-50 ms (DIS3) (Figure1).

In 75% of the (noDIS and DIS) trials, a dog facing left (37.5%) or right (37.5%) indicated in which ear (left or right) the target sound would be played (informative cue). In the other 25% of the trials, a dog facing front did not provide any indication in which ear (left: 12.5% or right: 12.5%) the target sound would be played (uninformative cue).

A total of eighteen different sounds were used as distracting sounds (e.g., clock-alarm, phone ringtone). These sounds loudness was subjectively equalized by two listeners (Masson & Bidet-Caulet, 2019).

To compare responses to acoustically matched sounds, the same distracting sounds were played for each distractor occurrence condition (DIS1, DIS2, or DIS3) in the informative condition. Each distracting sound was played four times during the experiment, but no more than twice during each block to minimize habituation.

The inter-trial-interval duration (post target offset) was jittered between 3700 and 3900ms.

Task

The stimuli were presented to the participants either passively (passive condition, see below) or actively (Active Audio-Visual condition). Although the different stimuli serve as cues, targets, or distracting sounds only in the active condition, the same terminology is used for clarity in the passive conditions.

In the Active Audio-Visual condition (AAV), participants were instructed to perform a detection task by pressing a mouse button as fast as possible when they heard the target sound (i.e., the dog bark) and to ignore the distracting sounds. The AAV condition included 3 blocks of 48 trials (total with informative cue: 54 NoDIS, 18 DIS1, 18 DIS2, and 18 DIS3 trials; total with uninformative cue: 18 NoDIS, 6 DIS1, 6 DIS2 and 6 DIS3 trials).

In the Passive Audio-Visual condition (PAV), participants were instructed to passively watch and hear the same visual and auditory stimuli as in AAV, without providing any response. The PAV condition included 1 block of 48 trials (total with informative cue: 18 NoDIS, 6 DIS1, 6 DIS2 and 6 DIS3 trials; total with uninformative cue: 6 NoDIS, 2 DIS1, 2 DIS2, and 2 DIS3 trials).

Two additional passive blocks were added as control conditions. In the Passive Visual (PV) condition, only the visual cue was presented, in 24 trials (18 with informative cues and 6 with uninformative cues). Participants were instructed to passively watch the visual stimuli. In the Passive Auditory (PA) condition, only distracting and target sounds were presented, in 48 trials (24 NoDIS, 8 DIS1, 8 DIS2, and 8 DIS3 trials). Participants were instructed to passively listen to the sounds. Data from these control conditions are presented in supplementary data section (SupFigure1).

Procedure

Behavior

Participants were seated in a comfortable armchair at a 70-cm distance from a computer screen. All stimuli were delivered using Presentation software (Neurobehavioral Systems, Albany, CA, USA), which was also used to record the timing of behavioral responses. Sounds were delivered through circumaural headphones (Sennheiser 280HD). First, participants performed the PV block. Second, the

auditory threshold was determined for the target sound, in each ear, for each participant using the Bekesy tracking method, later allowing to present the target sound at 15dB SL and the distractor at 30 dB SL. Third, participants performed the PA and PAV blocks. Finally, they performed a short AAV training (10 trials), and three AAV blocks.

All participants performed the experimental blocks in the same order (PV, PA, PAV, AAV), but trials within blocks were pseudo-randomized differently for each participant to limit sequence effects.

The total duration of the experiment was 1h.

Pupillometry

The pupil size of one eye (right: 13; left: 7) was recorded during each block using an eye-tracking system (Eyelink 1000) in arbitrary units (au) in a room with controlled luminosity. The illumination at proximity of the participants was around 7.5 lux. Participants were placed at a 79 cm distance from the eye-tracker which was set up in a remote mode at a sampling rate of 500 Hz. Each block started with a five-point eye-tracker calibration followed by a five-point validation procedure. Participants were instructed to blink naturally but minimize eye movements during the whole recordings. They were instructed to keep their gaze fixed on a blue cross, which was displayed continuously, except during the cue presentation.

Data preprocessing

Data preprocessing was performed using the software package for electrophysiological analysis (ELAN Pack) developed at the Lyon Neuroscience Research Center (elan.lyon@inserm.fr; Aguera et al. 2011) and custom MATLAB and Python programs.

Behavioral data

Reaction times (RT) limits after target onset for correct detections were chosen based on previous studies (Hoyer at al., 2021, 2023a, 2023b). The RT lower limit was 150ms and the RT higher limit was the mean of RT plus 2 standard deviations in each subject. A button-press before the RT lower limit was considered as a false alarm. A trial with a button-press after the upper limit was considered as a late response. A trial with no button-press before the next cue onset was considered as a miss. The median of RT to targets was calculated on positive RTs for each subject.

