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The effect of phasic auditory alerting on visual perception

Anders Petersen [a,*], Annemarie Hilkjær Petersen [b], Claus Bundesen [a], Signe Vangkilde [a], Thomas Habekost [a]

[a] Department of Psychology, University of Copenhagen, Denmark
[b] Center for Rehabilitation of Brain Injury, Copenhagen, Denmark

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ABSTRACT

Phasic alertness refers to a short-lived change in the preparatory state of the cognitive system following an alerting signal. In the present study, we examined the effect of phasic auditory alerting on distinct perceptual processes, unconfounded by motor components. We combined an alerting/no-alerting design with a pure accuracy-based single-letter recognition task. Computational modeling based on Bundesen's Theory of Visual Attention was used to examine the effect of phasic alertness on visual processing speed and threshold of conscious perception. Results show that phasic auditory alertness affects visual perception by increasing the visual processing speed and lowering the threshold of conscious perception (Experiment 1). By manipulating the intensity of the alerting cue, we further observed a positive relationship between alerting intensity and processing speed, which was not seen for the threshold of conscious perception (Experiment 2). This was replicated in a third experiment, in which pupil size was measured as a physiological marker of alertness. Results revealed that the increase in processing speed was accompanied by an increase in pupil size, substantiating the link between alertness and processing speed (Experiment 3). The implications of these results are discussed in relation to a newly developed mathematical model of the relationship between levels of alertness and the speed with which humans process visual information.

1. Introduction

Alertness refers to the brain's general readiness to respond to an upcoming event (Posner & Petersen, 1990). The ability to prepare and sustain alertness is an important attentional function, which, if impaired, can result in severe attentional problems. A broad distinction is made between tonic and phasic alertness (Sturm & Willmes, 2001): Tonic (intrinsic) alertness denotes the sustained long-term intensity level of attention, whereas phasic (extrinsic) alertness refers to a short-lived increase of attention elicited, for example, by a warning signal preceding an upcoming event. Phasic alertness has been found to reduce reaction times in response to various stimuli (Fan, McCandliss, Sommer, Raz, & Posner, 2002; Posner & Boies, 1971), which was originally attributed to faster preparation and/or execution of the motor response (Posner, 1978; Sanders, 1980). Evidence, however, is accumulating showing that phasic alertness also affects earlier perceptual processes. For instance, Matthias et al. (2010) presented a visual alerting cue prior to a whole report letter display (Sperling, 1960) and used mathematical modeling based on the Theory of Visual Attention (TVA; Bundesen, 1990) to show that phasic visual alerting increased visual processing speed and changed the spatial distribution of attentional resources. These findings are particularly interesting because they were obtained using pure accuracy-based measures, unconfounded by motor components. Phasic auditory alertness has also been reported to affect early perception (Jepma, Wagenmakers, Band, & Nieuwenhuis, 2009; Kusnir, Chica, Mitsumasu, & Bartolomeo, 2011; Robertson, Mattingley, Rorden, & Driver, 1998; Weinbach & Henik, 2011). However, most of these studies rely on reaction time-based measures, by which it is difficult to disentangle effects on early perception from effects on later, response-based processes (although see Finke et al., 2012; Robertson et al., 1998; and Brown et al., 2015). Thus, in this article we use pure accuracy-based measures and TVA-based modeling to examine how phasic auditory alertness influences early visual perception. In contrast to most previous research on phasic alerting, we do not rely on uniform foreperiod distributions (i.e., distributions of the time interval between the cue and the target) because such distributions confound the alerting effect with the build-up of temporal expectancy as time elapses (Weinbach & Henik, 2012). Instead, we use a non-aging foreperiod distribution (Niemi & Näätänen, 1981) to reduce the effect of temporal expectancy (but see Lawrence & Klein, 2013 for a more sophisticated, yet less

* Corresponding author.
E-mail address: anders.petersen@psy.ku.dk (A. Petersen).

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simple, approach). A non-aging distribution has a constant hazard rate (i.e., a constant probability that the target appears during the next little period of time, given that the target has not yet appeared), resulting in a distribution with many short and only a few long foreperiods. Experiment 1 was a single-letter recognition task in which a high-intensity alerting cue (85 dB) was presented prior to a backward-masked target letter in 1/3 of the trials, and TVA-estimates of visual processing speed and perceptual threshold were compared between the alerting and no-alerting conditions. In Experiment 2, we investigated the effect of alerting intensity on TVA-estimates by including both high (85 dB) and low (40 dB) intensity cues in an experimental design similar to the design used in Experiment 1. Finally, in Experiment 3 we replicated Experiment 2 but included measures of pupil size to examine physiological effects of auditory alerting (see, e.g., Kahneman, 1973; Tona, Murphy, Brown, & Nieuwenhuis, 2016).

Based on previous findings by Matthias et al. (2010), we hypothesized that presentation of an auditory alerting cue, similar to the presentation of a visual alerting cue, increases visual processing speed. Further, theoretical considerations by Bundesen, Vangkilde, and Habekost (2015; see discussion) suggest that the intensity of alerting should correlate with the observed estimates of processing speed. It has previously been reported that increasing levels of auditory alerting prior to an imperative stimulus lead to faster response times (Behar & Adams, 1966; Keuss, 1972), but to the best of our knowledge this is the first time effects of alerting intensity on early perceptual processes have been investigated using pure accuracy-based measures, unconfounded by motor processes.

