## Running head: A METHOD OF INFLUENCING NOISE IN HUMAN BRAIN ACTIVITY

# A Non-Invasive Method of Influencing the Distribution of Noise in Human Brain Activity Michael V. Bronstein

Advised by

Tyler S. Lorig

## Author Note

Contact should be directed to Michael V. Bronstein, Parmly Hall 204 West Washington Street, Lexington, VA or to bronsteinm15@mail.wlu.edu

Submitted in partial fulfillment of the requirements for the B.S. in Psychology with Honors

I declare no conflict of interest with any material contained here-in

I gratefully acknowledge invaluable assistance from Dr. T S. Lorig in completing this thesis. I am also grateful for Dr. Wythe Whiting's generous contributions of time and talent to my efforts to realize the paradigm detailed in this paper. I would also like to acknowledge R. Strong for completing initial pilot work and would like to thank B. Bowring for her assistance in running participants and maintaining our laboratory.

## Abstract

While noise in brain activity has been studied for many years, new theoretical considerations suggest that this noise may be an important and even essential part of normal brain functioning. Here we describe a technique to non-invasively manipulate noise levels in the brain using visual stimuli. Fifteen participants viewed a variety of visual scenes containing different levels of visual noise. EEG was recorded from a montage of 78 electrodes after each scene type. Analysis of the entropy present in participants' brain activity suggests that noisy visual scenes alter the entropy in brain activity and that this induction is more accurately assessed with EEG measures that characterize entropy than with traditional metrics such as alpha.

# Dedication

I would like to dedicate this thesis to those individuals who have earned psychology the status of being a true science. It is my great hope that my future career might honor the spirit of your efforts.

### Acknowledgements

Along the path to producing my thesis, I have had the fortune of having the sage guidance of the men and women of the Washington and Lee University Department of Psychology. Although each member of the department contributed in important ways to this endeavor, I would like to specifically acknowledge the efforts of the following faculty members:

- Dr. Johnson, for teaching me the statistical tools to test my ideas and for always being willing to offer me his assistance in expanding my knowledge of psychology
- Dr. Murdock, for her adroit advising as well as her helpful encouragement of my study of clinical psychology
- Dr. Whiting, for his expert assistance with the attentional aspects of the studies which comprise this thesis
- Dr. Lorig, for helping me go from being a freshman who asked too many questions after lectures to a senior with the tools to answer them for himself; for being a superior mentor

I am incredibly grateful to each of you for helping me to take my place in the community of science.

A Non-Invasive Method of Influencing the Distribution of Noise in Human Brain Activity

Despite the ongoing debate about what exactly constitutes noise in the nervous system (e.g., Stein et al., 2005), it is often assumed that information in this system is transmitted against a background of random activity, called neural noise (c.f., Kail, 1998). Neural noise, which arises from various sources in the brain (see Faisal et al., 2008 for a review), significantly influences the precision and reliability of neuron spike timing (Schneidman et al., 1998; Carpenter, 1999; Kuriscak et al., 2012). Because behavior is governed by neuronal activity, this influence of neural noise on spike timing intimates that neural noise might have non-negligible effects on the reliability and precision of behavior as well. Support for the notion that neural noise has such effects on behavior can be found in studies assessing working memory (Bays, 2014), the speed of general cognition (Kail, 1998), as well as the ability to sense and perceive stimuli (Skoczenski & Norcia, 1998; Wiesenfeld & Moss, 1995). These studies have yielded converging evidence that neural noise influences behavior by influencing signal detection.

In light of this converging evidence, the goal of the present study was to further explore the influence of neural noise on behaviors involving signal detection. A visual search task was created to accomplish this goal. This task type was selected because observer performance in visual search tasks has a strong basis in signal detection theory (Whiting et al., 2014; Wolfe, Butcher, Lee & Hyle, 2003), making these tasks a good tool for investigations of factors impacting signal detection behavior. This task type was also selected because neural noise increases should multiplicatively compound the processing of distracters in visual search displays (Whiting et al., 2014; Lu & Dosher, 2008). Due to this multiplicative relationship, even small changes in neural noise levels should have the potential to engender detectable behavioral changes in visual search tasks. Finally, this task type was selected because it relies heavily on the sensory and perceptual systems. The performance of these systems is both augmented and limited by neural noise. The notion that noise is a limiting factor in these systems is implied by the existence of an absolute threshold for every perceptual task at any given moment (Lu & Dosher, 2008). The notion that noise is an augmenting factor in these systems is supported by the fact that these systems display stochastic resonance (c.f. Mori & Kai, 2002; Moss et al., 2004; Douglass et al., 1993), which is the increase in the detection or information content of weak signals in the presence of an appropriate amount of neural noise (Moss et al., 2004). Because neural noise level alterations may alter these limiting and augmenting effects of neural noise, changes in neural noise levels should meaningfully impact behaviors arising from the sensory and perceptual systems. Thus, the reliance of visual search tasks on these systems increases the likelihood that altering neural noise levels will cause detectable changes in behavior during visual search tasks.