Pupil dilation data

Full blinks were detected and marked by the eye tracker. Segments with blinks or missing data were interpolated with linear interpolation. Trials with more than 60% of interpolated data were removed from further analysis (Seropian et al., . Trials with false alarms or miss responses were also excluded.

The final mean % of rejected trials was (mean ± standard deviation) 2.3 ± 4.4 % in AAV, 1.8 ± 4.3 % in PAV, 0.6 ± 1.2% in PA & 2.1 ± 6.1 in PV. Finally, data were low-pass filtered using a bi-directional Butterworth filter with an 80Hz cut-off.

Pupil dilation responses (PDR) were analyzed locked to either the cue or the distractor events. cue-locked PDR was baseline-corrected by subtracting the 250ms period before cue onset. Concerning DIS-locked PDR, for each distractor onset time-range, surrogate DIS-locked PDR were created in the NoDIS trials and subtracted from the actual DIS-locked responses. The obtained PDR to the distractor was thus clear of cue-related activity. PDR to the distractor was further baseline-corrected by subtracting the 250ms period before DIS onset.

Statistical analysis

Frequentist statistical analyses were conducted using packages rstatix, emmeans, and PMCMRplus of R (version 4.2.2). Shapiro-Wilk test was used to test data normality. When data were found normally distributed, parametric analyses were performed; otherwise, non-parametric analyses were chosen.

Behavior (AAV condition)

Median RTs were submitted to a repeated-measure ANOVA with cue (two levels: informative, uninformative) and distractor (four levels: NoDIS, DIS1, DIS2, DIS3) as within-participant factors. *F* values, probability levels and generalized eta squared (η^2G) for effect sizes are provided. ηG2 values, representing the proportion of total variance explained by a factor, generally range from 0 to 1. According to Cohen's interpretation guidelines (Cohen, 1988), the closer the value of ηG2 is to 1, the greater the effect of the factor. Conversely, the closer it is to 0, the weaker the effect. Significant main effects obtained with ANOVAs were further examined with pairwise paired t-test comparisons and the Bonferroni multiple testing correction method.

Pupillometry

For statistical analysis of the pupil dilation, since data were not normally distributed (all p-value inferior to .05) non-parametric tests were used. Wilcoxon signed-rank tests were conducted when only two paired conditions were compared, and Friedman tests were conducted when three paired conditions were compared.

Statistical analysis of the cue-locked PDR (NoDIS trials) was conducted on the mean PDR amplitude in the 0-500ms, 500-1000ms, 1000-1500ms, 1500-2000ms, 2000-2500ms and 2500-3000ms time windows following the cue. First, to test the task effect, PDR amplitudes in the AAV and PAV conditions were compared using paired unilateral Wilcoxon signed-rank tests (AAV > PAV). Second, to test the cue effect on the task engagement, mean difference in PDR amplitude between AAV and

PAV conditions (AAV – PAV) were computed in the informative and uninformative conditions and compared using paired unilateral Wilcoxon signed-rank tests (Informative > Uninformative).

To test the task effect on the tonic pupil size changes, the mean pupil size over the -250 to 0ms period preceding cues after pre-cue baseline correction (-250 to 0ms) was compared between AAV and PAV conditions (AAV – PAV) using a paired bilateral Wilcoxon signed-rank test.

Statistical analyses of the DIS-locked PDR were conducted on the mean PDR amplitude in the 0-500ms, 500-1000ms, 1000-1500ms and 1500-2000ms time windows following the distractor. First, to test the existence of a DIS-locked PDR, in the PAV condition, the mean amplitude of the DIS-locked PDR was compared to 0 using unilateral Wilcoxon signed-rank test (>0). Second, to test the task effect, DIS-locked PDR amplitudes in the AAV and PAV conditions were compared using paired unilateral Wilcoxon signed-rank tests (AAV > PAV). Third, to test the cue effect on the task engagement, mean difference in DIS-locked PDR amplitude between AAV and PAV conditions (AAV – PAV) were computed in the informative and uninformative conditions and compared using paired bilateral Wilcoxon signed-rank tests.

To test the distractor position effect, mean difference in DIS-locked PDR amplitude between AAV and PAV conditions (AAV – PAV) in the DIS1, DIS2, and DIS3 conditions were computed in consecutive 500 ms wide time windows (i.e., 0-500ms, 500-1000ms, 1000-1500ms, 1500-2000ms, 2000-2500ms and 2500-3000ms) following a distractor and compared using a Friedman test.

Because pupil size immediately preceding the distractor might depend on the timing of the distractor's appearance relative to the cue and target, statistical analyses were conducted on the mean pupil size amplitude over the -250 to 0ms period preceding distractor after pre-cue baseline correction (-250 to 0 ms). The mean differences in amplitude between AAV and PAV conditions (AAV – PAV) in the DIS1, DIS2, and DIS3 conditions were compared using a Friedman test.