2. Theory of Visual Attention

The behavioral data in this article were analyzed by use of Bundesen's (1990) Theory of Visual Attention (TVA). In this section, we introduce TVA and the way it was used to analyze data from the single-letter recognition task. In general, TVA proposes that an object x in the visual field is encoded into visual short-term memory (VSTM) by encoding one or more categorizations of the object into VSTM. A categorization has the form "object x belongs to category i" (or equivalently "object x has feature i"), where i is a perceptual category (e.g., a certain letter shape, color, size, or orientation). Consider the hazard rate, $v(x,i)$, of the event that the categorization "x belongs to i" becomes encoded into VSTM at a given time t. If $f(t)$ and $F(t)$ are the probability density and distribution functions of the event, the hazard rate is $f(t)/[1-F(t)]$, which is a measure of the speed of processing at time t. By the rate equation of TVA,

$$v(x,i) = \eta(x,i)\beta_i \frac{w_x}{\sum_{z \in S} w_z}, \tag{1}$$

where $\eta(x,i)$ is the strength of the sensory evidence that object x belongs to category i, β_i is the perceptual bias associated with category i, and w_x is the attentional weight of object x, which is divided by the sum of attentional weights across all objects in the visual field, S. When several objects are presented simultaneously in the visual field, they compete for access to the limited storage space of VSTM. Objects that are likely to win the competition are those that differ from their local surroundings (feature contrast) and those that are relevant for the task (feature relevance). Such objects get high attentional weights (see Nordfang, Dyrholm, & Bundesen, 2012), and task-relevant categorizations of objects with high attentional weights are likely to become encoded into VSTM (see Eq. (1)).

As an example, consider the task of reporting the identity of red letters (targets) among equally salient blue letters (distractors). According to TVA, the visual system solves this task by setting the attentional weights high for red objects and low for blue objects. This makes categorizations of red objects faster than categorizations of blue objects. Furthermore, to facilitate that only task-relevant categorizations of letter shapes are encoded into VSTM, the perceptual biases associated with letter shapes (i.e., $\beta_A, \beta_B, \ldots, \beta_Z$) are set high, whereas perceptual biases for task-irrelevant categories are set at values near zero.

TVA is a general model of visual perception (see Bundesen, 1990; Bundesen, Habekost, & Kyllingsbæk, 2005). In this article, we use TVA to model data from a simple, single-letter recognition task, which greatly reduces the complexity of the model. If we neglect the storage limitation of VSTM and neglect potential perceptual confusions by setting $\eta(x,i) = 0$ for all incorrect categorizations of object x, the probability of encoding object x into VSTM can be expressed as,

$$p = \begin{cases} 1 - e^{-v_x(\tau - t_0)} & \tau > t_0 \\ 0 & \tau \leqslant t_0 \end{cases}, \tag{2}$$

where v_x is the processing speed of object x (i.e., the speed of the process of correctly categorizing object x), τ is the exposure duration of object x, and t_0 is the longest ineffective exposure duration (a.k.a. the threshold of perception). That is, if the exposure duration of an object is shorter than or equal to t_0, the probability of encoding the object into VSTM is zero. However, if the exposure duration of the object is longer than t_0, the probability of encoding the object into VSTM increases exponentially as a function of $\tau - t_0$. An instance of the model (corrected for guessing, see method section of Experiment 1) is provided in Fig. 2 with t_0 interpreted visually as the exposure duration at which the curve rises from pure guessing performance and v as the slope of the curve at t_0.

3. Experiment 1

To investigate the effect of phasic auditory alerting on visual perception we conducted an experiment in which participants were to report the identity of a post-masked letter presented for varying exposure durations. This made it possible to perform a TVA-based modeling of the data for each individual subject. In one third of the trials, a loud 85 dB auditory alerting cue preceded the presentation of the letter. In the remaining two thirds of the trials, the letter was presented without a preceding cue. The TVA-based modeling of the data was performed independently for the two conditions.

3.1. Method

3.1.1. Participants

28 Danish students (23 females, 5 males, mean age = 22.8 years, SD = 1.8 years) were paid a standard fee by the hour (18 students) or received course credits (10 students) for participating in the experiment. All had normal or corrected-to-normal vision and performed within the normal hearing range on a screening audiometer test (Oscilla® USB-310). The study was approved by the departmental board of ethics (No. 2012/2).

3.1.2. Design

In one third of the trials, an 85 dB auditory cue was played prior to the presentation of a target letter (85 dB cue condition), whereas in the remaining two thirds of the trials no auditory cue was given (no cue condition; see Fig. 1). This distribution of trials was chosen to allow for longer periods with low alertness while leaving enough trials in the cue condition for TVA-based modeling. To avoid habituation to a specific auditory stimulus, the cue was played equally often at either a high pitch of 900 Hz or at a low

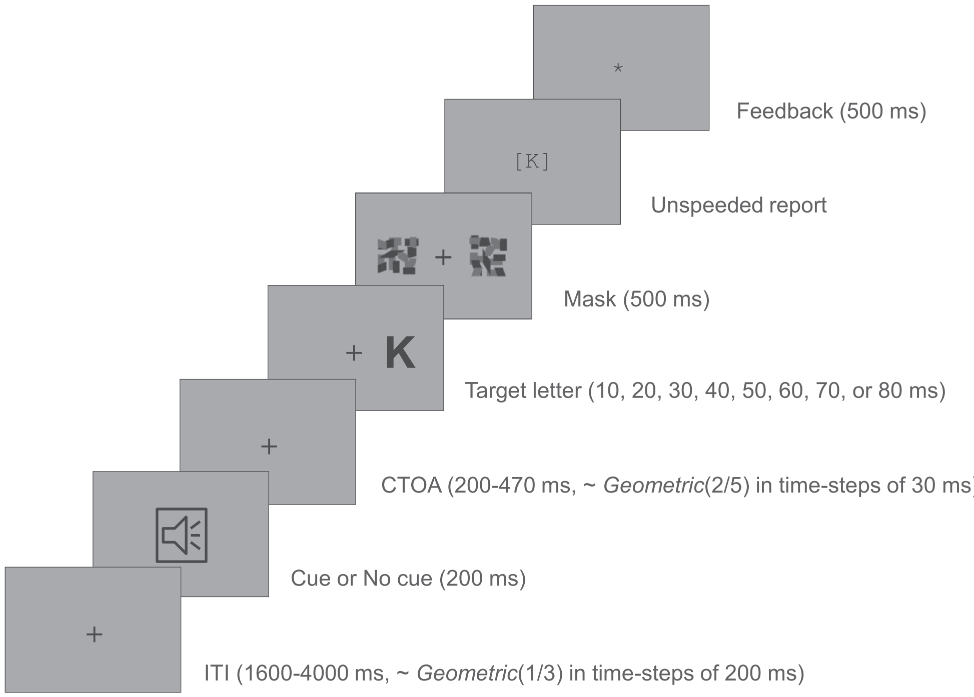

Fig. 1. Trial outline for Experiments 1 and 2.