These factors in tandem make using visual search tasks a logical method of increasing one's chances of having adequate statistical power to detect the putative effects of neural noise on behaviors involving signal detection. In the visual search task created in this study, visual external noise was added directly to search displays in a manner similar to that used in Whiting et al. (2014). The decision to add visual external noise to search displays in this way was driven primarily by the fact that mathematical models of inconsistency in observers' reports of visual stimuli suggest that neural noise can be induced at a rate that is directly proportional to the amount of external visual noise in an image (Burgess & Colborne, 1988). It follows from these models that one should be able to manipulate neural noise levels in participants by manipulating the amount of external visual noise in the displays of a visual search task. This method seems likely to yield detectable changes in observers' signal detection ability during a visual search task given the long history of using external noise methods to successfully characterize the intrinsic perceptual limitations of human observers as well as the changes in these limitations (Lu & Dosher, 2008). Thus, this manipulation is amenable to this study's goal of further exploring the role of neural noise in signal detection behaviors.

In order to quantitatively measure the response of neural noise levels to this manipulation of external visual noise, electroencephalographic (EEG) data were recorded from participants after they completed each third of the visual search task. The entropy of these data was then computed. This quantification of neural noise levels using noise in brain activity allowed us to better ensure that neural noise levels were being altered by our external visual noise manipulation, increasing the internal validity of this study's assessment of the effects of neural noise on behaviors involving signal detection. Further, this quantification of neural noise levels allowed us to provide a preliminary test of Burgess & Colborne's (1988) induced noise model in that if this model is correct, changes in neural noise levels should be observable in the present study with changes in external visual noise.

Because the goal of this study required assessing the changes in signal detection behaviors that resulted from these changes in neural noise levels, several dependent measures for this study were selected from the outcomes of visual search tasks. These measures included canonical signal detection metrics (hits, false alarms, etc.). These measures also included ex-Gaussian reaction time parameters (see Whelan, 2008) that might be indicative of signal detection ability. For example, the tau parameter is thought to reflect the inability of the subject to reach a decision regarding the identity of a target (Ratcliff, 1993). This decision uncertainty may be a natural consequence of increased neural noise levels. Thus, it was expected that the tau parameter would change with changes in neural noise levels in this study. In summary, the present study sought to examine the effect of neural noise on signal detection behavior. This was done by having participants complete a visual search task with three different levels of external visual noise and then ascertaining the changes in both behavior and the amount of noise in participants' brain activity that resulted from this manipulation.

#### Method

## **Participants**

Fifteen participants (9 males and 6 females, ages 18-22) were recruited from the undergraduate population of a small liberal arts college. Participants were recruited via flier and email, and were offered extra credit in exchange for their participation. A computerized version of the Ishihara-like color blindness test was used to ensure that only individuals with normal color vision participated in this study.

## **Visual Search Task Materials**

The stimuli used in this study consisted of 480 randomly generated feature or conjunctive visual search displays. The foregrounds of these displays varied in their number of distracter objects and also varied as to whether or not a target object was present in them. Feature search displays contained a horizontal black rectangle with distracter objects limited to horizontal white rectangles outlined in black. In contrast, conjunctive search displays' distracter objects included both horizontal white rectangles outlined in black and vertical black rectangles. Thus, in feature search displays, the target (a horizontal black rectangle) could be differentiated from the distracters using a single feature (color). In contrast, in conjunctive search displays, two features (color, orientation) were needed to differentiate the target from distracters. Distracter objects subtended 2.09 degrees of visual angle by 0.41 degrees of visual angle when oriented horizontally or subtended 0.41 degrees of visual angle by 2.09 degrees of visual angle when oriented

vertically. The total number of these distracter objects varied in both the feature and conjunctive search displays. In one half the displays of each search type (conjunction and feature), there were either seven or eight distracter objects depending on whether or not the target was present (respectively). This half of the displays formed the small set size condition. In the other half of the displays there were either 15 or 16 distracter objects, again depending on whether or not the target was present. This second half of the displays formed the large set size condition. The target, a horizontal black rectangle, subtended 2.09 degrees of visual angle by 0.41 degrees of visual angle and was present in one half of the displays of each search type. See Figure 2 for representative examples of stimuli from each set size and search type.

In addition to this variation in the foreground of the search displays, the background of all displays varied in the amount of external visual noise that they included. Either 1800, 3600, or 5400 rectangles of external visual noise were added to the displays in the low, medium, or high external visual noise conditions, respectively. In each display, an equal number of these rectangles were colored red (248 R, 9 G, 0 B), green (0 R, 255 G, 30 B), and blue (8 R, 0 G, 232 B). These rectangles were constructed using colors with equal luminance, and differed significantly from the targets in size, shape, and color so that they could be clearly distinguished from potential target objects. Further, each of these rectangles varied randomly and independently in size, subtending a maximum visual angle of 0.39 by 0.11 degrees and a minimum visual angle of zero degrees squared (exclusive). Thus, the external visual noise pattern of each search display was different from that of all other displays used in this experiment. Care was taken to ensure that this external visual noise, which was randomly generated, did not obscure any of the potential target objects. See Figure 1 for representative examples of stimuli containing each level of external visual noise.

Despite these variations among the search displays, they were united by one important similarity. This similarity was that the same 16 equally spaced locations where targets and distracters could potentially appear were used in all search displays. Targets or distracters appeared in all 16 of these locations in large set size search displays, and appeared in a randomly selected subset of 8 of these locations in small set size displays. This similarity is important because it allowed the amount and density of external visual noise to which participants were exposed to remain constant across the set sizes within a given block of trials, thus making the detection of potential set size effects possible.