Statistic values (Z for Wilcoxon and X^2 for Friedman), probability levels and effect sizes (r for Wilcoxon and Kendall's W for Friedman) for each test were provided. For the Wilcoxon effect size, r value was calculated as Z statistic (extracted from permutation test) divided by the square root of the sample size. For the Friedman test effect size, the Kendall's W are calculated by dividing the Friedman statistic value X^2 by the product of the sample size N and one less than the number of measurements per subjects (K-1). Interpretation of r and Kendall's W uses the Cohen's interpretation guidelines (Cohen, 1988) of 0.1 to 0.3 (small effect), 0.3 to 0.5 (moderate effect) and >= 0.5 (large effect).

Significant effects from Friedman tests were further examined by pairwise comparisons using paired bilateral Wilcoxon signed-rank tests, p-values are adjusted using the Bonferroni multiple testing correction method.

For non-significant effects, Bayesian non-parametric Wilcoxon signed-rank test were conducted using JASP software (JASP—A Fresh Way to Do Statistics, 2021; Version 0.14.1). In contrast to Frequentist statistics, Bayesian analyses allow one to assess the credibility of both the alternative and null hypotheses. We reported Bayes factor (BF10) as a measure of evidence in favor of the null hypothesis (BF_{10} 0.1–0.33, 0.01–0.1, and lower than 0.01: moderate, strong, and decisive evidence, respectively) and in favor of the alternative hypothesis (value of 3–10, 10–100, and more than 100: moderate, strong, and decisive evidence, respectively, Lee and Wagenmakers, 2014).

Results

Behavior

Participants correctly performed the AAV blocks with (mean ± standard deviation) 93.7% ± 2.62% of hits, 3.4% ± 1.4% of late responses, and 2.8% ± 2% of false alarms.

Reaction times

RTs were significantly shorter for informative than for uninformative cues, as shown by a significant main cue effect ($F_{(1, 19)} = 8.484$, $p = .009$, $\eta^2G = .072$) (Figure 2).

A significant main effect of distractor ($F_{(3, 57)} = 61.636$, $p = 6.88 \times 10^{-18}$, $\eta^2G = 0.583$) was also observed. Pairwise comparisons showed that the RTs were significantly shorter in DIS1 than NoDIS and DIS3 (all $p < .0001$) and in DIS2 than NoDIS and DIS3 (all $p < .0001$). No significant cue by distractor interaction was found ($p = .729$). (Figure 2).

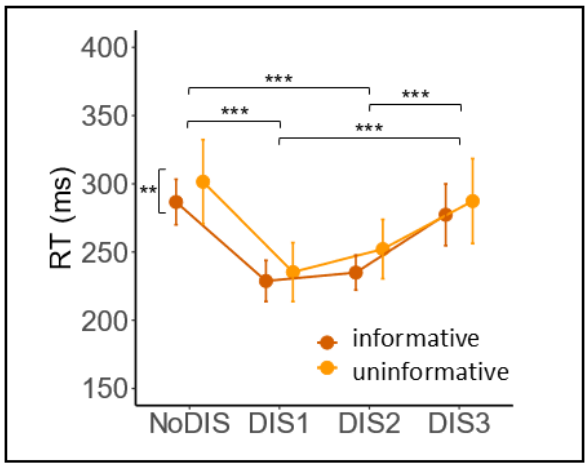

Figure 2. Behavioral results. Mean reaction time as a function of cue type (informative in brown or uninformative in orange) and distractor condition (NoDIS, DIS1, DIS2, DIS3). Error bars represent within-subject standard errors of the mean. ** p < .01, *** p < .001 (after Bonferroni correction).

Pupil Dilation Response

In the PAV condition and in the absence of distracting sound, from the cue-locked PDR, we first observe a large pupil constriction, also visible in the PV but not the PA condition (see SupFigure1). This constriction can be attributed to the pupillary light response to the cue, which is brighter than the fixation cross (for review see Mathôt, 2018). Then we observe a small pupil dilation, corresponding to the response to the "target" sound, also visible in the PA but not the PV condition.

PDR to cues, without distracting sounds

The PDR to the relevant cue is larger in amplitude in the active condition compared to the passive condition. This task effect on the cue-locked PDR amplitude is larger after an informative rather than an uninformative cue.

To test the task effect on the cue-locked PDR, mean amplitudes of the PDR in trials with no distracting sound were compared in the PAV and AAV conditions. From 1500 to 3000ms post cue (i.e., in three consecutive 500-ms time windows), the mean amplitude of the cue-locked PDR was found larger in the active than in the passive condition (1500-2000 ms: Z = 196, p = .0001, r = .76; 2000-2500ms: Z = 206, $p = 6.7 \times 10^{-6}$, r = .84; 2500-3000ms: Z = 193, p = .0002, r = .73) (Figure 3A). No significant effect of the task was found on the other time-windows (All $p > .10$).