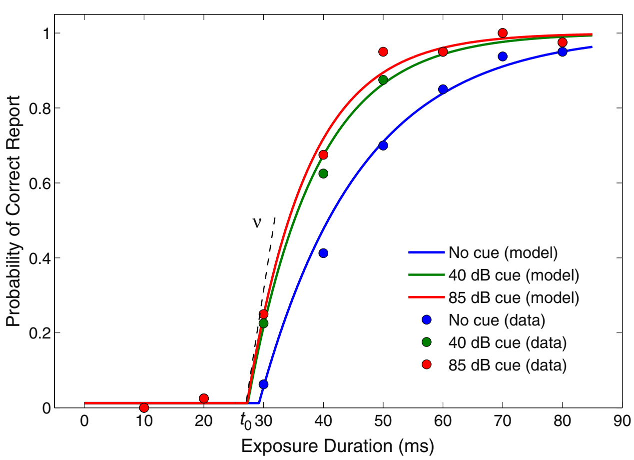

Fig. 2. Model fitted to data from a single subject. The observed (dots) and predicted (solid lines) probability of a correct response as a function of exposure duration for the No cue (blue), 40 dB cue (green), and 85 dB cue conditions (red). Model parameters are illustrated on the figure: t_0 (the perceptual threshold) is the exposure duration at which the curve rises from pure guessing performance and v (the processing speed) is the slope of the curve at t_0. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

pitch of 500 Hz. Target letters were chosen randomly without replacement from a set of 20 letters (ABDEFGHJKLMNOPRSTVXZ), such that each letter was presented once and only once for each exposure duration in the cue condition and twice for each exposure duration in the no cue condition. Exposure durations were chosen from a set of eight durations (10, 20, 30, 40, 50, 60, 70, and 80 ms) such that each exposure duration was used equally often in both conditions. This 20 × 8 factorial design resulted in one session of the experiment comprising 160 cue trials and 320 no cue trials. To reduce dynamics related to temporal expectancy, the intertrial interval (ITI) and cue-target onset asynchrony (CTOA) were drawn from distributions with constant hazard rates (*nonaging* distributions; cf. Luce, 2008; Näätänen, 1971; Thomas, 1967). More specifically, the ITIs were distributed geometrically using time-steps of 200 ms and a hazard rate of 1/3 (i.e., the probability that the cue would appear at the next possible time point given that it had not yet appeared). This resulted in a distribution with many short and only a few long ITIs ranging from 1600 to 4000 ms and with an expected ITI of 2000 ms. Accordingly, the CTOAs were distributed geometrically using time-steps of 30 ms and a hazard rate of 2/5 resulting in CTOAs ranging from 200 to 470 ms and an expected CTOA of 244 ms.

3.1.3. Procedure

Stimuli were presented on a 21" CRT monitor running at 100 Hz using E-prime 2 software in a semidarkened room with participants seated approximately 65 cm from the monitor with their heads supported by a chinrest to ensure constant viewing distance and position throughout the experiment. During the ITIs, a black fixation cross (0.44° × 0.44° of visual angle, 0.39 cd/m^2) was presented centrally on a grey background (17.5 cd/m^2) and participants were instructed to keep fixation on the cross throughout the presentation of the cross. In the cue condition, a trial was initiated by a 200 ms, 85 dB cue played by two loud speakers located next to the monitor. The presentation of the cue was followed by a varying CTOA during which the fixation cross was still presented, thus in the no cue condition the effective ITI was ITI + CTOA. A trial proceeded with the presentation of a target letter for a varying exposure duration either 3.4° of visual angle to the left or the right of the fixation cross (measured center-to-center). The location of the letter was chosen such that in both the cue and no cue conditions a letter was equally often presented at both locations. The letters were written in the font Arial (broad) with a letter point size of 68 corresponding to 2.0° × 2.5° of visual angle and terminated by two pattern masks presented for 500 ms, one at each of the two locations. The pattern masks were made from black and dark grey letter fragments measuring 3.3° × 3.3° of visual angle which completely covered the letters. Masks were presented at both locations to reduce automatic eye movements to the target location. Following the offset of the masks, participants reported the identity of the letter presented. Participants were instructed to make a non-speeded report of the identity of the letter if they were "fairly certain" of having seen it (i.e., to use all available information but refrain from pure guessing). If participants had no information on the identity of the letter, they conveyed this by starting the next trial without making a report. A 500 ms feedback display informed participants of whether their report was correct ('*') or not ('–'). Participants completed a total of 960 trials (i.e., 2 sessions of 480 trials) which were presented in blocks of 40 trials each. Participants were encouraged to take small breaks between blocks. See Fig. 1 for an outline of a trial in Experiment 1.

3.1.4. Modeling

For each condition (no cue, 85 dB cue), v and t_0 parameters were estimated separately for each subject by a maximum-likelihood estimation using the Nelder-Mead simplex optimization algorithm in Matlab (see Fig. 2). Despite the instruction to refrain from pure guessing, subjects did occasionally guess on the identity of the presented letters. To improve the estimation of parameters, a high-threshold guessing model was introduced, which assumes that with a certain probability, p_g, subjects guess randomly among the 20 letters if they fail to encode the presented letter into VSTM. That is, the probability of correctly reporting a single letter presented for an exposure duration of τ is given by

$$p = \begin{cases} 1 - e^{-v(\tau - t_0)} + e^{-v(\tau - t_0)} p_g \frac{1}{20} & \tau > t_0 \\ p_g \frac{1}{20} & \tau \leqslant t_0 \end{cases}. \quad (3)$$

3.2. Results

Fig. 3a shows the average estimates of v and t_0 across participants for the two conditions in Experiment 1. Paired t tests revealed an increase in processing speed v, $t(27) = 4.71$, $p < 0.001$, $d_z = 0.89$, and a decrease in the perceptual threshold t_0, $t(27) = 3.52$, $p = 0.002$, $d_z = 0.67$, when a 85 dB cue is presented prior to the letter. No significant difference was found between conditions for the guessing parameter, $\bar{p}_{g,\text{No cue}} = 0.67$ and $\bar{p}_{g,\text{85dB cue}} = 0.55$, $t(27) = 1.24$, $p = 0.23$. For both conditions, the model explained on average 98% of the variance in the data.

