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Inter-individual variations in internal noise predict the effects of spatial attention

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ABSTRACT

Individuals differ considerably in the degree to which they benefit from attention allocation. Thus far, such individual differences were attributed to post-perceptual factors such as working-memory capacity. This study examined whether a perceptual factor – the level of internal noise – also contributes to this inter-individual variability in attentional effects. To that end, we estimated individual levels of internal noise from behavioral variability in an orientation discrimination task (with tilted gratings) using the double-pass procedure and the perceptual-template model. We also measured the effects of spatial attention in an acuity task: the participants reported the side of a square on which a small aperture appeared. Central arrows were used to engage sustained attention and peripheral cues to engage transient attention. We found reliable correlations between individual levels of internal noise and the effects of both types of attention, albeit of opposite directions: positive correlation with sustained attention and negative correlation with transient attention. These findings demonstrate that internal noise – a fundamental characteristic of visual perception – can predict individual differences in the effects of spatial attention, highlighting the intricate relations between perception and attention.

1. Introduction

Individuals often vary greatly in their performance in behavioral tasks. Differences in observers' performance are usually treated as noise in the data, and the majority of studies of human behavior focus on averages across individuals. However, individual differences could be very informative, and they likely arise from a multitude of factors, such as differences in optical, neural, and cognitive processes (de-Wit & Wagemans, 2015; Mollon, Bosten, Peterzell, & Webster, 2017; Wilmer, 2008). When regarding performance in attentional tasks, individual differences are well documented (e.g., Huang, Mo, & Li, 2012; Marciano & Yeshurun, 2017; Moosbrugger, Goldhammer, & Schweizer, 2006; Rosenberg, Finn, Scheinost, Constable, & Chun, 2017). Nevertheless, the correlates of performance in attentional tasks are not yet well understood. In this study we focused on covert spatial attention – the deployment of attention to a location in the visual field in the absence of eye movements. Covert attention is often divided into two distinct subtypes (e.g., Carrasco, 2011; Jonides, 1981; Nakayama & Mackeben, 1989; Posner, 1980). Sustained attention is the slower, long-lasting voluntary deployment of attention that usually occurs in response to a symbolic central cue such as an arrow that points towards the to-be-attended location. Transient attention is the fast, automatic capture of attention triggered by the sudden onset of a cue that is usually presented peripherally near the to-be-attended location. These two types of attention could produce differential effects on perceptual processes, suggesting that they may be mediated by different mechanisms (e.g., Barbot, Landy, & Carrasco, 2012; Briand, 1998; Briand & Klein, 1987; Carrasco, 2011; Giordano, McElree, & Carrasco, 2009; Hein, Rolke, & Ulrich, 2006; Jigo & Carrasco, 2020; Müller & Rabbitt, 1989; Yeshurun, Montagna, & Carrasco, 2008). For instance, some studies have demonstrated external noise reduction and signal enhancement following a peripheral cue but only external noise reduction following a central cue (Lu & Dosher, 2000; Lu & Dosher, 2005). Additionally, several neurophysiological studies suggested that these two types of attention result in distinct patterns of neural activation (e.g., Corbetta & Shulman, 2002; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Ibos, Duhamel, & Hamed, 2013). Regardless of the type of covert attention, the investigation of individual differences in performance in spatial attention tasks has focused mostly on factors such as working memory (e.g., Bengson & Mangun, 2011; Fukuda & Vogel, 2011; Kreitz, Furley, Memmert, & Simons, 2015; Machizawa & Driver, 2011), brain structure and functionality (Chechlacz, Gillebert, Vangkilde, Petersen, & Humphreys,

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2015; Niogi, Mukherjee, Ghajar, & McCandliss, 2010; Störmer, Passow, Biesenack, & Li, 2012), and personality traits (Bates & Stough, 1997; Robinson, Zabelina, Ode, & Moeller, 2008). Yet, the possibility that perceptual mechanisms are related to individual differences in the ability to benefit from the advance allocation of spatial attention remains mostly unexplored. Here, we examined the relation between individual differences in spatial attention and a fundamental characteristic of the perceptual system – internal noise.

Internal noise can be conceptualized as variability in an observer's internal response that is not due to variability in the external stimulus. To illustrate, in a typical psychophysical experiment, when the observers are presented with the same stimulus on different trials, their response will often vary, even though the visual stimuli presented were identical. This behavioral variability is attributed to internal noise. Internal noise is introduced at every stage of visual processing from stimulus to perception (Hurlbert, 2000), and several sources of variability are thought to contribute to internal noise in the visual system. Noise is introduced at the molecular, cellular, and synaptic level (Faisal, Selen, & Wolpert, 2008) due to mechanisms such as photoreceptor sampling errors (Geisler, 1989) and variance of neuronal firing rate (Tolhurst, Movshon, & Dean, 1983). Psychophysical methods have been developed throughout the years to estimate a participant's level of internal noise based on behavioral variability (Burgess & Colborne, 1988; Green, 1964; Pelli & Farell, 1999). These methods have been used to characterize internal noise as a feature of the perceptual system (Neri, 2010; Vilidaite, Yu, & Baker, 2017) and to investigate the role of internal noise in perceptual tasks (Diependaele, Brysbaert, & Neri, 2012; Ratcliff, Voskuilen, & McKoon, 2018). In particular, the double-pass consistency method is regarded as a 'gold standard' for directly estimating internal noise in the human perceptual system (e.g., Burgess & Colborne, 1988; Diependaele et al., 2012; Gold, Bennett, & Sekuler, 1999; Hasan, Joosten, & Neri, 2012; Lu & Dosher, 2008; Ratcliff et al., 2018; Tolhurst et al., 1983; Vilidaite et al., 2017). This method relies on the core assumption that if the same stimulus is presented twice to an observer, any inconsistency in the response to the stimulus should be attributed to internal noise. In the double-pass procedure, external variability is added to a stimulus, usually in the form of random Gaussian noise, generating a number of unique instances of the stimulus. Each unique instance of the stimulus is repeated in a second pass creating pairs of identical trials. Agreement in the participant's response is measured as the proportion of pairs of identical trials in which the participant gave the same answer, no matter if the answer was correct or not. In general, high agreement in the double-pass procedure indicates a low degree of internal noise and low agreement indicates a high degree of internal noise. Additionally, fitting a computational model to the double-pass data can generate an estimation of internal noise based on a given model. For instance, the Perceptual Template Model (PTM; Lu & Dosher, 2008) is a prominent observer model that includes two internal sources of variance: internal additive noise, which remains constant at all signal levels, and internal multiplicative noise, which is proportional to the signal strength. When stimuli are relatively weak, the response is mainly limited by additive internal noise, but when stimuli are strong multiplicative noise becomes the main limiting factor (Kontsevich, Chen, & Tyler, 2002; Lu & Dosher, 2000; Solomon & Tyler, 2017). In other words, performance near the detection threshold is affected mainly by additive noise while performance in supra-threshold discrimination is affected mainly by multiplicative noise. Additive internal noise can be considered to reflect mainly spontaneous neural activity (Kontsevich et al., 2002), while multiplicative noise is mostly linked to specific neural responses (Harris & Wolpert, 1998; Kontsevich et al., 2002). Additionally, multiplicative noise is the basis for Weber-law behavior while additive noise is the basis for absolute sensory thresholds (Lu & Dosher, 2000). Fitting the PTM to the double-pass data would yield a parameter that estimates additive internal noise and another that estimates multiplicative internal noise.

The main goal of the current study was to test whether individual differences in internal noise predict individual differences in the effects of sustained attention and/or transient attention. To that end, we examined the relationship between internal noise and attention using both central and peripheral spatial cues. Internal noise reduction has been suggested as a possible mechanism through which attention might enhance performance (Lu & Dosher, 2000; Yeshurun & Carrasco, 1999). In addition, studies have found evidence of reduced neural variability following attentional cues (Arazi, Yeshurun, & Dinstein, 2019; Cohen & Maunsell, 2009; Mitchell, Sundberg, & Reynolds, 2007). For instance, a recent study demonstrated reduced variability in the EEG signal following a central spatial cue that informed the participants of the most likely location of an upcoming target (Arazi et al., 2019). Here, we did not ask which aspects of perception are affected by spatial attention, as did many of the previous studies that considered the relations between attention and internal noise (e.g., Arazi et al., 2019; Cohen & Maunsell, 2009; Lu & Dosher, 2000; Lu & Dosher, 2005). Instead, we asked a complementary question: whether a core aspect of visual perception – internal noise – predicts the extent to which attention affects performance. Importantly, we focused on behavioral variability measured in a psychophysical procedure that was separate from the measurement of attentional effects.