#### **Visual Search Task Procedure**

The visual search task in this study used a  $2 \times 2 \times 2 \times 3$  within-subjects design. The independent variables manipulated in this task were the type of the search display (feature or conjunctive), the set size of the display (small or large), whether the target was present or absent in the display, and the level of external visual noise in the display (high vs. medium vs. low). Several behavioral dependent measures were recorded in order to study the effects of these manipulations. These dependent measures included the number of trials in each condition on which participants committed a miss or a false alarm, the response time it took participants to judge whether or not the target was present each display, and the ex-Gaussian parameters (mu, sigma, and tau) that described the distribution of participants' reaction times at each display noise level. The tau parameter is a metric of decision uncertainty, and describes the right-most tail of the canonically skewed reaction time distribution. The mu parameter reflects average performance, and describes the normal portion of the reaction time distribution. The sigma parameter reflects variability in reaction times when discounting extremes in performance, and describes the variability in this normal portion of the reaction time distribution.

In order to carry out these manipulations and record these behavioral dependent measures, participants were seated approximately 1.04 meters in front of a 0.61 meter computer monitor. The participants were then asked to stare at a fixation cross for one minute. Following this minute, the participant completed 480 trials of a visual search task administered using MATLAB R2011b (The MathWorks, Inc.). In each trial of this task, participants searched for a target (a horizontal black bar) in a search display. Search displays remained onscreen for 105 ms. This presentation was followed by a visual noise mask that was presented for 30 ms. Following this mask, a screen which read "respond" appeared. Upon seeing this screen, participants were instructed to indicate whether or not the target was present in each display as quickly as possible without sacrificing accuracy. Participants did this by pressing the 'p' key on a standard keyboard if the target was present and the 'a' key if it was not present. For each of these trials, the accuracy of participant's responses was recorded, as was the reaction time of participants for trials on which the participant responded correctly only.

These 480 visual search task trials were divided into three blocks of 160 trials. These trials were organized such that the external visual noise levels of all of the visual search displays within a given block were equal. This was done in order to guard against the potential carryover effects that could arise from inducing different neural noise levels in quick succession. The order in which participants encountered these three blocks of trials was randomized. Within each block, the difficulty of the visual search task (conjunctive vs. feature) and target presence randomly varied. The set size of displays within a block was also manipulated: a mini-block of 80 trials within each external visual noise block had a large set size (16 potential targets), and a second mini-block of 80 trials within each external visual noise block was randomly varied within each full block.

After each full block of trials, participants were given a two minute forced break (with the option to extend it for as long as he or she pleased) in order to increase the chances that neural noise levels in the brain would return to baseline before the next block. During the first minute of this break, participants stared at a fixation cross. No break was given in between the trials that made up a block.

## **Procedure for Collecting EEG Data**

Participants were fitted with a set of 78 electrodes arranged in manner adhering to the extended 10-20 system, using CMS and DRL electrodes for noise reduction, and attached to an analog-to-digital converter and amplifier (Biosemi Systems). Electrodes were prepared at low noise levels, typically with a root mean square noise level of 50uV. Electrodes with higher noise levels (>50uV) were excluded from analysis and replaced in the montage. Biosemi is a common mode rejection system and therefore impedances are not available. Signa Gel (Parker Laboratories) was used at each electrode site. After setting up the EEG system in this manner, data were recorded from participants while they stared at a fixation cross at four different times during the experiment. The first of these times was in the minute before the participants began the visual search task. This collection period was included in order to obtain the participants' baseline resting EEG. The remaining three times that EEG data were collected came during the first minute following each block of 160 trials of the visual search task. Throughout all four of these one minute collection periods, EEG data were recorded for four consecutive seconds and were discarded for the next two seconds. This cycle continued for the duration of each collection period. This was done in order to allow for a more representative sampling of the random variation in participants' resting EEG activity. This EEG data collection paradigm is summarized visually in Figure 3.

## **Statistical Procedures**

All analyses involving were conducted using SPSS Statistics 21 (SPSS Inc., Chicago, IL, USA). All pairwise comparisons were conducted using Bonferroni corrections to limit type I error rate. ANOVAs were conducted using H-F corrections (Huynh & Feldt, 1976) to limit type I error rate in the presence of violations of assumptions regarding data sphericity.

#### Results

### **EEG Data**

EEG data were obtained after the onset of the fixation cross at baseline and following each block of visual search trials. These data were initially subjected to artifact rejection using FASTER software (Nolan et al., 2010). This software was used to remove artifacts, including eve blinks, in the electroencephalographic data via independent component analysis. The EEG data were then further reduced by discarding the data from the first 500 ms after each onset of the fixation cross in order to avoid including the event-related potential caused by the onset of the fixation cross in the data that were analyzed in this study. Data points further than 3500 ms from the onset of the fixation cross were also discarded. This procedure caused the data set to consist of only the EEG data from 500-3500 ms after each onset of the fixation cross. The entropy of these data was then computed separately at each level of the external visual noise independent variable. Entropy was calculated using permutation entropy according to the method outlined in Unakafova & Keller (2013). Permutation entropy is strongly related to the widely used Kolmogorov-Sinai (KS) entropy but takes greater advantage of the overlapping nature of time series data in order to allow for faster calculation speeds. This entropy calculation was done in order to quantify the amount of neural noise at each level of external visual noise in this study.

For an extended explanation of how entropy can be used to measure noise in brain activity, please see Appendix 1.