4. Experiment 2

In Experiment 1, we found a clear effect of phasic auditory alerting on visual perception: An alerting cue reduced the perceptual threshold and increased the processing speed of visual information compared with a condition in which no alerting cue was presented. To quantify these effects further, we ran a second experiment investigating the effect of the alerting intensity by including both trials with high (85 dB) and low (40 dB) intensity cues before letter presentation. Previous researchers have reported that an increase in the intensity of alerting auditory stimuli speeds up reaction times (e.g., Behar & Adams, 1966), but the present study appears to be the first investigation of the effect of the intensity of alerting auditory stimuli on pure accuracy-based measures of visual perception.

4.1. Method

4.1.1. Participants

29 Danish students were paid a standard fee by the hour for participating in the experiment. All participants were naïve to the experiment and had normal or corrected-to-normal vision and normal hearing. One participant was diagnosed with ADHD and was on medication. This participant was excluded from the

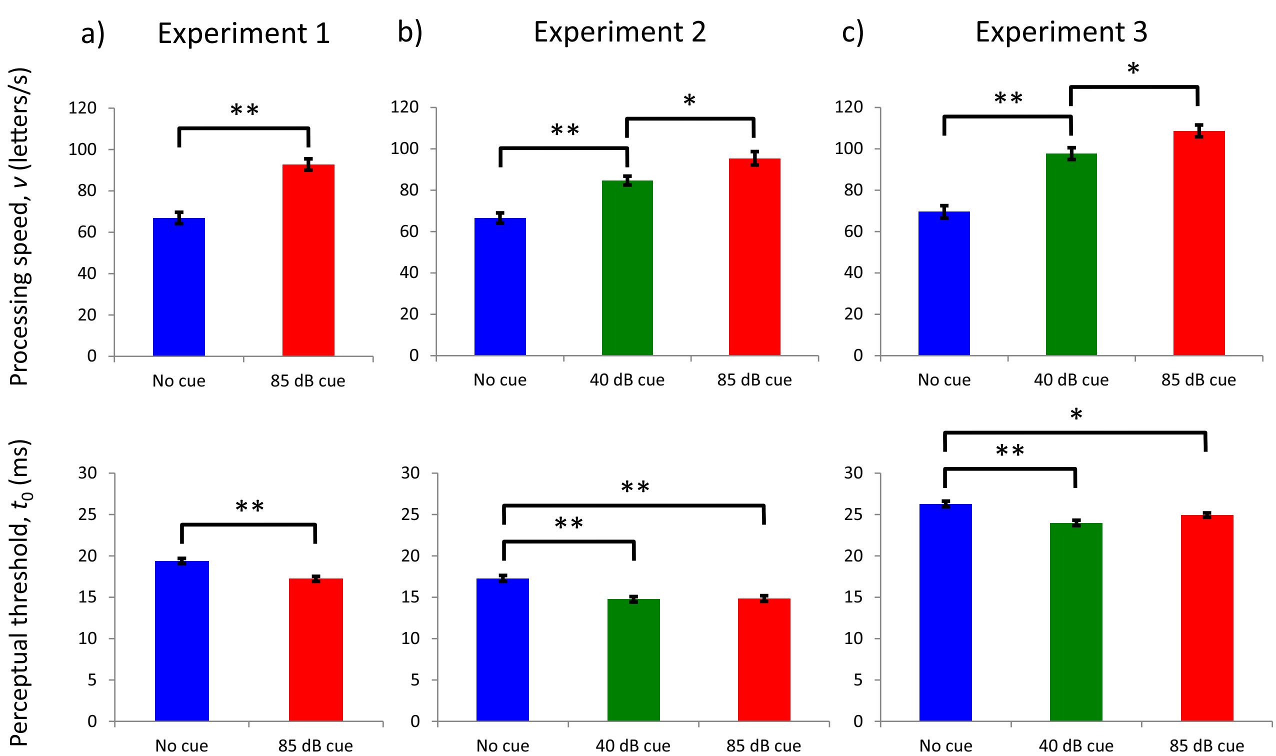

Fig. 3. TVA parameter estimates for Experiments 1, 2 and 3. Bars represent the mean estimate of the processing speed (upper panel) and the perceptual threshold (lower panel) for the No cue (blue), 40 dB cue (green), and 85 dB cue conditions (red) in Experiments 1 (a), 2 (b), and 3 (c). Error bars represent standard errors of the mean (corrected for between-subject variability; Cousineau, 2005). Statistically significant differences between conditions are indicated by * $p < 0.05$, ** $p < 0.01$.

analysis resulting in a final sample size of 28 Danish students (25 females, 3 males, mean age = 23.8 years, *SD* = 1.6 years).

4.1.2. Design

In one half of the trials, a 40 dB auditory cue (40 dB cue condition) or an 85 dB auditory cue (85 dB cue condition) was played equally often prior to the presentation of a target letter, whereas in the remaining one half of the trials no auditory cue was played (no cue condition). The three conditions were randomly intermixed in each testing block. Similar to Experiment 1, the cues were played equally often at either a high pitch of 900 Hz or at a low pitch of 500 Hz to avoid habituation to a specific auditory stimulus. All other aspects of the design were equal to Experiment 1 resulting in 160 low intensity cue trials, 160 high intensity cue trials, and 320 no cue trials per session.

4.1.3. Procedure

Similar to Experiment 1 (see Fig. 1). Participants completed a total of 1280 trials (i.e., 2 sessions of 640 trials) presented in blocks of 40 trials each.