We built on the aforementioned double-pass procedure employed with centrally presented tilted gratings (Gabor patches) and an orientation discrimination task. We then estimated individual levels of internal noise by fitting the PTM to the results of the double-pass procedure. In separate sessions, we measured attentional effects using a spatial cueing paradigm (Posner, 1980) in two different versions. In the sustained attention paradigm, we employed central cues to direct attention, and in the transient attention paradigm, a small horizontal line presented peripherally served to attract attention to a location. Given that a significant positive correlation has been found between individual levels of EEG variability and effects of sustained attention on accuracy (Arazi et al., 2019), we expected to find a positive correlation between the level of internal noise estimated with the double-pass procedure and the effect of spatial attention on accuracy when using a central cue. This hypothesis was not specific to one type of internal noise (additive or multiplicative) as this distinction was not discussed in Arazi et al. Furthermore, the relation between internal noise (neuronal or behavioral) and transient attention was not examined before, and although many have found similar effects for transient and sustained attention, some have found different patterns of effects (e.g., Barbot, Landy, & Carrasco, 2012; Briand, 1998; Briand & Klein, 1987; Carrasco, 2011; Giordano, McElree, & Carrasco, 2009; Hein et al., 2006; Jigo & Carrasco, 2020; Lu & Dosher, 2005; Müller & Rabbitt, 1989; Yeshurun, Montagna, & Carrasco, 2008). Thus, we did not have a specific hypothesis regarding the correlation between internal noise and spatial attention when using peripheral cues.

2. Methods

2.1. Participants

Thirty-two students from the University of Haifa participated in this study. One participant was removed due to an exceedingly high proportion of eye movements in the sustained attention task (22%) and another due to a particularly low level of agreement in the double-pass procedure (56% compared to the group mean of 76% with an SD of 5%). Therefore, the results reported here are based on data from the remaining thirty participants. All participants reported normal or corrected to normal vision and no history of neurological disorders. Participants were naïve to the purpose of the study. The study was approved by the ethics committee of the University of Haifa.

The sample size was chosen based on a study that examined the relationship between EEG variability and attention (Arazi et al., 2019). Pearson's correlations in said study ranged between $r = 0.41$ and $r = 0.61$. A power analysis conducted with G*Power (Faul, Erdfelder, Lang,

& Buchner, 2007) using the average effect size of $r = 0.48$ and an alpha level of 0.05 indicated that a sample size of 30 participants ensures sufficient statistical power (0.87).

2.2. Stimuli and apparatus

2.2.1. General

Stimuli were generated and presented using Psychopy (Peirce et al., 2019) on a 19-in. linearized monitor of an IBM-compatible PC (1280 × 1024 resolution at a refresh rate of 85 Hz). Eye movements during the sustained attention task were recorded from the right eye with an Eye-Link 1000 eye tracker (temporal resolution of 1000 Hz; SR Research, Ottawa, ON, Canada) to ensure participants fixated the center of the screen at all times.

2.2.2. Double pass procedure

The method of constant stimuli was used in this task. Stimuli were presented on a gray background. The fixation mark was a black square outline spanning 2°x2° of visual angle with a line width of 0.1°. The target stimuli were Gabor patches (Gaussian windowed sinusoidal gratings) tilted 45° to the left or to the right from vertical (Fig. 1a). The gratings were rendered on a 64 × 64 pixel grid, which amounted to approximately 2°x2° of visual angle. Gaussian white noise images were created using 2 × 2 pixel elements to also span a 64 × 64 pixel grid. The contrast of each element was drawn from a Gaussian distribution with a mean of 0 and an SD of 0.10 (low external noise condition) or 0.33 (high external noise condition). For each external noise condition, 5 different target contrast levels were chosen for each participant in a calibration session. Stimuli in the calibration session were identical to those used in the experimental session except that a wider range of target contrasts was used for each noise level. A psychometric function was fit to the results of the calibration session and five contrast levels were chosen to be used in the experimental session to span a wide range of performance levels.

2.2.3. Sustained attention paradigm

Stimuli were presented on a black background. The fixation cross was a white plus sign spanning 1 × 1° of visual angle. The target was a white outline square (side: 1°, line width: 0.1°). The square contained a small aperture, either on its left side or on its right side (Fig. 1b). The size of the aperture was determined separately for each individual in a calibration session using a QUEST procedure (Watson & Pelli, 1983) that was performed just prior to starting each of the attention paradigms. We aimed for an aperture size that would lead to performance of about 75% correct. In the valid and invalid trials, the cue was a white arrow spanning 0.5 × 0.5°, and in the neutral trials, the cue was a white circle with a diameter of 0.5°. The target was displayed in one of four possible locations at an eccentricity of 5.5° from the center of the display, and it was followed by a random dot square mask of size 1.4° at the same location.

2.2.4. Transient attention paradigm

The stimuli in this task were identical to those in the sustained attention paradigm except for the following: The cue was a white horizontal line spanning 0.5 × 0.14° of visual angle positioned 0.1° above the cued location. The neutral cue was comprised of 4 such lines, one over each possible location (Fig. 1c).

2.3. Procedure

2.3.1. General

The participants placed their head on a chin rest throughout the

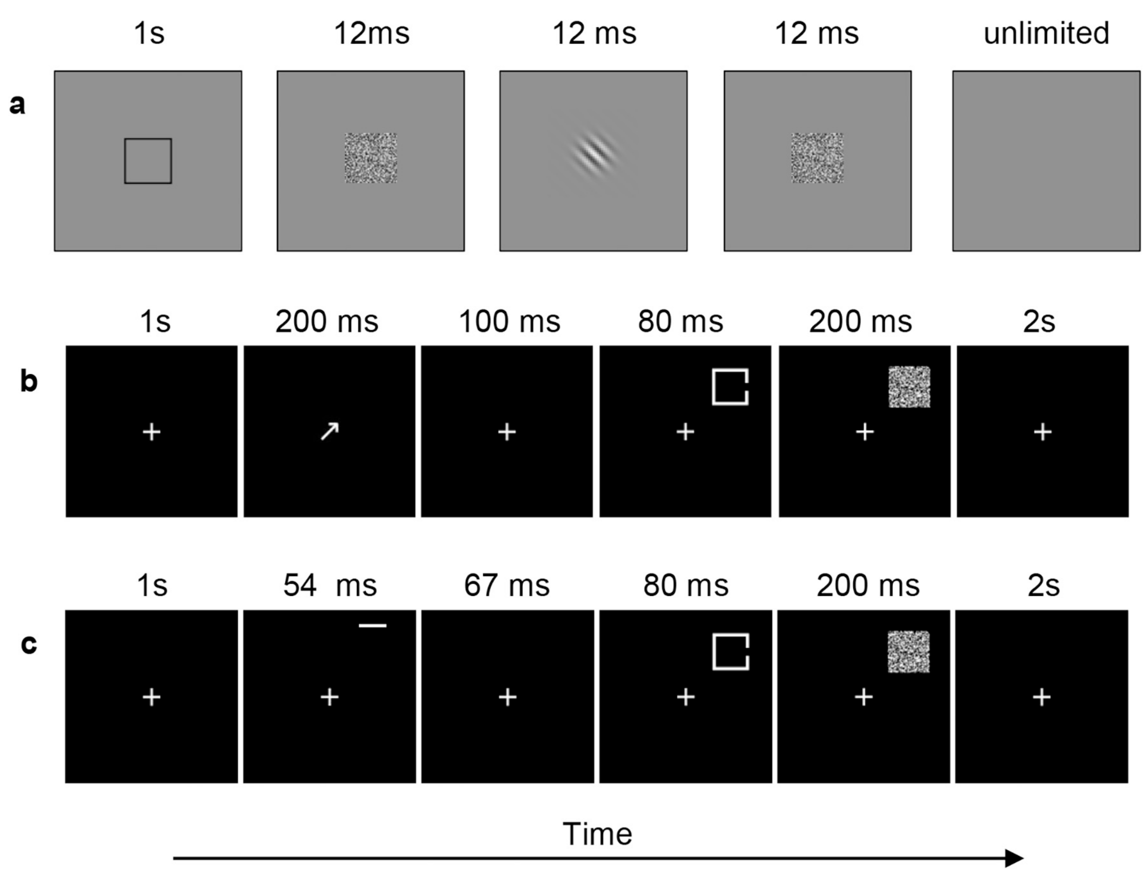

Fig. 1. The sequence of events in a single trial of the different tasks employed in this study. (a) Double-pass procedure. (b) Sustained attention paradigm. (c) Transient attention paradigm.