Then, to test the cue effect on the cue-locked PDR, the mean differences in amplitude between active and passive conditions (AAV-PAV) in trials with no distracting sound were compared in the informative and uninformative cue conditions. From 1000 to 1500ms, the mean AAV-PAV difference in amplitude was larger after an informative than after an uninformative cue (Z = 60, p = .048, r = .38) (Figure 3B). No significant effect of the cue was found on the other time-windows (All $p > .07$).

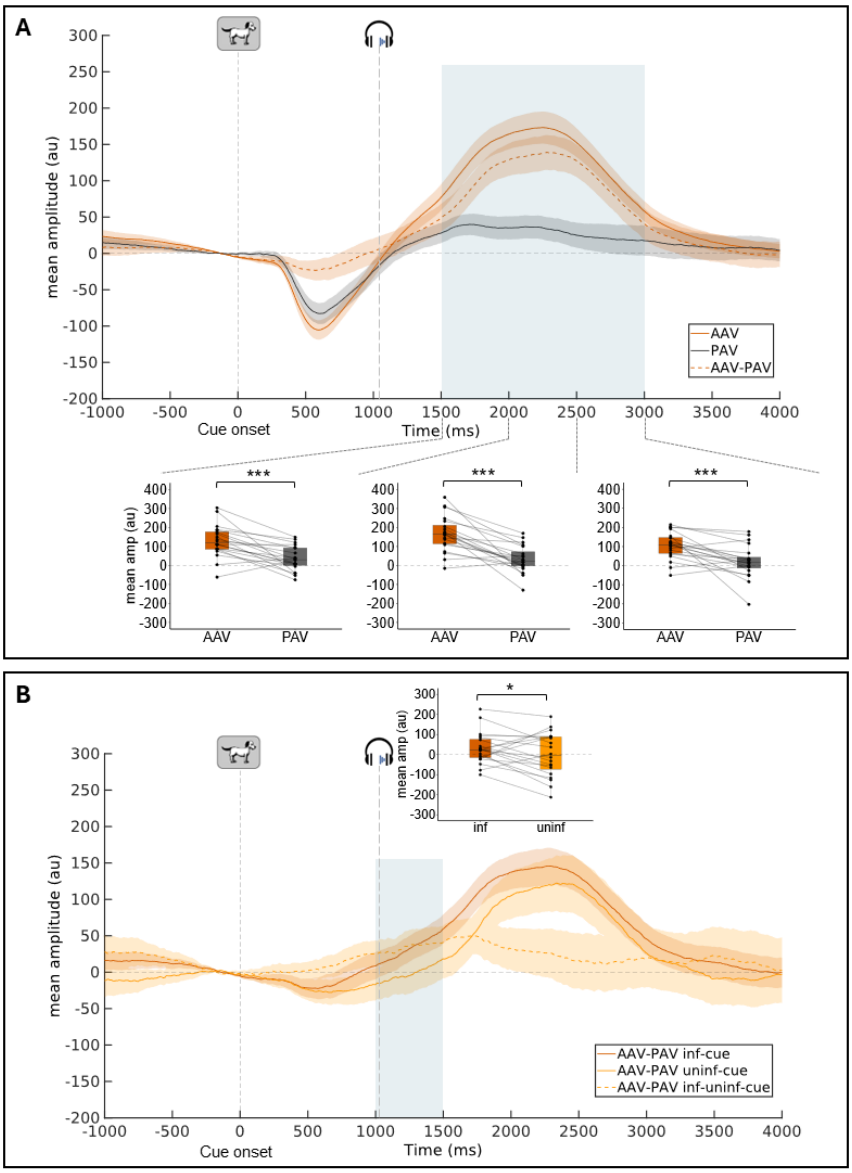

Figure 3. Cue-locked pupil dilation (group-average, 250-ms pre-cue baseline subtraction) **in trials without distractor (NoDIS trials). A:** Mean pupil dilation in AAV, PAV conditions and the subtraction between the two. **B:** Mean pupil dilation in informative & uninformative conditions and the subtraction between the two for AAV-PAV subtraction. Shadowed areas surrounding the curves represent standard errors of the mean. Examples of stimuli presented to participants are shown at their relative onset (for the target, the mean onset latency is indicated). Blue areas indicate time-windows where the task (A) or the cue (B) effect are significant. For these time windows, boxplots with individual data are depicted (mean pupil dilation amplitude in 500ms time-windows). Within each boxplot, the horizontal line represents the group median, the box the first and third quartiles, the whiskers the largest value under 1.5*IQR. (IQR = inter-quartile range). Superimposed to each boxplot, the dots represent individual means. * $p < 0.05$, *** $p < 0.001$. AAV: Active Audio-Visual condition, PAV: Passive Audio-Visual condition, inf: informative, uninf: uninformative.