4.2. Results

As in Experiment 1, model parameters were estimated separately for each subject and condition (see Fig. 2). Averages of the estimated v and t_0 parameters are presented in Fig. 3b. Paired *t* tests between the no cue and 40 dB cue conditions, $t(27) = 5.44$, $p < 0.001$, $d_z = 1.03$, and between the 40 dB cue and 85 dB cue conditions, $t(27) = 2.20$, $p = 0.037$, $d_z = 0.41$, revealed a significant increase of processing speed, v, when a 40 dB cue was presented prior to the letter, and a further increase when a 85 dB cue was presented. Paired *t* tests also revealed a decrease in the perceptual threshold, t_0, both when a 40 dB cue, $t(27) = 4.21$, $p < 0.001$, $d_z = 0.80$, and when an 85 dB cue, $t(27) = 3.90$, $p = 0.001$, $d_z = 0.74$, was presented prior to the letter display compared with the condition in which no cue was presented. Interestingly, no difference in perceptual threshold was observed between the two cue conditions, $t(27) = 0.17$, $p = 0.869$. No significant differences were found between conditions for the guessing parameter, $\bar{p}_{g,\text{No cue}} = 0.52$, $\bar{p}_{g,\text{40dB cue}} = 0.56$, and $\bar{p}_{g,\text{85dB cue}} = 0.41$, all $ts \leq 1.54$, all $ps \geq 0.135$. For all conditions, the model explained on average 98% of the variance in the data.

5. Experiment 3

The purpose of Experiment 3 was twofold. One goal was to replicate the findings in Experiment 2, another to perform simultaneous measures of changes in pupil size and thus examine the physiological effect of different intensities of phasic auditory alerting. Hess and Polt (1960) showed that pupil size increased with the presentation of arousing stimuli thus establishing a link between pupil dilation and cognitive processes. Later, Hess and Polt (1964) demonstrated that difficulty of mental calculations correlated positively with pupil size, and Beatty and Kahneman (1966) found that pupil dilation is directly related to the length of a to-be-recalled string of digits. Based on these and other findings Kahneman (1973; see also Beatty, 1982) suggested that pupillary responses are physiological markers of cognitive effort and that phasic pupillary responses correspond to the intensity aspect of attention. Many subsequent studies have demonstrated a relationship between pupil dilation and cognitive effort (Ahern & Beatty, 1979; Laeng, Ørbo, Holmlund, & Miozzo, 2011) or memory load (Granholm, Asarnow, Sarkin, & Dykes, 1996; Peavler, 1974; Piquado, Isaacowitz, & Wingfield, 2010; Van Gerven, Paas, Van Merriënboer, & Schmidt, 2004) and, furthermore, a tight link between pupil size and activation in neurons of the locus coeruleus (LC) has been established (Joshi, Li, Kalwani, & Gold, 2016; Murphy, O'Connell, O'Sullivan, Robertson, & Balsters, 2014; Nieuwenhuis, De Geus, & Aston-Jones, 2011; Reimer et al., 2016). LC is involved in many aspects of attention through the regulation the neurotransmitter norepinephrine, for which LC is the primary source (for a review see Aston-Jones & Cohen, 2005). Importantly, LC is assumed to play a role in changes in alertness or vigilance. For instance, Posner and Petersen (1990) distinguished between the alerting, orienting, and executive networks of the brain, and later imaging studies suggested that the alerting network encompasses the LC as well as areas of the right frontal and parietal cortex (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Posner & Rothbart, 2007). In Experiment 3, we recorded changes in attentional intensity by use of a desktop mounted eye tracker measuring phasic pupil responses following the presentation of the auditory and visual stimuli.

5.1. Method

5.1.1. Participants

26 Danish students were paid a standard fee by the hour for participating in the experiment. All participants were naïve to the experiment and had normal or corrected-to-normal vision and normal hearing. One participant made above 50% incorrect responses (i.e., did not refrain from pure guessing as instructed) and was excluded from further analysis resulting in a final sample of 25 Danish students (19 females, 6 males, mean age = 24.4 years, *SD* = 2.3 years).

5.1.2. Design

The design was identical to the design of Experiment 2, but in order to provide sufficient time for measuring pupil dilations, a retention interval was introduced after the offset of the mask display. Participants were instructed to sustain fixation at the center of the screen until the fixation cross disappeared, marking the end of the retention interval (see Fig. 4). The duration of the retention interval was distributed geometrically using time-steps of 100 ms and a hazard rate of 2/5. This resulted in a retention interval ranging from 1500 to 2500 ms and an expected interval of 1640 ms.

5.1.3. Procedure

Similar to the procedure used in Experiment 2. However, to avoid pupil dilation caused by changes in luminance, the fixation cross, letters, and masks were presented in colors equiluminant with the background (17.5 cd/m^2). The fixation cross and letters were red, whereas masks were made from red and blue letter fragments. See Fig. 4 for an illustration of the trial outline in Experiment 3.

5.1.4. Pupillometry

Pupil diameter for the left eye was measured using a desktop mounted Eyelink 1000 eye tracker (SR research) sampling at a rate of 250 Hz. Gaze position was calibrated via a standard Eyelink 9-point procedure at the start of the experiment. Pupil diameter was originally recorded in arbitrary pixels, but was converted into units of mm by scaling the original diameter according to the size of a 'model pupil' of known diameter measured under the same physical conditions used for testing the participants. Eye-blinks and other noise transients were removed offline using a custom linear interpolation algorithm (see also Murphy, Vandekerckhove, & Nieuwenhuis, 2014) replacing artifactual sections of data shorter than 1.5 s. Remaining artifactual samples were identified by applying amplitude (any sample < 1 mm) and gradient (any difference in consecutive samples > 0.075 mm) thresholds to the interpolated data. A trial was excluded from further analysis if it contained at least one artifactual sample within the window −1 to 2.5 s relative