experiment and were asked to fixate the center of the screen. All participants completed the tasks over two days in the same order: The double-pass calibration followed by the sustained attention paradigm on the first day, and the double-pass procedure followed by the transient attention paradigm on the second day. Each daily session took approximately 75 min to complete. We chose to administer the tasks in a fixed order to minimize the impact of task-order on individual differences (Goodhew & Edwards, 2019). Note that the main focus of this study was individual differences, therefore a fixed order was chosen to avoid a possible confound between task order and the effect of individual differences. In some cases, counterbalancing might be considered in order to reduce the effect of learning or fatigue on task outcomes, but this comes at the cost of introducing additional inter-individual variability to the data. That is, counterbalancing not only increases 'irrelevant' variance in the data, it also introduces a confound with individual differences, because it is hard to tell which aspects of the differences between individuals arise from the different tasks' order and which from actual individual differences. Furthermore, even though a direct comparison of the magnitude of the effects of the two types of attention was not at the focus of this study, in order to minimize the effects of learning on accuracy in the attentional tasks, task difficulty was determined individually for each participant before they performed each of the attentional tasks.

2.3.2. Double-pass procedure

A trial commenced with the fixation mark in the middle of the screen which lasted for 1 s (Fig. 1a). Then the external noise image was displayed for 12 ms (the duration of 1 frame) followed by the target for 12 ms and then the same external noise image was displayed again for 1 frame. Temporal summation of the noise and target stimuli was used instead of direct summation to guarantee linearity in the summation process (e.g., Lu & Dosher, 2000; Lu & Dosher, 2008; Xu, Lu, Qiu, & Zhou, 2006). Note that due to the rapid presentation of the frames this sequence results in perceptual merging of the target and the noise. This is normally done in PTM experiments to allow finer adjustments of target contrast (e.g., Lu & Dosher, 1998; Park, Schauder, Zhang, Bennetto, & Tadin, 2017). Participants had unlimited time to indicate whether the grating was tilted to the left or to the right. A total of 600 (2 external noise levels x 5 target contrast levels x 60 repetitions) unique combinations of target contrast and external noise were presented to the participants. The same 600 trials were repeated in the same order in a second pass as soon as the first pass was completed. Participants were unaware of the fact that trials were repeated a second time.

2.3.3. Sustained attention paradigm

Each trial began with a fixation cross in the center of the display for 1 s (Fig. 1b). The cross was replaced either by the arrow cue pointing to one of four possible locations or the circle cue (neutral condition). The cue was displayed for 200 ms, followed by a 100 ms ISI (Inter-Stimulus-Interval). The target was then displayed for 80 ms before being replaced by the mask for 200 ms. The arrow cue correctly predicted the target location on 75% of cued trials (valid condition). On the remaining 25% of cued trials, the target appeared in one of the other 3 locations (invalid condition). Following the neutral cue, the target could appear equally often in each of the four locations. The participants had to indicate, as fast and as accurately as possible, which side of the target had an aperture. If 2 s had passed without a response the current trial ended and the next trial began. We chose this task because it has been repeatedly demonstrated that it is affected by the allocation of spatial attention (e.g., Bonder, Gopher, & Yeshurun, 2018; Montagna, Pestilli, & Carrasco, 2009; Yeshurun & Carrasco, 1999; Yeshurun & Levy, 2003). The 3 cueing conditions (valid, invalid, neutral) were randomly mixed within a block. Each participant completed 20 practice trials prior to the experimental trials. There were 144 valid, 48 invalid, and 96 neutral trials for a total of 288 experimental trials.

2.3.4. Transient attention paradigm

The procedure was identical to the sustained attention procedure described above except for the following: the cue was displayed for 54 ms with an ISI of 67 ms between cue and target (Fig. 1c). In cued trials, the target had a 50% chance of appearing at the cued location and a 50% chance of appearing at one of the other locations. Each participant completed 60 valid, 60 invalid, and 60 neutral trials for a total of 180 experimental trials.

2.4. Model fitting

We fit the double-pass data with the PTM to estimate internal multiplicative noise and additive internal noise parameters. The mathematical basis for the double-pass procedure was developed extensively by Burgess and Colborne (1988) and it was later extended and adapted to the PTM by Lu and Dosher (2008; see Appendix for a brief description). The proportion of correct trials and the proportion of agreement between the passes was calculated for each participant for each level of external noise and each target contrast level. The PTM equations were used to predict the proportion correct and the proportion agreement separately for each observer using the least-squares method. We used the R (Version 3.5.0; R Core Team, 2020) function optim with a simplex algorithm (Nelder & Mead, 1965) to find the parameters that produced the smallest prediction errors separately for each participant. To avoid local minima, the model fitting process was repeated a hundred times per participant with different starting parameters each time and the fit with the lowest degree of prediction error was selected.

3. Results

3.1. Data preparation

Trials containing eye movements were removed from the analysis (10% of all sustained attention paradigm trials). Trials with an RT larger/smaller than 2 SD from the mean of each observer were removed from all RT analyses (this resulted in the removal of approximately 5% of trials in the sustained attention paradigm and 4% of trials in the transient attention paradigm). Attentional effect scores were calculated for each participant as the difference in performance between the valid and invalid conditions separately for each of the attentional paradigms (e.g., Arazi et al., 2019; Bates & Stough, 1997; Bengson & Mangun, 2011). To calculate accuracy effects, we subtracted each individual's mean accuracy in the invalid condition from mean accuracy in the valid condition, so that a positive score would mean higher accuracy in the valid condition. To calculate RT effects, we subtracted each individual's mean correct RT in the valid condition from correct RT in the invalid condition, so that a positive score would mean faster RT in the valid condition.

Variables were assessed for normality using a Shapiro-Wilk test. The results for mean accuracy and RT in both attentional tasks as well as threshold sizes and multiplicative noise were not significant (all *p*-values above 0.235), suggesting that these samples likely come from a normally distributed population. However, in the case of additive noise, the Shapiro-Wilk test was significant ($p < .001$). Hence, non-parametric tests (Spearman correlations) were used wherever additive internal noise is concerned.

3.2. Double pass procedure

Agreement was calculated as the proportion of pairs of identical trials in which the participant provided the same response. Accuracy was calculated as the proportion of correct responses in both passes combined. The proportion of correct trials and the proportion of agreement between passes were calculated for each of our 30 participants for each level of external noise and each target contrast. To estimate individual levels of both additive and multiplicative internal noise, the PTM was fitted to individual data. On average, the fit explained 97% of the variance in the accuracy data and 90% of the variance in the agreement data (Fig. 2). The mean value of the estimated additive internal noise parameter was 0.007 (SD = 0.009). The mean value of the estimated multiplicative internal noise parameter was 1.332 (SD = 0.355). These values are similar to what has been reported by other studies (Lu & Dosher, 2008; Park et al., 2017).