The pre-cue pupil size was not significantly affected by the task. To test the task effect on the pre-cue pupil size, the mean differences in amplitude between active and passive conditions (AAV-PAV) was compared during the 250ms preceding the cue (-250-0ms) and resulted in no difference ($p > .24$).

PDR to distractors

The DIS-locked PDR is larger in amplitude in the active condition compared to the passive condition. This task effect on the DIS-locked PDR amplitude is not modulated by the cue conditions (informative vs. uninformative).

To assess the presence of a distractor-locked PDR in the PAV condition, the mean amplitude of the distractor-locked PDR was tested against zero. From 500 to 1500ms, the mean amplitude was larger than 0 (500-1000ms: Z = 164, $p < .05$, r = .83; 1000-1500ms : Z = 171, $p < .01$, r = 083) (Figure 4A). No significant effect was found on the other time-windows (All $p > .06$). To test the task effect on the DIS-locked PDR, the mean amplitudes of the PDR were compared in the PAV and AAV conditions. From 500 to 1500ms, the mean amplitude of the DIS-locked PDR was larger in the active than the passive condition (500-1000ms: Z = 177, $p = .003$, r = .60; 1000-1500ms: Z = 159, $p < .022$, r = .45) (Figure 4A). No significant effect of the task was found on the other time-windows (All $p > .05$). Then, to test the cue effect on the DIS-locked PDR, the mean differences in amplitude between active and passive conditions (AAV-PAV) were compared in the informative and uninformative cue conditions. No significant cue effect was found on this task difference ($p > .13$ for the 4 time-windows) (Figure 4B). Bayesian Wilcoxon tests showed no conclusive evidence for or against a cue effect from 0 to 1500 ms ($0.371 < BF_{10} < 1.185$) and positive evidence for no cue effect on the DIS-locked PDR from 1500 to 2000 ms ($BF_{10} = 0.277$).