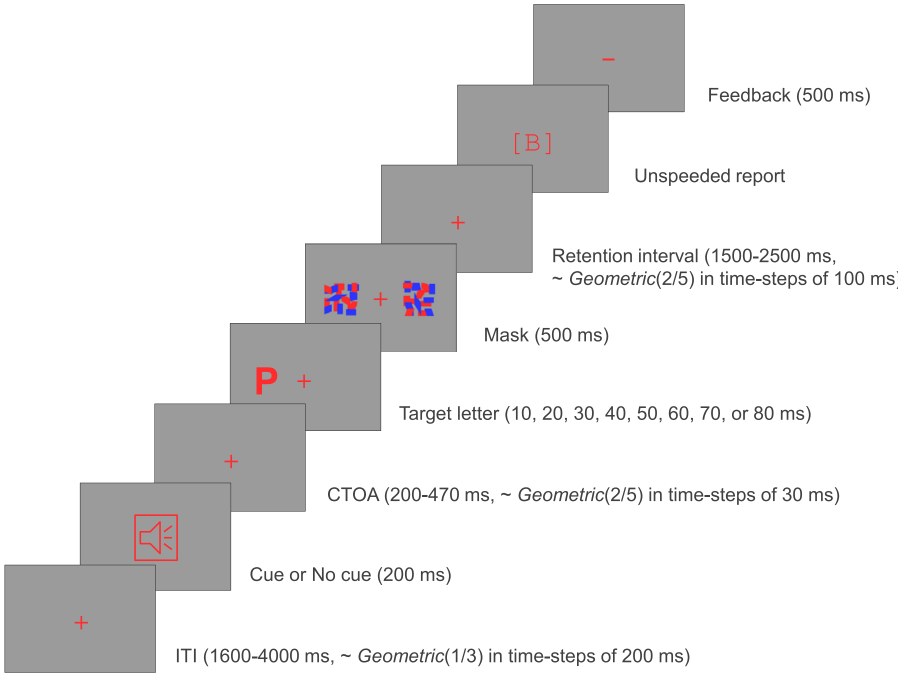

Fig. 4. Trial outline for Experiment 3.

to the time of cue onset (or the corresponding time point in the no cue condition).

5.2. Results

Fig. 3c shows mean estimates of the v and t_0 parameters from Experiment 3. As in Experiment 2, paired t tests between the no cue and 40 dB cue conditions, $t(24) = 5.47$, $p < 0.001$, $d_z = 1.09$, and between the 40 dB cue and 85 dB cue conditions, $t(24) = 2.23$, $p = 0.035$, $d_z = 0.45$, revealed an increase in processing speed, v, when a 40 dB cue was presented prior to the letter, and a further increase when a 85 dB cue was presented. Experiment 3 also replicated the previous finding of a decrease in perceptual threshold, t_0, when a 40 dB cue, $t(24) = 3.72$, $p = 0.001$, $d_z = 0.75$, or a 85 dB cue, $t(24) = 2.61$, $p = 0.015$, $d_z = 0.53$, was presented prior to the letter display compared with trials in which no cue was presented. Also corresponding with the results obtained in Experiment 2, a paired t tests showed no difference in t_0 between the two cue conditions, $t(24) = 2.01$, $p = 0.056$. Further, no significant differences were found between conditions for the guessing parameter, $\bar{p}_{g,\text{No cue}} = 0.33$, $\bar{p}_{g,\text{40dB cue}} = 0.27$, and $\bar{p}_{g,\text{85dB cue}} = 0.28$, all $ts \leq 0.743$, all $ps \geq 0.465$. For all conditions, the model explained on average 99% of the variance in the data.[1]

Technical problems prevented recording of pupil size in one of the 25 participants included in the behavioral analysis above. This resulted in a sample size of 24 (19 females, 5 males, mean age = 24.3 years) for the examination of the physiological effect of the alerting manipulation. For the remaining subjects, an average of 5% of the trials were excluded because of artifacts. Fig. 5 shows the grand average of pupil diameter for a −1 to 2.5 s window relative to the time of cue onset. Baseline pupil diameter on each trial is defined as the mean pupil diameter in the interval 1 s prior to cue onset. In the cue conditions, a biphasic pupil response is observed with one component peaking around 550 ms after cue onset and a second component with a peak around 1400 ms after cue onset. A similar biphasic pupil response to an auditory signal has previously been observed by Wetzel, Buttelmann, Schieler, and Widmann (2016) and Shiga and Ohkubo (1979), and has been associated with separate activation of the parasympathetic (early dilation) and sympathetic nervous system components (late dilation), which are involved in the generation of pupillary dilation during cognitive tasks (Steinhauer & Hakerem, 1992). A pupil response is also observed in the no cue condition which is most likely generated by the correct detection of the presented letters (Hakerem & Sutton, 1966). If so, part of the pupil response in the cue conditions must also be attributed to letter detection, such that only the differences between conditions will give an estimate of the physiological effect of the auditory cues per se. Note, that Hoeks and Levelt (1993) found the effects of auditory and visual signals on pupil response to be additive.

To compare the pupil response between conditions, we identified the maximum peak for each subjects' mean pupil dilation relative to the baseline in an early (300–800 ms after cue onset) and late time window (800–2000 ms after cue onset) for each of the three conditions. Paired t tests comparing peak pupil dilation in the early time window showed a significant difference between the no cue condition ($M = 0.056$ mm, $SD = 0.049$) and 40 dB cue condition ($M = 0.092$ mm, $SD = 0.056$), $t(23) = 8.34$, $p < 0.001$, $d_z = 1.70$, and between the 40 dB cue condition and the 85 dB cue condition ($M = 0.124$ mm, $SD = 0.52$), $t(23) = 5.43$, $p < 0.001$,