3.3. Sustained attention paradigm

To assess the behavioral effect of attention, a repeated-measures one-way analysis of variance (ANOVA) with cueing condition (valid, invalid, neutral) as the independent variable was performed on both correct RT and accuracy data. The RT analysis revealed a significant effect of cueing condition ($F_{(2, 58)} = 39.382$, $p < .001$; $\eta_p^2 = 0.576$, Fig. 3a). Planned comparisons revealed the expected attentional effect: the mean RT in the valid condition was significantly shorter than the mean RT in the invalid condition ($t_{(29)} = 7.974$, p < .001, one-tailed, 95% CI [26.693, 45.108]). We also found a benefit for valid cues: mean RT was significantly faster in the valid condition than in the neutral condition ($t_{(29)} = 7.365$, p < .001, one-tailed, 95% CI [26.561, 46.986]). We did not find a cost for invalid cues: mean RT in the invalid condition was not significantly different from mean RT in the neutral condition ($t_{(29)} = 0.187$, $p = .573$, one-tailed, 95% CI [−10.440, 8.695]). Please note that one-tailed tests are used here as the effect of attention on perceptual tasks involving spatial resolution is well documented (e.g., Bonder et al., 2018; Carrasco, Williams, & Yeshurun, 2002; Montagna et al., 2009; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 1999; Yeshurun & Levy, 2003; see Carrasco & Yeshurun, 2009 for a review). Since attention has been consistently shown to improve spatial resolution, there is no theoretical reason to expect an effect in the opposite direction. One-tailed tests are explicitly reported whenever used. All tests that are not explicitly reported as one-tailed are two-tailed. The accuracy analysis (Fig. 3b) did not reveal a significant effect of cueing condition (this lack of a significant effect will be discussed later on). Importantly, there was no evidence of a speed-accuracy trade-off.

3.4. Transient attention paradigm

We performed a one-way (cueing condition – valid, invalid, neutral) repeated-measures ANOVA on correct RT and accuracy data of this paradigm. The RT analysis revealed a significant effect of cueing condition ($F_{(2, 58)} = 28.581$, $p < .001$, $\eta_p^2 = 0.496$; Fig. 4a). As with the sustained attention paradigm, we found a significant attentional effect: Participants were significantly faster in the valid condition than in the other conditions (invalid: $t_{(29)} = 7.386$, p < .001, one-tailed, 95% CI [26.699, 47.148]; neutral: $t_{(29)} = 5.011$, p < .001, one-tailed, 95% CI [13.727, 32.663]). Participants were also significantly faster to respond in the neutral condition than in the invalid condition ($t_{(29)} = 2.657$, $p = .006$, one-tailed, 95% CI [3.161, 24.296]), indicating that peripheral cues produced a benefit when appearing at the correct location and a cost when appearing at an incorrect location.

The accuracy analysis also revealed a significant effect of cueing condition ($F_{(2,58)} = 4.598$, $p = .014$, $\eta_p^2 = 0.137$; Fig. 4b). Planned comparisons revealed significantly higher accuracy in the valid condition compared to the other conditions (invalid: $t_{(29)} = 3.156$, $p = .002$, one-tailed, 95% CI [0.013, 0.060]; neutral: $t_{(29)} = 2.028$, $p = .026$, one-tailed, 95% CI [0.000, 0.047]). The difference in accuracy between the invalid condition and the neutral condition was not statistically significant ($t_{(29)} = 0.974$, $p = .169$, one-tailed, 95% CI [−0.014, 0.040]). Given that similar effects were found for RT and accuracy we can rule out the presence of a speed-accuracy trade-off in this task as well.

3.5. General task parameters and relationships with internal noise

Participants completed all paradigms in a fixed order: the sustained attention paradigm was completed during the first session and the transient attention paradigm was completed during a second session on a different day. To minimize the potential effect of perceptual learning on accuracy, we measured threshold size (i.e., the opening size that leads to an accuracy level of about 75%) prior to each attentional paradigm and used the obtained threshold size in the corresponding experimental session. As expected, we found that threshold size in the sustained attention paradigm (M = 0.226°, SD = 0.087) was significantly larger ($t_{(29)} = 3.554$, $p = .001$, 95% CI [0.021, 0.077]) than threshold size in the transient attention paradigm (M = 0.177°, SD = 0.077), indicating a significant effect of perceptual learning. Importantly, the difference in accuracy between the sustained attention (M = 0.753, SD = 0.13) and the transient attention (M = 0.767, SD = 0.12) sessions was not significant ($t_{(29)} = 0.546$, $p = .589$, 95% CI [−0.067, 0.039]), indicating that we were indeed able to minimize the effects of perceptual learning on accuracy. Still, participants were significantly faster ($t(29) = 7.089$, p < .001, 95% CI [50.644, 91.714]) in the transient attention paradigm (M = 525 ms, SD = 75) than in the sustained attention paradigm (M = 596 ms, SD = 91). This finding could also be attributed to perceptual learning but it could also be attributed to other task-related factors such as changes in motor preparation due to practice. Critically, the internal noise parameters did not significantly predict overall accuracy, RT, or

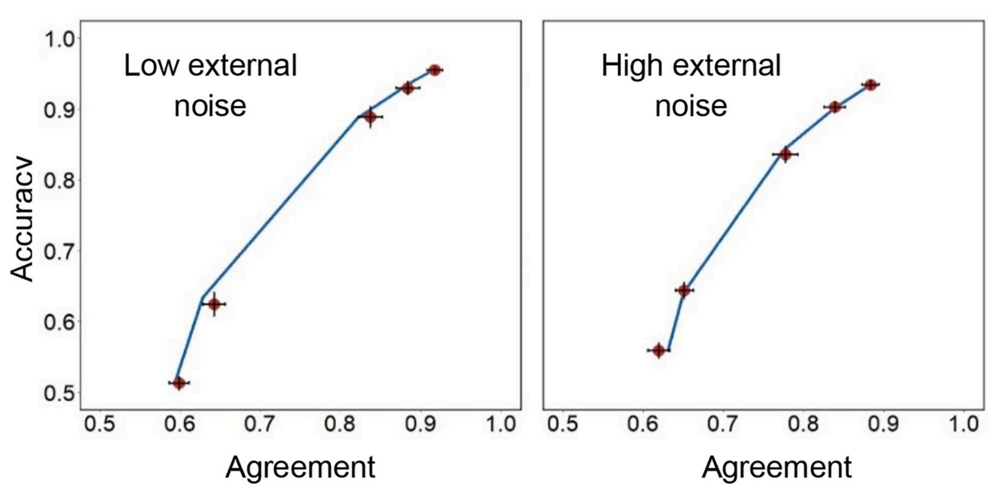

Fig. 2. Accuracy (proportion of correct responses in both passes) and agreement (proportion of trials in which the same answer was given in the two passes, regardless of accuracy) in the double-pass procedure. Red dots represent observed data and blue lines represent PTM predictions. Error bars correspond to ±1 standard error (SE) of the mean.

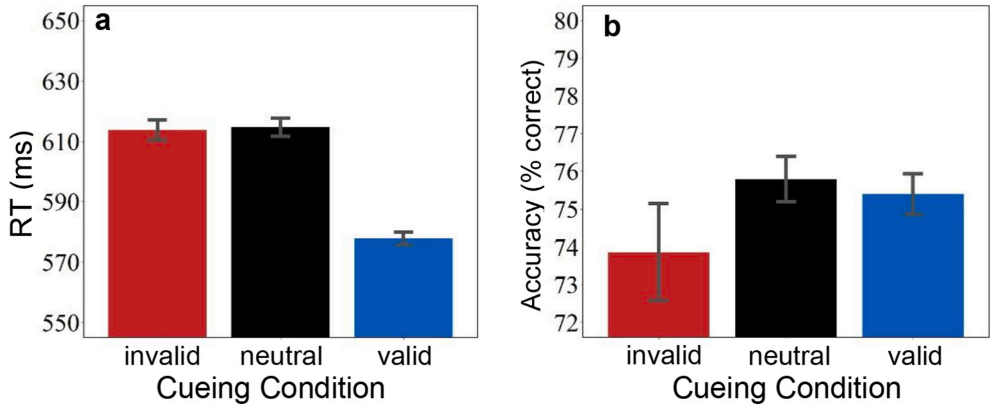

Fig. 3. (a) mean RT and (b) accuracy as a function of cueing condition in the sustained attention paradigm. Error bars correspond to ±1 within-subject SE (Cousineau, 2005).