The entropy values generated in this manner were then subjected to a 3(external visual noise level) × 2 (hemisphere) × 3 (anterior-central-posterior) repeated measures *ANOVA*. The results of this *ANOVA* indicated that, as might be expected, there was a greater amount of entropy over the anterior cortex than over the posterior cortex of participants, F(2,28) = 5.79, H-F corrected p = .030, partial eta squared =.29. Such a difference between anterior and posterior entropy levels over the cortex is to be expected and provides support for the validity of the data collection and processing procedures used in this study. This main effect was qualified by a marginally significant interaction between external visual noise level and anterior-posterior electrode position in determining the amount of entropy in the EEG of subjects, F(2,28) = 2.97, H-F corrected p = .079, partial eta squared = .18. This interaction can be best characterized by the fact that there was a difference in entropy between the anterior (M = 0.9835, SD = 0.00997) and posterior (M = 0.9808, SD = 0.00974) portions of participants' brains at the low level of external visual noise, t(14) = 3.78, Bonferroni corrected p = .006, which disappeared at the medium and high levels of external visual noise.

This *ANOVA* also revealed that there was an interaction (shown in Figures 4 and 5) between the external visual noise level in the search displays and the hemisphere of interest in determining the amount of entropy in subjects' EEG, F(2,28) = 8.22, H-F corrected p = .002, partial eta squared = .37. Follow up *t*-tests revealed no significant differences between the cell means in this *ANOVA* that survived Bonferroni correction. However, the above interaction can be accounted for by the fact that in the left hemisphere the difference between the entropy in participants' brains at successive external visual noise levels was largest when comparing the low

and medium levels of external visual noise, t(14) = 2.37, Bonferroni corrected p = .20, while in the right hemisphere this same comparison yielded the smallest difference between successive external visual noise levels, t(14) = .09, Bonferroni corrected p > .99.

These results using entropy as the dependent variable were then compared with identical analyses substituting alpha activity as the dependent variable. For the purposes of this comparison, alpha activity was calculated by first converting the EEG data into event-related spectral perturbations from a zero baseline using EEGLAB (Delorme & Makeig, 2004). Activity within the 8-12 Hz window was integrated over the same time window used for the entropy analyses. Then, like the entropy analyses, these data were grouped into electrode clusters for six scalp regions and submitted to analysis of variance.

This comparison suggested that entropy is a more sensitive dependent measure than alpha for detecting changes in the amount of noise in brain activity. This suggestion stemmed from the fact that using alpha as a dependent measure yielded effects of a smaller size than using entropy as a dependent measure did across several analyses. For example, when using alpha as a dependent measure the marginally significant interaction between external visual noise level and anterior-posterior electrode position found above using entropy as a dependent measure was not detected. As might be expected from this difference in detection, the effect size of this interaction when using alpha as a dependent measure (partial eta squared = .001) was smaller than that obtained when using entropy as a dependent measure (partial eta squared = .18). Even when the same significant interactions were detected using both dependent measures, using alpha as a dependent measure resulted in a smaller effect size being observed. For instance, the interaction between external visual noise level and hemisphere of interest observed when using alpha as a dependent measure .20 (F(2.28) = 3.55, H-F corrected p =

.042). This is less than the effect size of .37 for the same interaction obtained above using entropy as a dependent measure. This difference in sensitivity can also be observed visually by examining the changes in entropy over the external visual noise conditions and comparing them to the difference in alpha, as can be seen in Figure 4.

#### **Behavioral Data**

#### **Reaction Time**

As recommended by Whelan (2008), ex-Gaussian parameters were used to characterize the distribution of reaction times in each display noise level condition. These parameters were then compared using 3 separate one-way *ANOVAs* with 3 cells each, one for each parameter across the levels of display noise. As predicted, increases in display noise level increased the tau parameter, F(2,28) = 4.94, H-F corrected p = .023, partial eta squared = .26. Follow-up repeated measures *t*-tests suggested that there was a significant difference between the tau parameters at the low (M = 0.17, SD = 0.10) and medium (M = 0.25, SD = 0.12) levels of display noise, t(14) =3.53, Bonferroni corrected p = .009, as well as at the high (M = 0.25, SD = 0.15) and low levels of display noise, t(14) = .027, Bonferroni corrected p = .027. There was no significant difference between the tau parameters at the medium and high levels of display noise, nor were there any significant main effects of display noise level on the mu or sigma parameters at any noise level. Reaction time data is summarized in Table 1.

These differences in the behavioral data across external visual noise levels suggest that the paradigm used in this study altered neural noise levels enough to produce effects on behavioral outcomes. In order to strengthen this suggestion further, metrics of participants' performance on each block of visual search trials were correlated with the deviation of their entropy levels from baseline after that block. For the purposes of these correlations, the deviation of participants' entropy levels was calculated as the entropy in the participants' EEG prior to completing any trials of the visual search task subtracted from the entropy in the participants' EEG after completing a given block of visual search trails. One participants' data was excluded from these analyses because of their extremely large deviations from baseline entropy levels after all three blocks of visual search trials. This excluded participants' deviations from baseline entropy levels were all greater than 0.17, and were confirmed to be outliers using Tukey's outlier filter. After removing this participants' data, 42 data points remained. All of these remaining data points were tested for their correlation with the behavioral metrics of performance used in this study. These data points formed a significant positive correlation between participants' deviation from resting state entropy levels after a given block of trials and the value of the mu parameter describing the distribution of their reaction times on that block, r = .38, p = .012,  $R^2 = .15$ . This correlation can be seen in Figure 6.