[1] For Experiment 1, a likelihood ratio test showed that a 2 × 3-parameter model (one set of v, t_0, and p_g parameters for each of the two experimental conditions) was a significantly better model compared with a 1 × 3-parameter model (same set of v, t_0, and p_g parameters across conditions), $\chi^2(84) = 491.60$, $p < 0.001$. For Experiment 2, likelihood ratio tests showed that a 2 × 3-parameter model (one set of parameters for the no cue condition; same set of parameters across the two cue conditions) was significantly better compared with a 1 × 3-parameter model (same set of parameters across all conditions), $\chi^2(84) = 810.76$, $p < 0.001$. However, neither a 3 × 3-parameter model (one set of parameters for each of the three experimental conditions) nor a 3 + 4-parameter model (one set of parameters for the no cue condition; separate v but same t_0 and p_g parameters for the two cue conditions) were found to be significantly better compared with the 2x3-parameter model, $\chi^2(84) = 78.63$, $p = 0.645$; $\chi^2(28) = 30.65$, $p = 0.333$. For Experiment 3, likelihood ratio tests showed that the 2 × 3-parameter model should be preferred over the 1 × 3-parameter model, $\chi^2(75) = 708.38$, $p < 0.001$. But neither the 3 × 3-parameter model nor the 3 + 4-parameter model were found to be significantly better compared with the 2 × 3-parameter model, $\chi^2(75) = 68.17$, $p = 0.699$; $\chi^2(25) = 21.52$, $p = 0.663$.

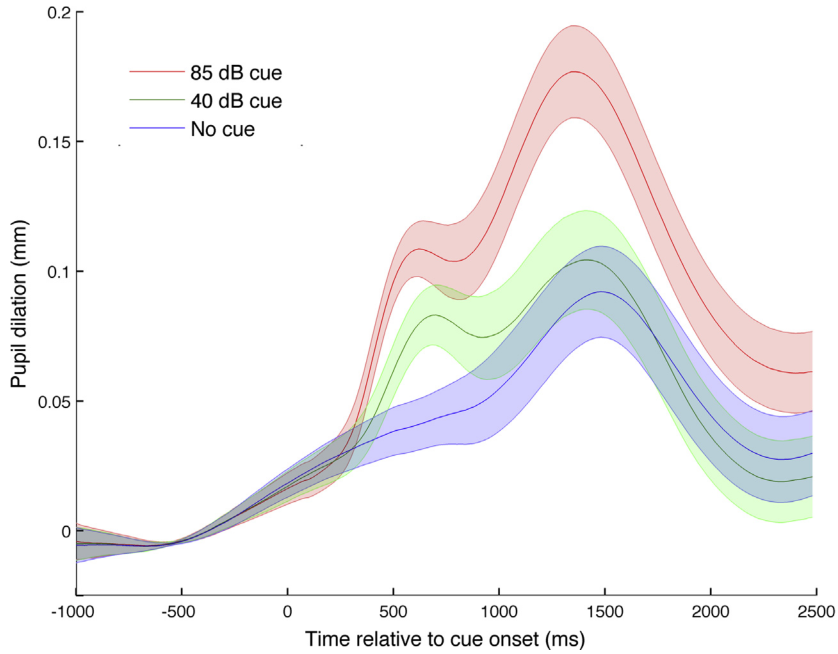

Fig. 5. Phasic pupillary responses in Experiment 3. Grand average of pupil dilation for the No cue (blue), 40 dB cue (green), and 85 dB cue conditions (red) time-locked to cue onset. Confidence bands represent standard error of the mean.

$d_z = 1.11$. Similarly, paired t tests comparing peak pupil dilation in the late time window showed a significant difference between the no cue condition ($M = 0.107$ mm, $SD = 0.082$) and 40 dB cue condition ($M = 0.122$ mm, $SD = 0.084$), $t(23) = 3.67$, $p = 0.001$, $d_z = 0.75$, and between the 40 dB cue condition and the 85 dB cue condition ($M = 0.187$ mm, $SD = 0.086$), $t(23) = 7.99$, $p < 0.001$, $d_z = 1.63$. We further identified subjects' peak pupil dilation for each individual exposure duration in the late time window. Consistently for all three experimental conditions, we found that subjects' peak pupil dilation correlated positively with their processing speed estimate, v, for exposure durations of 30 ms (all $rs > 0.41$, all $ps < 0.05$, cross-subject correlations) and 40 ms (all $rs > 0.42$, all $ps < 0.05$), but not for higher or lower exposure durations (except for 20 ms in the 40 dB cue condition, $r = 0.53$, $p < 0.05$). That is, we found a positive relationship between pupil dilation and processing speed but only when subjects were maximally challenged with exposure durations near threshold-level for which letter identification was difficult but not impossible (providing crucial information about the slope of the behavioral performance curve; see Fig. 3).

6. Discussion

In three experiments, we investigated the effect of phasic auditory alertness on early visual perception. In Experiment 1, we found that alertness lowered the perceptual threshold and increased the processing speed of visual information, running counter to the idea that alerting only speeds up motor responses and does not influence perceptual information processing (Posner, 1978; Posner & Petersen, 1990; Sanders, 1980). Presenting a visual alerting cue prior to a whole report display, Matthias et al. (2010) provided equivalent evidence that alerting increases processing speed, but they did not investigate effects on the perceptual threshold. Instead, they examined the effect of alerting on visual short-term memory (VSTM) capacity and on the spatial distribution of attentional resources, finding no modulation of VSTM capacity but a short-lived rightward shift of attentional resources following alerting. The effect of alerting on perceptual thresholds has, however, been addressed by Kusnir et al. (2011), who asked subjects to detect and discriminate near-threshold visual stimuli preceded by a phasic alerting cue in 50% of trials. Equivalent to our findings, Kusnir et al. (2011) reported faster and more accurate responses to near-threshold stimuli in alerting trials, suggesting that the limit for conscious perception is affected by states of arousal. Additionally, Jepma et al. (2009) investigated the effects of accessory stimuli on information processing by a diffusion model analysis. The accessory stimulus was a task-irrelevant sound presented very shortly before the visual stimulus to be identified; CTOA was 30 ms in one experiment and 100 ms in another one. According to the diffusion model analysis, the accessory stimulus speeded up the onset of the process of evidence accumulation (corresponding to a decrease in the t_0 parameter of TVA) but not the ensuing rate of evidence accumulation (corresponding to the v parameter of TVA). In our experiments, CTOA ranged between 200 ms and 470 ms with a mean of 244 ms. The contrast between our results and those of Jepma et al. may have resulted from participants using different strategies depending on the time available for processing the cue. In any case, the results of Experiment 1 are in line with previous research showing that phasic alerting influences early perception by both lowering the visual threshold and increasing the processing speed.