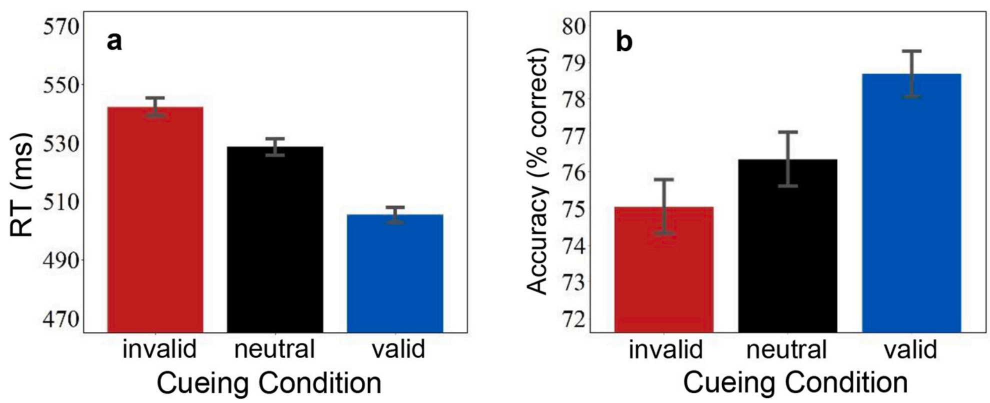

Fig. 4. (a) Mean RT and (b) accuracy as a function of cueing condition in the transient attention paradigm. Error bars correspond to ±1 within-subject SE.

threshold size in either task (all p values > .103). Thus, it is unlikely that the noise parameters reported here reflect a general ability to control attention or arousal level. Finally, attentional effects in the sustained and transient paradigms were not significantly correlated with each other in RT ($r_{(30)} = 0.039$, $p = .836$) or in accuracy ($r_{(30)} = 0.299$, $p = .109$). This is not surprising considering these are two different types of attention. However, this last observation should be taken with caution because a direct comparison between the two types of attention was not the aim of this study, and accordingly the design of our study was not optimized for such a comparison (e.g., transient attention was consistently tested after sustained attention which might introduce order effects).

3.6. Individual differences in attentional effects

Fig. 5a shows the distribution of individual attentional effects on accuracy for both sustained attention and transient attention paradigms. As can be clearly seen, the variance in the size of the attentional effect is considerably larger with sustained attention than transient attention. A two-sided F-test that compares variances confirmed that the variance observed with the sustained attention paradigm was significantly larger than that observed with the transient attention paradigm ($F_{(29,29)} = 2.172$, $p = .041$). This difference is likely due to the more voluntary nature of sustained attention that affords the participants more control (and thereby produces more variability) over the utilization of attentional mechanisms.

Fig. 5b shows the distributions of individual attentional effects on RT for both sustained attention and transient attention paradigms. Here, the two distributions of the attentional effect are quite similar ($F_{(29,29)} = 0.811$, $p = .5763$). This may be related to the fact that RT is partially mediated by motor preparation which could be a less controlled mechanism. Indeed, previous studies have suggested that accuracy and RT reflect only partially overlapping processing stages, and particularly that changes in RT may be due to motor preparation (e.g., Correa, Lupiáñez, & Tudela, 2005; Van der Lubbe, Vogel, & Postma, 2005; Handy, Kingstone, & Mangun, 1996; Luck & Thomas, 1999; Rinkenauer, Osman, Ulrich, Müller-Gethmann, & Mattes, 2004; Santee & Egeth, 1982).

To further examine individual variability in the effects of spatial attention, we broke down these attentional effects into attentional benefit (i.e., the difference between the valid and neutral conditions) and attentional cost (i.e., the difference between invalid and neutral conditions). Fig. 5c depicts these benefit and cost effects on accuracy for both types of attention. Starting with sustained attention, a noteworthy result is the considerably larger variance of the cost in comparison to that of the benefit ($F_{(29,29)} = 2.212$, $p = .036$). In contrast, the variability that emerged for the benefit and cost effects with transient attention did not differ significantly ($F_{(29,29)} = 1.332$, $p = .445$). Likewise, no differences were found between the variances of the cost and benefit effects with RT (Fig. 5d), regardless of the type of attention (sustained: $F_{(29,29)} = 0.878$, $p = .728$, transient: $F_{(29,29)} = 1.246$, $p = .558$).

3.7. The relationships between internal noise and sustained attention

This section and the following one are most critical, given the goal of this study, because they test the hypothesis that the variability in the size of the attentional effect (valid vs. invalid) observed for different participants is related to their level of internal noise. As stated in the

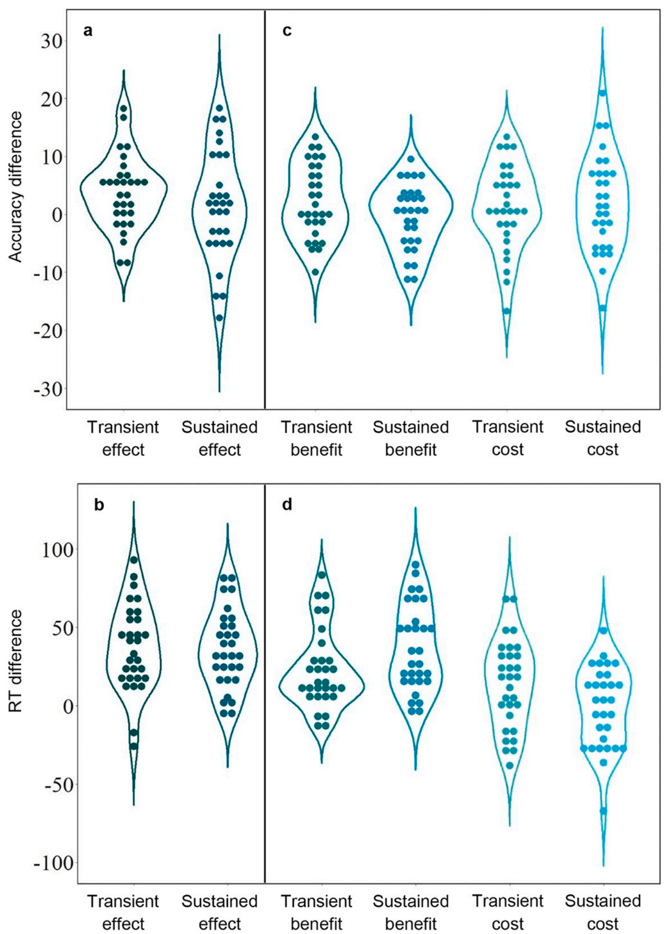

Fig. 5. Violin plots and dot plots (binned individual data points) for (a) The attentional effect (valid - invalid) on accuracy. (b) The attentional effect (invalid - valid) on RT. (c) The attentional benefit (valid – neutral) and cost (neutral - invalid) on accuracy. (d) The attentional benefit (neutral - valid) and cost (invalid - neutral) on RT.

introduction, when considering individual variability in the sustained attention paradigm (Fig. 5a and c), our hypothesis was directional – we expected larger effects with higher levels of noise. Indeed, we found a significant positive correlation ($r_{(30)} = 0.363$, $p = .024$, one-tailed; Fig. 6a) between individual levels of multiplicative internal noise and the effect of attention on accuracy. Note that this effect would be significant even if a two-tailed test had been employed ($p = .048$). Individuals with higher levels of internal noise displayed larger accuracy effects in the sustained attention paradigm compared to individuals with low levels of internal noise. This finding is in line with a previous study showing that individuals with higher levels of neural variability display larger attentional effects (Arazi et al., 2019). Individual RT effects were not significantly correlated with multiplicative internal noise levels ($r_{(30)} = -0.096$, $p = .615$, Fig. 6c), and the additive internal noise parameter did not significantly predict attentional effects in neither accuracy ($r_{s(30)} = 0.013$, $p = .946$, Fig. 6b) nor RT ($r_{s(30)} = -0.281$, $p = .132$, Fig. 6d) in the sustained attention paradigm.