#### **Signal Detection Parameters**

No significant changes were found in signal detection parameters (misses, false alarms, hits, correct rejections) as a result of changes in external visual noise in the visual search displays.

#### Discussion

Although no significant changes were found in these direct measures of signal detection ability as a result of neural noise level changes, more indirect measures of this ability were sensitive to neural noise level changes in this study. For example, the significant alterations in the tau parameter describing reaction time distributions across the neural noise level conditions in this study are consistent with the notion that signal detection ability was indeed altered as a result of changes in participants' neural noise levels. This conclusion follows from the fact that when signal to noise ratios are decreased (e.g., with increases in neural noise levels), more time must elapse for the amount of signal necessary to reach an observer's criterion of selection (assuming this remains constant) to be accumulated. Because of this, the observer should respond more slowly than normal to trials in which especially high neural noise levels are present, a behavior pattern captured by the tau parameter. The sensitivity of this indirect measure of signal detection ability to neural noise level alterations is consistent with the idea that neural noise impacts behaviors involving signal detection in the human visual system. Thus, with greater statistical power it is plausible that this study would have detected effects of neural noise level changes on more direct measures of participants' signal detection abilities.

The results of this study are also consistent with Burgess & Colborne's (1988) claim that neural noise might be induced by noise in the external environment at a rate proportional to the amount of external visual noise present. This consistency exists because this study suggests that neural noise levels are altered with external visual noise levels, which is a necessary but not sufficient condition for Burgess & Colborne's (1988) claim to be true. It is important to note, however, that the preliminary evidence for the induction of neural noise through external visual noise changes presented in this study comes with one major caveat. This caveat is that because task difficulty varied directly with external visual noise levels in this study, one cannot be certain that external visual noise level increases per se led to the alterations of neural noise levels in the brain described above.

In order to assess the severity of this caveat, we examined whether or not there was an interaction between the set size and external visual noise independent variables in determining the amount of noise in participants' brain activity. Because the large set size condition should be more difficult than the small set size condition, if difficulty were the main cause of the variations

in the amount of noise in participants' brain activity that were observed in this study than there should be more of this noise in the large set size condition than in the small set size condition at any given level of external visual noise. Thus, these variables would interact in determining the amount of noise in participants' brain activity. This interaction was not found to be significant. In light of this, these difficulty differences are unlikely to explain the results presented above. Nevertheless, it is noteworthy that the measurement of noise in brain activity used in this study could be useful in quantifying the changes in neural noise levels that should occur with changes in the difficulty of a signal detection task. These changes are likely to occur because as a signal detection task becomes more difficult, the gain on both the signal and internal noise must be increased by an observer in order to maintain a given level of performance.

If changes in the external visual environment do indeed lead to changes in the amount of noise in brain activity, as this study suggests is the case, this intimates that induced neural noise might help the brain to make sense of the visual world around it through stochastic facilitation. This intimation stems from the fact that brain parameters which reliably change with features of the visual environment could logically be used to facilitate the gathering of information about that environment. This seems especially likely to be the case if these changing parameters, like neural noise, might potentially also be detrimental to existing signals in the brain. In such a situation, the induction of neural noise would need to facilitate this information gathering to a significant degree to be maintained by evolution, as this maintenance likely requires that the computational mechanisms that exist in the brain would perform less well in the absence of neural noise (c.f. McDonnell & Ward, 2011). In light of this intimation, it is worth considering potential ways in which induced neural noise might help the brain gather information about the visual world.

One way in which this induced noise may help the human brain to interpret the visual world is that it may aid in the detection of weak visual signals via stochastic resonance. This possibility is consistent with theoretical evidence suggesting that neural noise is induced at a rate proportional to the amount of external visual noise present in a scene (Burgess & Colborne, 1988) because a signal would be relatively weaker in the presence of greater amounts of external visual noise and may therefore need greater aid from phenomena such as stochastic resonance to be detected reliably. It is also consistent with observations of stochastic resonance occurring in human visual cortex (e.g., Mori & Kai, 2002).

Induced neural noise may also help brains to interpret their world by allowing the visual system to take advantage of unattended stimuli in order to localize attended stimuli in space. If Burgess & Colborne's (1988) assertion that neural noise is induced at a rate proportional to the amount of external visual noise in a scene is correct, the often uneven distribution of external visual noise in a given visual scene could combine with the receptive field structure of the early visual system (see Carandini, 2004 for a review) in order to create a gradient of neural noise across the early visual system neurons that are most sensitive to different regions of the scene being viewed. Because very low neural noise levels lead to a reproducible rate of neuron spiking while higher noise levels lead to a more variable spiking rate (Stein et al., 2005), this gradient could engender a corresponding gradient in the variability of neuron spiking rates in response to a repeated stimulus. This corresponding variability gradient could allow a rate code to be used in order to determine the location of a visual stimulus in space with greater accuracy. Although this latter possibility is admittedly less well supported than the former, both merit further investigation in future research.