In Experiment 2, we investigated how alerting intensity influences visual perception and found that processing speed increased with the intensity of the alerting cue (higher processing speed in the 85 dB cue condition compared with the 40 dB cue condition), whereas the perceptual threshold was unaffected (equal thresholds in the 85 dB and 40 dB cue conditions). Thus, the results of Experiment 2 indicate a direct correspondence between levels of alertness and processing speed, whereas the perceptual threshold seems to be equally reduced regardless of the level of phasic alerting. It should be noted however that the differences between the cue conditions were of modest effect sizes (see also post hoc model comparisons; Footnote 1).

Behar and Adams (1966; see also Adams & Behar, 1966; Loveless & Sanford, 1975; Ulrich & Mattes, 1996) have previously investigated how different levels of auditory alertness influence reaction times to visual stimuli and found that reaction times decreased with increasing intensities. Also, Keuss (1972) had subjects make a speeded response to an auditory stimulus preceded by an auditory alerting cue and found a decrease in reaction time with increasing cue intensities. Our results are consistent with these findings, but additionally show that intensity manipulation of alertness is directly linked to changes in early perceptual processes and not only motoric processes. To the best of our knowledge, this is the first time that the relation between manipulation of alerting intensity and a pure accuracy-based measure of early visual perception, unconfounded by motor processes, has been investigated.

Bundesen et al. (2015) have proposed a mathematical relationship between levels of alertness and visual processing speed by decomposing the visual bias, β_i, associated with category i in the rate equation of TVA (see Eq. (1)), into a product of three terms:

$$\beta_i = Ap_iu_i, \tag{4}$$

where A is the level of alertness, p_i is the subjective prior probability of being presented with feature i, and u_i is the subjective importance (utility) of identifying feature i. This multiplicative structure suggests that the visual processing speed increases monotonically with the level of alertness, A, which is in agreement with our behavioral data (see Fig. 3).

Eq. (4) may also be understood in neural terms. According to the neural interpretation of TVA (NTVA) proposed by Bundesen et al. (2005), β_i corresponds to the level of activation in the population of cortical cells that represents the categorization i (e.g., "M" in case of letter recognition). If the level of alertness A is increased, β_i is similarly upscaled, which results in faster processing of the visual categorization i. At the neural level, an increase in alertness should therefore be reflected in a directly proportional increase of activity in the cells that are specialized to represent the categorization.

Additional research will, however, be required to further validate the multiplicative structure of Eq. (4) by, for instance, setting up more complicated factorial designs, in which the level of alertness, A, is systematically varied in combination with manipulations of either the prior probability of being presented with a certain feature, p_i, or the utility of identifying a certain feature, u_i.

Changing the level of alertness, of course, also has more general effects in the brain. In Experiment 3, we replicated the results of Experiment 2 and also examined the general neurophysiological effects of phasic auditory alerting by measuring the pupil size of participants. Phasic pupillary responses have previously been linked to the intensity aspect of attention (alertness); larger pupillary responses indicating higher levels of attentional involvement (e.g., Kahneman, 1973). Also at the neurophysiological level, a close relationship has been established between pupil size and the norepinephrine system (Aston-Jones & Cohen, 2005) that is centrally involved in the brain's regulation of alertness (Posner & Rothbart, 2007; Tona et al., 2016). By manipulating alerting intensities, we found systematic relations between phasic pupillary responses and visual processing speed: At the general level, both pupillary responses and visual processing speed increased significantly when participants were phasically alerted. In addition, both measures increased further when the phasic alerting was intensified from 40 dB to 85 dB. At the individual level, participants with relatively high visual processing speed exhibited larger pupillary responses at exposure durations near threshold-level (see also Hakerem & Sutton, 1966), in all three conditions of the experiment, compared to participants with relatively low visual processing speed. Both the general and individual patterns of results provide support for a systematic relationship between visual processing speed and the level of alertness. A plausible interpretation of the general pattern of results is that auditory phasic alerting increases the brain's level of arousal, evident in larger pupillary responses, which also causes an increase in visual processing speed as described in Eq. (4). The individual pattern of results can similarly be accounted for by assuming that participants who are more strongly alerted by the auditory cue, as reflected in larger pupil responses, also tend to have higher visual processing speed than other participants (in accordance with Eq. (4)). The fact that participants with larger pupil responses tend to have higher visual processing speed even in the baseline condition (i.e., no cue condition) might be explained by the alerting effect of the letter stimuli: Participants must concentrate strongly in order to identify the brief letter stimuli, and the sudden onset of the stimulus display on the screen presumably has an alerting effect by itself. Participants who are more strongly alerted than others by the onset of the display, reflected in larger pupil responses, should also receive a larger boost in their visual processing speed (cf. Eq. (4)).

Our findings also have potential implications for studies of phasic alerting in patients with visual neglect after right hemisphere damage. It has been shown that the spatial imbalance in attentional weighting that is characteristic of neglect patients can be briefly normalized by phasic alerting (Robertson et al., 1998). Finke et al. (2012) followed up on this finding to study the effects of phasic alerting on specific TVA parameters in patients with visual neglect. As well as normalizing the spatial distribution of attentional weights, Finke et al. found that phasic alerting increased the patients' visual processing speed. Given the findings of the present investigation, it would be interesting to study whether visual processing speed in neglect patients also increases monotonically with alerting intensity.

Together, the three experiments of the present study provide support for a close relationship between phasic alerting and specific aspects of visual perception: visual processing speed and the perception threshold. Whereas perceptual thresholds seem to be lowered regardless of the level of alerting, a positive relationship was found between the intensity of the alerting manipulation and the resulting level of visual processing speed. These findings are in accordance with a newly proposed extension of the mathematical TVA model, which incorporates alerting effects into this general model of visual attention.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2017.04.004.

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