The significant correlation between internal noise and the effect of attention on accuracy suggests that the lack of a significant cueing effect on accuracy at the group level (see ANOVA above) might be, at least partially, due to individual differences in multiplicative internal noise. To examine this possibility, a median split was performed to divide participants into low and high internal noise groups (mean multiplicative internal noise = 1.056, 1.608, respectively). Noise level (low internal noise, high internal noise) was entered as a between-participants factor to a two-way mixed-design ANOVA with cueing (valid, invalid, neutral) as a within-participant factor and accuracy as the dependent variable. A significant noise x cueing interaction ($F_{(2,56)} = 3.857$, $p = .027$, $\eta_p^2 = 0.121$; Fig. 6e and f) was revealed. The main effects of cueing ($F_{(2,56)} = 1.109$, $p = .34$, $\eta_p^2 = 0.038$) and noise level ($F_{(1,28)} = 0.518$, $p = .37$, $\eta_p^2 = 0.028$) were not significant. To clarify the nature of the interaction, further analyses were conducted for each noise group separately. A one-way repeated-measures ANOVA revealed a significant main effect of cueing for the high internal noise group ($F_{(2,28)} = 3.474$ $p = .045$, $\eta_p^2 = 0.199$). When we inspected the nature of this main effect, we found that participants in the high internal noise group were significantly more accurate in the valid condition than in the invalid condition ($t_{(14)} = 1.843$, $p = .043$, one-tailed, 95% CI [−0.008, 0.106]). We also found significantly higher accuracy for the neutral condition compared to the invalid condition ($t_{(14)} = 2.124$, $p = .026$, one-tailed, 95% CI [0.000, 0.104]), but there was no significant difference in accuracy between the valid and neutral conditions ($t_{(14)} = 0.229$, $p = .589$, one-tailed, 95% CI [−0.030, 0.025]). This pattern of findings suggests that the attentional effect found for the high internal noise group can be attributed to the cost of attending an incorrect location in invalid trials. In a second repeated-measures ANOVA for the low internal noise group, the main effect of cueing condition was not significant ($F_{(2,28)} = 0.657$ $p = .526$, $\eta_p^2 = 0.045$). These results suggest that the cueing condition affected accuracy only for the high internal noise group and not for the low internal noise group.

3.8. The relationships between internal noise and transient attention

In this section we examine whether the individual variability in the size of the attentional effect (valid vs. invalid) observed in the transient attention paradigm (Fig. 5b and d) is also related to the level of internal noise. However, with transient attention we could not form a directional hypothesis and therefore all tests are two-tailed. We found a significant negative correlation between multiplicative internal noise and the RT attentional effect ($r_{(30)} = -0.398$, $p = .029$; Fig. 7c); individuals scoring higher levels of multiplicative internal noise tended to achieve smaller RT attentional effects. However, the multiplicative internal noise parameter was not significantly correlated with the attentional effect on accuracy ($r_{(30)} = 0.057$, $p = .766$, Fig. 7a). Once again, the additive internal noise parameter did not significantly correlate with the measures of accuracy ($r_{s(30)} = 0.239$, $p = .203$, Fig. 7b) or RT ($r_{s(30)} = -0.096$, $p = .611$, Fig. 7d).

When the level of internal noise (low internal noise, high internal noise) was entered as a between-participants factor to a two-way mixed-design ANOVA with cueing (valid, invalid, neutral) as a within-participant factor and RT as the dependent variable, only the main effect of cueing ($F_{(2,56)} = 28.874$, $p < .001$, $\eta_p^2 = 0.508$) was significant. Neither the main effect of noise level ($F_{(1,28)} = 1.725$, $p = .200$, $\eta_p^2 = 0.058$) nor the noise x cueing interaction ($F_{(2,56)} = 1.298$, $p = .281$, $\eta_p^2 = 0.044$) were significant (Fig. 7e and f).

4. Discussion

This study employed psychophysical and computational methods to examine the relationships between internal noise and two types of spatial attention: sustained attention and transient attention, while focusing on individual differences. To this end, we measured the effects of these two types of attention on an acuity task, and we estimated individual levels of both additive and multiplicative internal noise by applying the PTM to data observed in a double pass procedure. First, we found a significant positive correlation between individual levels of multiplicative internal noise and sustained attention. Higher levels of multiplicative internal noise were associated with larger attentional effects on accuracy in the central cueing paradigm. We further found that participants with high levels of internal noise displayed a high cost of directing sustained attention towards the wrong location, while individuals with low levels of internal noise showed no benefit and also no

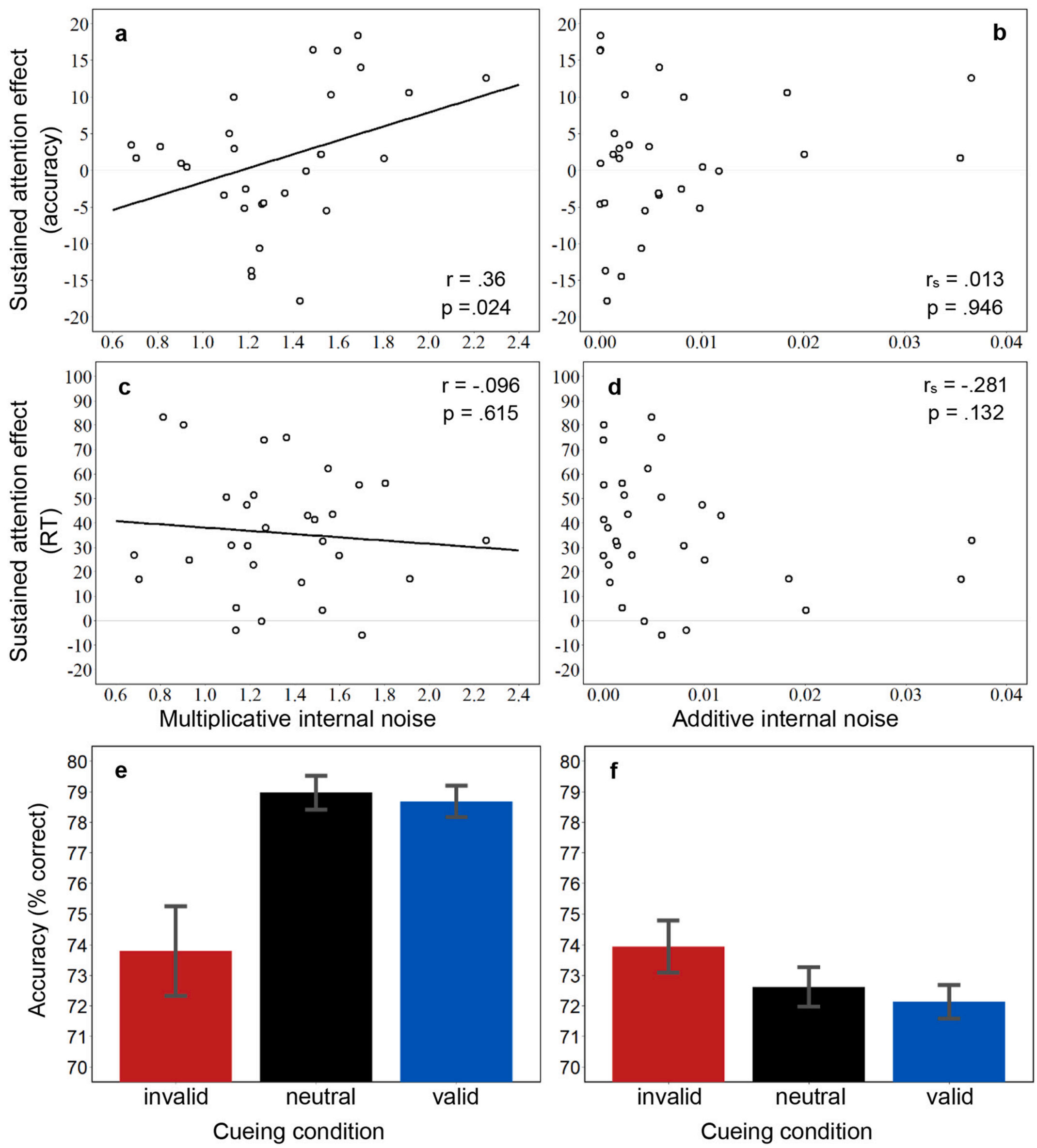

Fig. 6. The relations between internal noise and sustained attention. The individual attention effect on accuracy (valid – invalid) significantly correlated with multiplicative noise (a) but not additive noise (b). The effect of attention on RT (invalid-valid) did not correlate with multiplicative (c) or additive (d) noise. (e) Mean accuracy as a function of cueing condition for the high internal noise group. (f) Mean accuracy as a function of cueing condition for the low internal noise group. Error bars correspond to ±1 within-subject SE. Note that in (b) and (d) we calculated Spearman's correlations which test for a monotonic relation, therefore no regression lines are included.