The consistency of these results with the notion that neural noise might have a positive role in the visual system by helping the brain make sense of the visual world stands in contrast to the consistency of the behavioral results of this study with a detrimental role of noise in the brain. For example, the increase in reaction time distribution parameters that measure decision uncertainty (tau) as external visual noise levels increased from low to high and medium is consistent with the notion that neural noise might interfere with visual perception. These two contrasting consistencies suggest a dual role of neural noise in the visual system as both an inhibitor and augmenter of perception. Intriguingly, given that perception is a foundation for a variety of cognitive tasks (e.g., visual working memory tasks), it is possible that the ability of neural noise in the visual system to modulate perception (as demonstrated by Skoczenski & Norcia, 1998, and intimated in the present study) may have downstream effects on these tasks as well. This possibility is consistent with recent findings (Söderlund et al., 2007) showing that exposing a subject to white noise can increase or decrease performance on cognitive tasks as a function of individual difference variables (e.g., diagnostic status). This possibility is also consistent with recent findings showing that random variation in blood-oxygen level dependent (BOLD) signal is linked with modulations in the performance of a face matching task (Garrett et al., 2013).

A final point of interest regarding the results of this study is their consistency with the neural noise hypothesis of aging put forth by Welford (1965). This consistency stems from the positive correlation between participants' reaction times (mu) in a given block of this study's visual search task with the changes in their entropy levels (from resting state baseline) observed after that block (Figure 6). This correlation provides some support for the notion that even small increases in neural noise levels can influence reaction times and give the appearance of cognitive

slowing, which is consistent with the tenet of the neural noise hypothesis that increases in neural noise levels can lead to cognitive slowing.

#### Conclusions

In summary, this study supports the notion that neural noise levels in the brain vary with changes in the external environment. This is consistent with the view that neural noise has a significant role to play in determining the way in which the human brain interprets the visual world. This study also provides some evidence suggesting that neural noise impacts behaviors which are underlied by the human visual system and which involve signal detection. Given these consistencies, combined with previously published evidence for the diverse and important effects of neural noise on behavior, a reversal of the current trend of decreasing interest in the study of neural noise is warranted. It is hoped that the neural noise altering paradigm presented in this paper will aid in the fulfillment of this warrant by adding a relatively simple technique to the arsenal of tools which may be used to study neural noise.

#### References

- Bays, P. M. (2014). Noise in Neural Populations Accounts for Errors in Working Memory. *The Journal of Neuroscience*, 34(10), 3632-3645.
- Bernasconi, F., De Lucia, M., Tzovara, A., Manuel, A.L., Murray, M., & Spierer, L. (2011).
   Noise in brain activity engenders perception and influences discrimination sensitivity.
   *The Journal of Neuroscience*, *31*, 17971-17981.
- Burgess, A.E., & Colborne, B. (1988). Visual signal detection. IV. Observer inconsistency. *JOSA*, *5*, 617-627.
- Carpenter, R. (1999). A neural mechanism that randomizes behaviour. *Journal of Consciousness Studies*, 6, 13-22.
- Carandini, M. (2004). Receptive fields and suppressive fields in the early visual system. In Gazzaniga, M.S. (Ed.), *The Cognitive Neurosciences*. Cambridge, MA: MIT Press.
- Delorme, A., Makeig, S. (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9-21.
- Douglass, J., Wilkens, L., Pantezalou, E., & Moss, F. (1993). Noise enhancement of information transfer in crayfish mechanoreceptors by stochastic resonance. *Nature*, *365*, 337-340.
- Faisal, A., Selen, L., & Wolpert, D. (2008). Noise in the nervous system. Nat. Rev. Neuroscience, 9, 292-303.
- Garrett, D., McIntosh, A., & Grady, C. (2013). Brain signal variability is parametrically modifiable. *Cerebral Cortex*, *24*, 2931-2940.
- Huynh, H., & Feldt, L. S. (1976). Estimation of the Box correction for degrees of freedom from sample data in randomised block and split-plot designs. *Journal of Educational Statistics*, 1, 69-82.

- Kail, R. (1998). Speed of information processing in patients with multiple sclerosis. *Journal of Clinical and Experimental Neuropsychology*, 20, 98-106.
- Kuriscak, E., Marsalek, P., Stroffek, J., & Wunsch, Z. (2012). The effect of neural noise on spike time precision in a detailed ca3 neuron model. *Computational and Mathematical Models in Medicine*.
- Li, S., Lindenburger, U., & Silkstrom, S. (2001). Aging Cognition: From neuromodulation to representation. *TRENDS in Cognitive Sciences*, 5, 479-486.
- Lu, Z., & Dosher, B. (2008). Characterizing Observers Using External Noise and Observer Models: Assessing Internal Representations With External Noise. *Psychological Review*, 115, 44-82.
- McDonnell, M., & Ward, L. (2011). The benefits of noise in neural systems: bridging theory and experiment. *Nature Reviews Neuroscience*, *12*, 415-425.
- Mori, T., & Kai, S. (2002). Noise-induced entrainment and stochastic resonance in human brain waves. *Physical Review Letters*, 88(21), 218101.
- Moss, F., Ward, L. M., & Sannita, W. G. (2004). Stochastic resonance and sensory information processing: a tutorial and review of application. *Clinical Neurophysiology*, 115, 267-281.
- Nolan, H., Whelan, R., & Reilly, R. B. (2010). *FASTER*: Fully Automated Statistical
  Thresholding for EEG artifact Rejection. *Journal of Neuroscience Methods*, 192, 152-162.
- Ratcliff, R. (1993). Methods for Dealing with Reaction Time Outliers. *Psychological Bulletin*, *114*, 510-532.