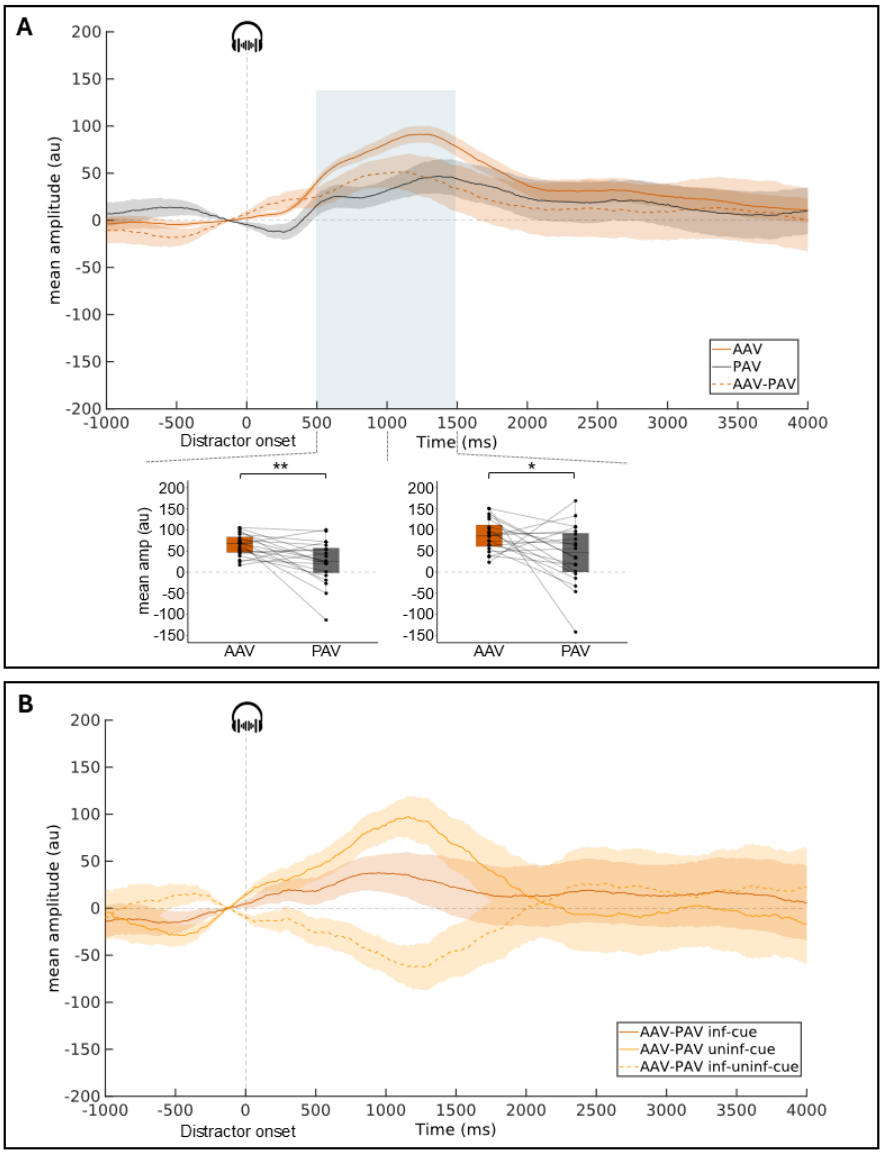

Figure 4. Distractor-locked pupil dilation (group-average, subtraction of the surrogate DIS-locked PDR & 250-ms pre-distractor baseline subtraction). **A:** Mean pupil dilation in AAV, PAV conditions and the subtraction between the two. **B:** Mean pupil dilation in informative & uninformative conditions and the subtraction between the two for the AAV-PAV subtraction curves. Shadowed areas surrounding the curves represent standard errors of the mean. The blue area (A) corresponds to the time windows where the task effect is significant. For these time windows, boxplots with individual data are depicted (mean pupil dilation amplitude in 500ms time-windows). Within each boxplot, the horizontal line represents the group median, the box the first and third quartiles, the whiskers the largest value under 1.5*IQR. (IQR = inter-quartile range). Superimposed to each boxplot, the dots represent individual means. * $p < 0.05$, ** $p < 0.01$. AAV: Active Audio-Visual condition, PAV: Passive Audio-Visual condition, inf: informative, uninf: uninformative.

The task effect on the DIS-locked PDR amplitude is larger after an early than a late distractor.

To test the distractor position effect on the DIS locked PDR, the mean differences in amplitude between active and passive conditions (AAV-PAV) were compared. A significant effect of the distractor position was found between 1000 and 3000ms post-distractor onset, i.e., in four consecutive 500-ms time windows (1000-1500ms: $X^2 = 11.1$, $p = .004$, W = 0.28; 1500-2000ms: $X^2 = 13.3$, $p = .001$, W = .33; 2000-2500ms: $X^2 = 17.2$, $p = .0002$, W = .43; 2500-3000ms: $X^2 = 12.4$, $p = .002$, W = .31; Figure 5A). No significant effect of the distractor position was found in the other time-windows ($p > .26$). From 1000 to 3000ms, pairwise Wilcoxon signed rank comparisons showed that the difference of mean amplitudes between active and passive conditions was significantly larger after DIS1 than DIS2 from 1500-2000ms (Z = 172, $p < .05$) and after DIS1 than DIS3 from 1000 to 3000ms (1000-1500ms: Z = 186, $p < .01$; 1500-2000ms: Z = 204, $p < .0001$; 2000-2500ms: Z = 210, $p < .0001$; 2500-3000ms: Z = 193, $p < .001$).

The task effect on the pre-distractor pupil size is lower before an early than a late distractor.

Finally, to test the distractor position effect on the pre-distractor pupil size, the mean differences in amplitude between active and passive conditions (AAV-PAV) were compared during the 250ms preceding the distractor onset (-250-0ms) after pre-cue baseline correction. A significant effect of the distractor position was found ($X^2 = 10.3$, $p = .01$, W = .54; Figure 5B). Pairwise Wilcoxon signed rank test showed that the difference of baseline between active and passive conditions was lower during the 250ms preceding DIS1 than DIS3 (Z= 16, $p < .001$). No other significant effect was found (All $p > .13$).