cost from central cueing. This positive correlation between behavioral trial-by-trial variability and sustained attention is in line with a previous study that showed a similar relationship between neural trial-by-trial variability and the effect of sustained attention (Arazi et al., 2019). While many different factors are likely to contribute to trial-by-trial variability, neural noise in early sensory areas is an important contributor (Faisal et al., 2008), and internal noise has been identified as a factor in perceptual variability (Osborne, Lisberger, & Bialek, 2005; Shadlen, Britten, Newsome, & Movshon, 1996). Interestingly, opposite relationships were found when we considered transient attention: multiplicative internal noise was found to be negatively correlated with the effect of attention on RT in the transient attention paradigm. That is, participants with higher levels of multiplicative internal noise tended to exhibit smaller RT advantages in the valid condition compared to the invalid condition than participants with low internal noise levels. It is important to note that the levels of internal noise were measured in a separate session in which all stimuli were presented at the center, and therefore all stimuli were attended. Hence, the correlations reported here cannot reflect attentional modulations of internal noise. Instead, they suggest that the degree to which the performance of a given participant is affected by the allocation of spatial attention is not determined solely by higher-level factors, as was thought thus far, rather it is linked to a fundamental characteristic of this participant's perceptual system – the level of internal noise.

It is well established that the allocation of attention to a given location could enhance the processing at the attended location (Carrasco, 2011; Yeshurun & Carrasco, 1999). However, the effect of spatial attention could also involve suppression of information at unattended locations, as is evident in the poorer performance that is typically observed for targets appearing at an unattended location (i.e., the invalid condition; Cheal & Gregory, 1997; Sylvester, Jack, Corbetta, & Shulman, 2008; Vanduffel, Tootell, & Orban, 2000). A suppression mechanism could improve performance by reducing noise from irrelevant locations (e.g., Luck, 1995), and balancing the competition for

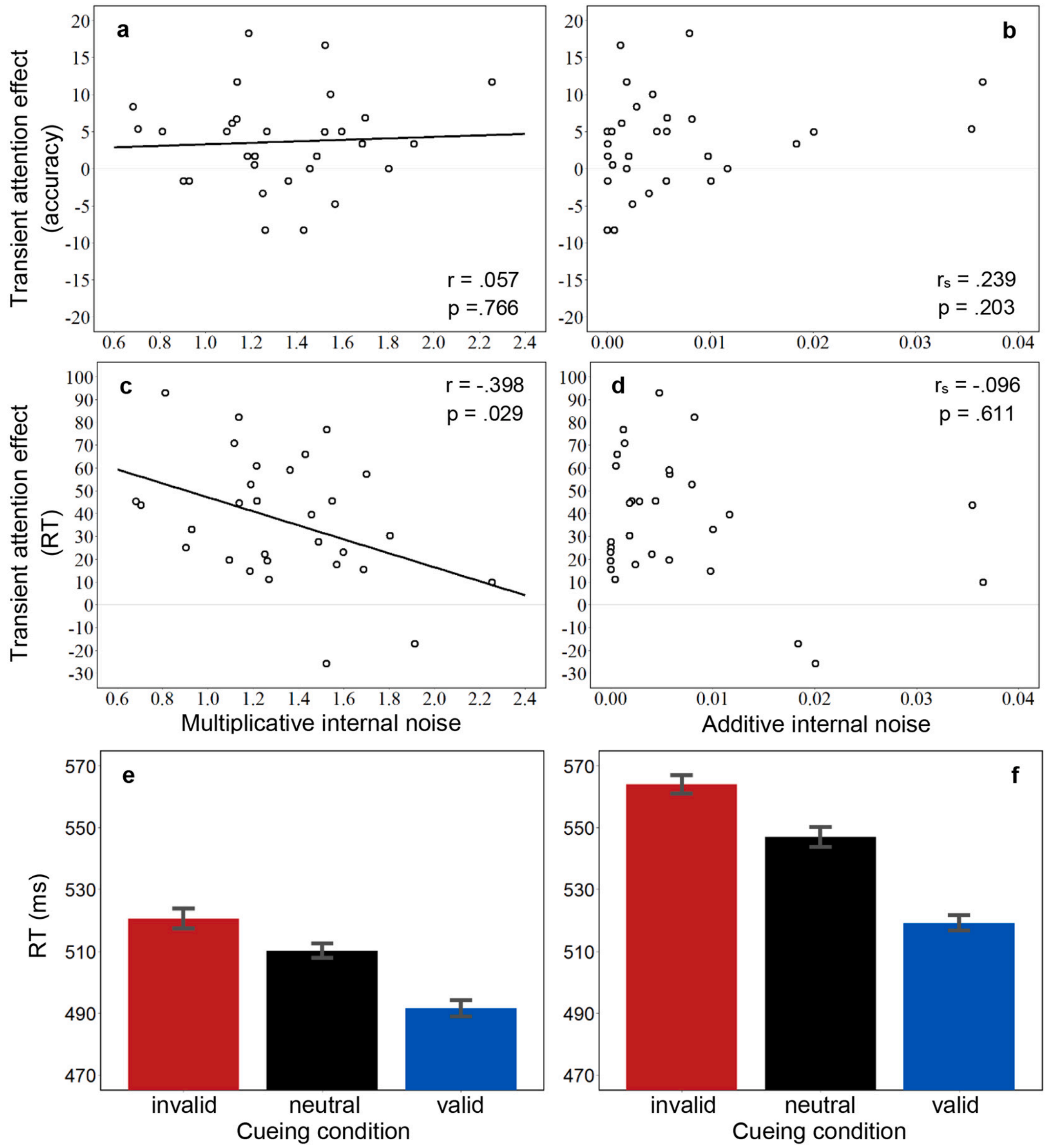

Fig. 7. The relations between internal noise and transient attention. The individual attention effect on accuracy (valid – invalid) was not correlated with multiplicative (a) or additive (b) noise. The effect of attention on RT (invalid – valid) was negatively correlated with multiplicative noise (c), but not with additive noise (d). (e) Mean RT as a function of cueing condition for the high internal noise group. (f) Mean RT as a function of cueing condition for the low internal noise group. Error bars correspond to ±1 within-subject SE. Note that in (b) and (d) we calculated Spearman's correlations which test for a monotonic relation, therefore no regression lines are included.

processing capacity in brain areas that are less retinotopically organized (e.g., Vanduffel et al., 2000). Such a suppression mechanism may underlie the finding that participants with higher levels of internal noise displayed a larger performance cost when attention was allocated to the wrong location than participants with lower levels of internal noise (Fig. 6b and c). Individuals with high levels of internal noise might tend to utilize such suppression mechanisms more often than individuals with low levels of internal noise in order to compensate for the relatively high levels of noise that are present in their perceptual systems. Thus, individuals with high levels of internal noise might apply inhibition more often to unattended locations leading to poorer performance when the target is presented there. It might be important to note that there is evidence that a suppression mechanism is active even when no distractors need to be ignored (Rihs, Michel, & Thut, 2007), as was the case in our study. Despite the fact that no distractors were employed in our paradigms, participants with high levels of internal noise would still benefit from reducing the amount of information being processed at unattended locations, because on most of the trials this would greatly reduce the amount of task-irrelevant information that needs to be processed at the same time as the task-relevant information. The view that variations in internal noise can account for a meaningful portion of the individual variability observed for the effect of sustained attention on accuracy in general, and on the attentional cost in particular, is also evident in Fig. 8. Clearly, the larger variability observed for sustained attention in comparison to transient attention (Fig. 5a), and for the cost effect in comparison to the benefit effect (Fig. 5c), is mainly due to individual variability in the sustained attention cost effect of the participants with high levels of noise. The lack of a similar difference in cost variability with transient attention may reflect the fact that participants have less control over the mechanisms triggered by a peripheral cue (e.g., Carrasco, 2011; Jonides, 1981; Posner, 1980).