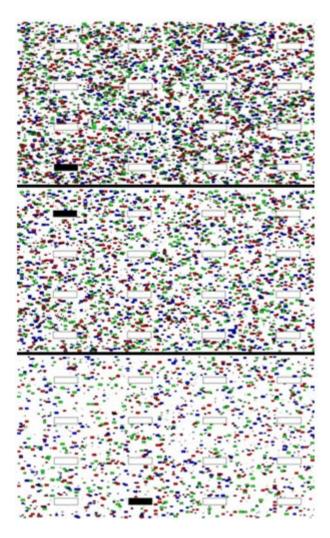
- Schneidman, E., Freedman, B., & Segev, I. (1998). Ion channel stochasticity may be critical in determining the reliability and precision of spike timing. *Neural Computation*, 10, 1679– 1703.
- Skoczenski, A., & Norcia, A. (1998). Neural noise limitations on infant visual sensitivity. *Nature*, 391, 697-700.
- Söderlund, G., Sikström, S., & Smart, A. (2007). Listen to the noise: Noise is beneficial for cognitive performance in ADHD. *Journal of Child Psychology and Psychiatry*, 48(8), 840-847.
- Stein, R., Gossen, E., & Jones, K. (2005). Neuronal variability: Noise or part of the signal? *Nature Reviews: Neuroscience*, 6, 389-396.
- Unakafova, V. A., & Keller, K. (2013). Efficiently Measuring Complexity on the Basis of Real-World Data. *Entropy*, *15*, 4392-4415.
- Welford, A. T. (1965). Performance, biological mechanisms and age: A theoretical sketch. *Behavior, aging, and the nervous system*, 3-20.
- Whelan, R. (2008). Effective Analysis of Reaction Time Data. *Psychological Record*, 58(3).
- Whiting, W. L., Sample, C. H., & Hagan, S. E. (2014). Top-down processing modulates older adults' susceptibility to noise. *Aging, Neuropsychology, and Cognition*, *21*(3), 370-385.
- Wiesenfeld, K., & Moss, F. (1995). Stochastic resonance and the benefits of noise: From ice ages to crayfish and SQUIDs. *Nature*, *373*, 33-36.
- Wolfe, J. M., Butcher, S. J., Lee, C., & Hyle, M. (2003). Changing your mind: on the contributions of top-down and bottom-up guidance in visual search for feature singletons. *Journal of Experimental Psychology: Human Perception and Performance*, 29(2), 483.

# Table 1

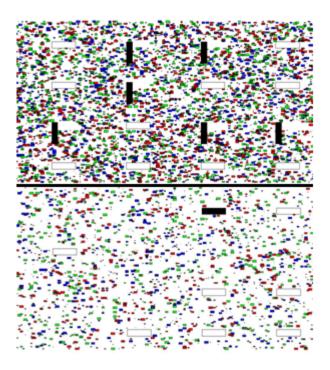
# Summary of Reaction Time Data

External visual noise Level		
Low	Medium	High
0.6022 (0.1458)	0.6804 (0.1623)	0.6982 (0.1839)
0.4261 (0.0853)	0.4328 (0.1024)	0.4476 (0.0922)
0.0566 (0.0268)	0.0567 (0.0305)	0.0683 (0.0429)
0.1719 (0.0998) <sup>A,B</sup>	0.2476 (0.1166) <sup>A</sup>	0.2493 (0.1464) <sup>B</sup>
	0.6022 (0.1458) 0.4261 (0.0853) 0.0566 (0.0268)	Low         Medium           0.6022 (0.1458)         0.6804 (0.1623)           0.4261 (0.0853)         0.4328 (0.1024)           0.0566 (0.0268)         0.0567 (0.0305)

*Note.* Shared capital letters following two values indicate a significant difference, p < .05. Values in parentheses are standard deviations. Reaction times in this table are in seconds.



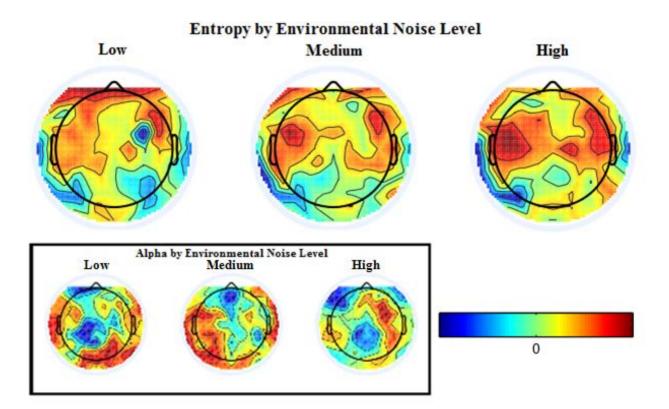
*Figure 1*. Representative examples of search displays with high (top), medium (middle), and low (bottom) levels of external visual noise that were used for the visual search task in this experiment. Targets are the horizontal black bars, while the distracter objects in these images are the white bars.