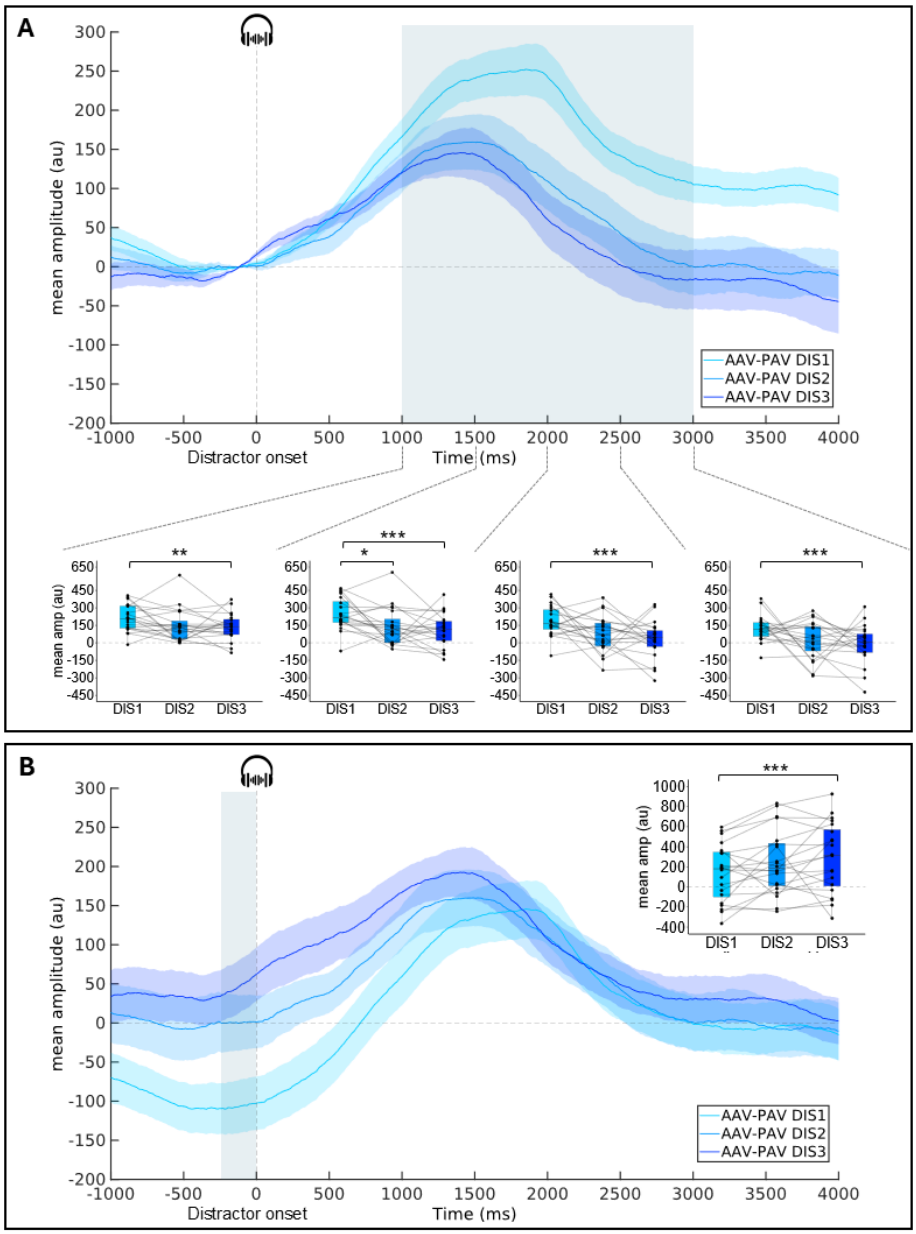

Figure 5. Distractor-locked pupil dilation (group-average, AAV-PAV subtraction curves) as a function of the distractor position (DIS1, DIS2, DIS3). **A**: with subtraction of the surrogate DIS-locked PDR & a 250-ms pre-distractor baseline subtraction. **B**: with a 250-ms pre-cue baseline correction. Shadowed areas surrounding the curves represent standard errors of the mean. Blue areas correspond to the time window where the distractor position is significant. For these time windows, boxplots with individual data are depicted (mean pupil dilation amplitude in 500ms time-windows). Within each boxplot, the horizontal line represents the group median, the box the first and third quartiles, the whiskers the largest value under 1.5*IQR. (IQR = inter-quartile range). Superimposed to each boxplot, the dots represent individual means. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. AAV-PAV: Active Audio-Visual - Passive Audio-Visual condition.

Discussion

This study used pupillometric responses during the Competitive Attention Task (CAT, Bidet-Caulet et al., 2015; Masson et Bidet-Caulet, 2019; Hoyer et al., 2021, 2023a, 2023b) to examine how attention influences arousal, according to task engagement and stimulus relevance. More precisely, we explored the impact of task engagement by comparing the pupil dilation responses (PDR) of participants who engaged in an auditory detection task or passively heard and saw the same sequences of events. In addition, we explored the impact of voluntary attention orienting on the PDR to relevant and irrelevant sounds.

Behavioral results obtained in the active condition agree with previous findings observed with a slightly different version of the CAT (e.g., Bidet-Caulet et al., 2015; Hoyer et al., 2023a, 2023b). Shorter reaction times were observed in trials with an informative compared to an uninformative cue (i.e., cue effect), confirming that more voluntary attention orienting is engaged after informative cues. Moreover, shorter reaction times were observed in presence of a distracting sound, with reaction times increasing as the distracting sounds got closer to the target. This dual effect of distracting sounds on RT replicates previously CAT results and can be explained by: (1) a phasic increase in arousal, which benefits reaction times, and (2) a distraction effect, which results in a cost in reaction times (Bidet-Caulet et al., 2015; Masson & Bidet-Caulet, 2019).