We also found evidence of a negative relationship between internal noise and the effect of transient attention on RT. One possible explanation is that the higher levels of perceptual or sensory noise interfere

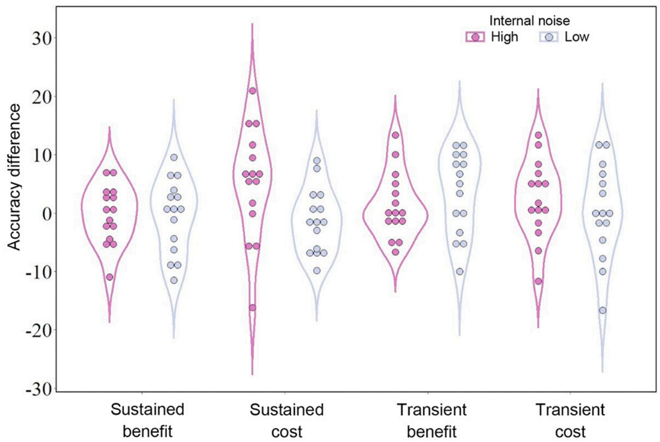

Fig. 8. Individual variability in the attentional benefit (valid – neutral) and cost (neutral - invalid) effects on accuracy as a function of noise level (high vs. low) and attention type (sustained vs. transient).

with the detection/localization of the peripheral cue. Thus, individuals with higher levels of internal noise might have been less efficient at locating the peripheral cues. Less efficient localization of the cues would lead to slower attention allocation to the cued location, reducing the RT advantage of the valid cue for individuals with high levels of internal noise and leading to a reduced effect of attention as was observed in this study. Although slowing down of attention allocation should reduce the attentional benefit manifested in response speed, it would not necessarily reduce the benefit manifested in response accuracy. If this slowing down is moderate, allowing attention to be, at least partially, involved in the processing of the target, that might be enough to enhance this processing, leading to improved accuracy. In our study, there was no evidence of a negative correlation between internal noise levels and the effects of transient attention on accuracy. This is consistent with the possibility that the impaired ability to detect the peripheral cue, brought about by high levels of noise, had a moderate influence on the ability of the participants to benefit from attention allocation to the target location. In the future, this possibility may be investigated by presenting peripheral cues with varying degrees of visibility. As visibility increases, the impact of internal noise on cue detection should decrease and the correlation between internal noise and the RT effect should diminish.

The additive noise parameter was not found to correlate with the effects of attention in any of the tasks used in this study. This is not surprising given the fact that additive noise is considered most relevant for stimuli presented near the detection threshold, but its relevancy is negligible with supra-threshold stimuli, for which multiplicative noise is more influential (Kontsevich et al., 2002; Lu & Dosher, 2000; Solomon & Tyler, 2017). In the sustained and transient attention paradigms we presented stimuli at full contrast (white stimuli on a black background). Hence, it is likely that due to the high contrast of the stimuli, internal additive noise did not play a meaningful role during these tasks. Instead, multiplicative internal noise was most likely the main source of internal variability in the attentional tasks presented here, as the influence of multiplicative internal noise is greater the higher the strength of the stimulus. However, it is possible that with near detection threshold stimuli the additive noise parameter would become a predictor of attentional effects instead of the multiplicative one.

To summarize, unlike previous studies who focused on higher processing levels as possible sources of individual variability in attentional effects (e.g., working memory; Fukuda & Vogel, 2011; Machizawa & Driver, 2011; or personality traits; Bates & Stough, 1997; Robinson et al., 2008), our study demonstrates that perceptual factors, like the level of internal noise, can also play a role in determining the degree to which spatial attention affects performance. Specifically, we found a positive correlation between multiplicative internal noise and the effect of sustained attention on accuracy and a negative correlation between multiplicative internal noise and the effect of transient attention on RT. These findings reveal the intricate relationships between perceptual and attentional processes. Clearly, a definitive conclusion regarding the nature of these relationships requires direct manipulation of the level of multiplicative internal noise. However, the finding that attention manipulations do not seem to modify the level of multiplicative internal noise (e.g., Dosher & Lu, 2000a; Dosher & Lu, 2000b; Lu & Dosher, 1998; Lu & Dosher, 2004; Lu, Liu, & Dosher, 2000) leads us to speculate that the correlation found here may at least partially reflect effects of multiplicative internal noise on the effectiveness of spatial attention. Thus, while many have shown in the past that spatial attention can affect various aspects of visual perception (e.g., Bonder et al., 2018; Carrasco, 2011; Hein et al., 2006; Montagna et al., 2009; Yeshurun, Montagna, & Carrasco, 2008; Yeshurun & Carrasco, 1999), we show here that the size of such attentional effects may, itself, be modified by perceptual factors, like the level of internal noise, though non-correlational experiments are required for a conclusive determination of causal relations.

Data availability

The data that support the findings of this study are available in the Open Science Framework repository, https://osf.io/34c5b/?view_only=5ac1efe8f23f4071af72ddf4e5004194

Author contributions

F.L. designed and conducted the experiments, analyzed and interpreted the data, and wrote the manuscript. Y.Y. designed the experiments, interpreted the data, and wrote the manuscript.

Declaration of Competing Interest

None.

Appendix A. PTM equations

The mathematical basis for the double-pass procedure was developed extensively by Burgess and Colborne (1988) and it was later extended to the PTM by Lu and Dosher (2008). Briefly here, according to the PTM, the input signal (including external noise) first passes through a perceptual template which is sensitive to a specific stimulus characteristic (such as orientation). Only the signal is enhanced by a gain factor β. Then, the output of the perceptual template is processed by a non-linear transducer function which amplifies the input to the γ_1^{th} power. In a multiplicative internal noise pathway, the input signal passes through a different perceptual template with a gain factor β_2 and a different non-linear transducer function γ_2. Multiplicative noise is added relative to the total stimulus strength and then additive noise is added to the final output.

In a 2-AFC task, the PTM can be used to calculate the proportion of correct responses in a given condition using the following equation:

$$P(C) = \int_{-\infty}^{\infty} g\left(x - \beta^{\gamma_1} c^{\gamma_1}, 0, \sqrt{\sigma_{\text{ext}}^{2\gamma_1} + N_{\text{mul}}^2\left[\sigma_{\text{ext}}^{2\gamma_2} + (\beta_2 c)^{2\gamma_2}\right] + \sigma_{\text{add}}^2}\right) \times G\left(x, 0, \sqrt{\sigma_{\text{ext}}^{2\gamma_1} + N_{\text{mul}}^2 \sigma_{\text{ext}}^{2\gamma_2} + \sigma_{\text{add}}^2}\right) dx \quad (1)$$

where $g(x, \mu, \sigma)$ is the probability density function and $G(x, \mu, \sigma)$ is the cumulative density function of a Gaussian random variable x with mean μ and SD σ. β, β_2, γ_1, γ_2, N_{mul} and σ_{add} are estimated parameters, c is the signal contrast and σ_{ext} is the SD of the external noise. The estimated parameters represent perceptual templates (β, β_2), transducer functions (γ_1, γ_2) and multiplicative and additive noise (N_{mul}, σ_{add}, respectively). In line with Lu and Dosher (2008), we followed the assumption that $\gamma = \gamma_1 = \gamma_2$. Similarly, agreement between passes for a given condition in the DP procedure can be calculated as follows:

$$\mathrm{P(A)} = \int_{-\infty}^{\infty} g\left(x - (\beta c)^{\gamma_1}, 0, \sqrt{2}\,\sigma_{\mathrm{ext}}^{\gamma_1}\right) \times \left\{ G^2\left(x, 0, \sqrt{N_{\mathrm{mul}}^2\left[2\sigma_{\mathrm{ext}}^{2\gamma_2} + (\beta_2 c)^{2\gamma_2}\right] + 2\sigma_{\mathrm{add}}^2}\right) + \left[1 - G\left(x, 0, \sqrt{N_{\mathrm{mul}}^2\left[2\sigma_{\mathrm{ext}}^{2\gamma_2} + (\beta_2 c)^{2\gamma_2}\right] + 2\sigma_{\mathrm{add}}^2}\right)\right]^2 \right\} dx \quad (2)$$

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