In the passive condition, we observed a pupil constriction in response to the bright visual cue followed by an increase in pupil dilation in anticipation of, and in response to, the “target” sound. Additionally, an increase in pupil dilation is triggered by the “distracting” sounds. Together, these findings suggest that all sounds are associated with an increase in phasic arousal. In the active condition, both relevant (target) and irrelevant (distractor) events elicited a larger increase in pupil dilation compared to the passive condition. This result is consistent with previous studies, showing that greater task engagement — whether through manipulating task difficulty, multitasking, or comparing active and passive tasks — is associated with larger pupil dilation responses (Kahneman & Beatty, 1967; Kramer et al., 2012; Lisi et al., 2015; Laeng et al., 2016; Liao et al., 2016). Engagement in a task (such as when requiring a motor response) involves focusing attentional resources (Tops and Boksem, 2010) and also results in increasing phasic arousal (Kahneman, 1973; Posner and Peterson, 1990; Aston-Jones and Cohen, 2005), as indicated by the increased pupil dilation. This increase in arousal, to both relevant and irrelevant events, suggests an interplay between task engagement and phasic arousal independent of stimulus relevance. This increase in phasic arousal could result in a global and transient increase in brain excitability.

Moreover, our results revealed a larger pupil dilation 1000 to 1500 ms after informative compared to uninformative cues. This increase starting immediately before target onset can reflect both anticipation of, and response to, the relevant target. This finding agrees with the few studies that have explored the effect of voluntary attention orienting on pupil dilation using visual cueing paradigms (Dragone et al., 2018; but see Aminihajibashi et al., 2020). In the present study, the increase in pupil dilation starts before target onset, which suggests a transient (phasic) increase in arousal, recruited via top-down attention mechanisms during target expectation (Totah et al., 2021; Aston-Jones & Cohen, 2005). In contrast, the pupil dilation response to the irrelevant distractor was not significantly affected by the cue information. Bayesian statistics partially speak for a similar pupil dilation response for both types of cues, suggesting that voluntary attention orienting does not further increase the phasic response to distraction. Thus, greater voluntary attention orienting within the task selectively increases phasic arousal to relevant sounds, suggesting a selective interplay between attention and arousal.

Interestingly, we also found a larger PDR to task-irrelevant distractors when they were presented long before the target, compared to those presented just before the target sound. Two speculative explanations might account for this result. First, the larger PDR to an early distracting sound could be due to less overlap with the PDR to the target sound. Second, the PDR to a distracting sound could decrease as attentional and motor preparation increase. Indeed, previous studies have shown that longer cue-to-target delays improve preparation (Posner et al., 1980; Niemi & Näätänen, 1981; Coull & Nobre, 1998; Hackley & Valle-Inclán, 1999; Griffin et al., 2001) and performance in detection tasks (Griffin et al., 2001). Thus, as the target approaches, top-down mechanisms, such as enhanced voluntary attentional orienting and inhibition, become more engaged, potentially reducing the phasic arousal response to irrelevant events. This second explanation also fits with the observation of increased pre-distractor baseline pupil dilation as the target onset approaches. Previous research suggests that changes in baseline pupil size are related to tonic activity in the locus coeruleus (LC), which is associated with tonic arousal or task engagement (Aston-Jones & Cohen, 2005; Gilzenrat et al., 2010; Jepma & Nieuwenhuis, 2011; Murphy et al., 2014; Unsworth & Robison, 2016, 2018; Konishi et al., 2017). Overall, these findings suggest that increase top-down attention during target anticipation is measurable through pupil dilation using the pre-distractor baseline (i.e. during the cue-target delay in the paradigm).

We observed that an increased arousal response to auditory stimuli is mediated by task engagement (active vs. passive), independently from the stimulus relevance. Importantly, we found that attention (manipulated using informative and uninformative cues) led to a further increase in arousal for relevant events (target sounds). Taken together, our results are consistent with the

Glutamate Amplifies Noradrenergic Effects (GANE) model (Mather et al. 2016) assuming that, increase in arousal —mediated by norepinephrine (NE) release— enhances the strong activity of neurons encoding high-priority mental representations while suppressing the low activity of neurons encoding lower-priority representations, thereby amplifying selectivity. Therefore, attention could differentially modulate the phasic LC-NE activity according to stimulus relevance, and the LC-NE system would, in turn, support selective attention (Dahl et al., 2022) by enhancing cortical excitability in response to relevant stimuli only.

Conclusion

We used pupil dilation in human as a measure of arousal and demonstrated that this marker is modulated by both task engagement and voluntary attention orienting. More precisely, our findings indicate that task engagement is associated with increased phasic arousal to both task-relevant and irrelevant sounds. Moreover, voluntary attention orienting further enhances phasic arousal to task-relevant sound only, with increased pupil dilation to auditory targets preceded by informative visual cues. These findings suggest that task engagement and voluntary attention orienting modulate phasic arousal in a global and a specific way, respectively. In agreement with the GANE model, increase in phasic arousal, mediated by the LC-NE system, would be more than a transient general enhancement of cortical excitation. These findings enhance our understanding of how attention and arousal interact, with implications for optimizing task design and learning environments.

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