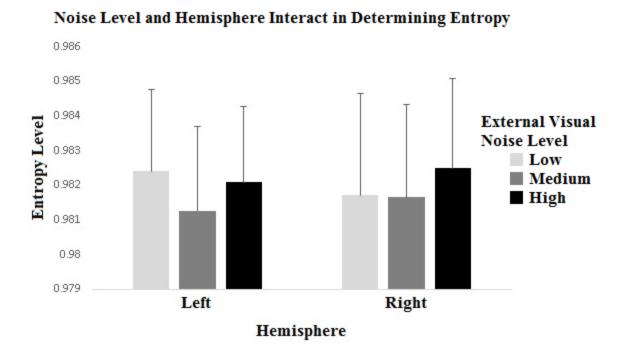
*Figure 2*. Representative example of a conjunctive search condition image with a large display size at the high noise level (top), and a representative example of a feature search condition image with a small display size at the low noise level (bottom). Targets are again the horizontal black bars, while the distracter objects in these images are the white bars and vertical black bars.

EEG recording:		
visual search task block	fixation cross	break

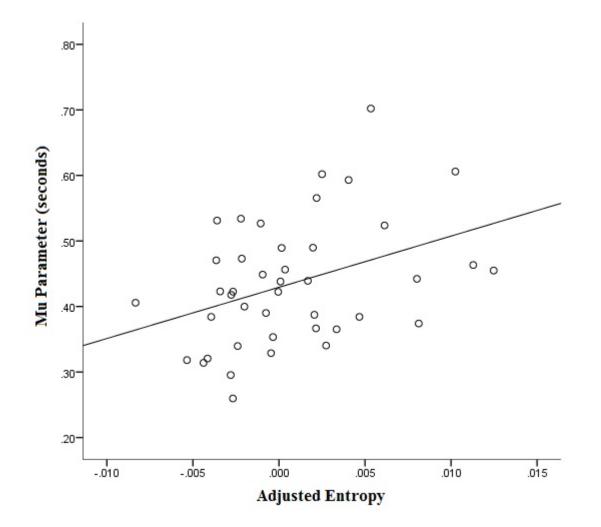
*Figure 3.* Diagram of how EEG data was recorded in relation to the activity completed by participants in one of the three blocks of this experiment. This recording pattern was identical in the other two blocks. At the top of the figure, light grey bars represent 4 second periods of recording. White spaces between these bars indicate 2 second periods where no recording occurred. The small black bar adjacent to the first grey bar represents the 500 ms period after the onset of the fixation cross during which no recording was made. In total, one minute of brain activity was recorded during each block.



*Figure 4.* Maps depicting the scalp distributions of the amount of entropy (main figure) and alpha power (inset; for reference) in the participants' electroencephalogram after completing visual search task blocks with low, medium, and high levels of external visual noise. Warmer colors indicate a larger amount of entropy or alpha power. Notice that the change in entropy over the external visual noise level conditions is relatively larger than the change in alpha power over the same conditions, indicating that entropy may be more sensitive to changes in psychological variables than traditional metrics of brain activity such as alpha power.



*Figure 5.* Interaction between noise level and hemisphere in determining the amount of entropy over participants' brains. This interaction can be seen in the fact that in the left hemisphere the difference between the entropy in participants' brains at successive external visual noise levels was largest when comparing the low and medium levels of external visual noise, while in the right hemisphere this same comparison yielded the smallest difference between successive external visual noise levels. Error bars represent SEMs.



*Figure 6.* The deviation of a participants' entropy from their baseline resting state entropy level after completing a block of the visual search task in this study is positively correlated, r = .38, with the mu parameter describing the distribution of their reaction times during that block of the visual search task. The abscissa denotes this difference in entropy. More positive numbers on the abscissa denote that the participants' entropy after completing a block of the task was successively larger than that when at baseline. Line of best fit shown, n = 42.

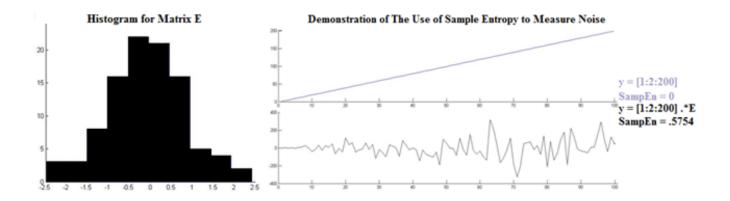
#### Appendix 1. Measuring Noise in Brain Activity with Entropy

In this appendix, the reader is given the background knowledge needed to understand how random noise can be quantified using entropy. An important part of this background knowledge is a basic understanding of equations for measuring the amount of entropy in a data set One typical example of such an equation is listed below.

## Equation A1: SampEn(dim, m, X, r, $\tau$ ) = -log(A/B)

This equation is a summary of the function for Sample Entropy, a very popular form of entropy measurement. The main input into this function is the time series, X, which contains the data whose entropy one wishes to measure. This time series is then optionally down-sampled by reducing time series X to a subsample of X consisting of every  $\tau^{th}$  member of X. The time series X (whether or not it has been down-sampled) is then divided into vectors of length m. This vector length is traditionally set to two (Zurek et al., 2012). These vectors are then randomly paired in all possible combinations and the maximum of the differences between corresponding members is found for each vector pair. The number of these vectors with maximum differences less than the tolerance, r, is recorded as A. This tolerance is usually set equal to one-fifth of the standard deviation of X (Zurek et al., 2012). Each of these vectors is then reduced to m-1 members by removing the final member of the vector. These vectors are again paired in every possible combination and the maximum difference between the corresponding members of each pair is found in the same manner. The number of these vectors with a maximum difference less than r is recorded as B. The negative log is then taken of the ratio of A to B. This operation results in the SampEn function's output, which is a logarithmic transformation of the probability that if the maximum difference between two subsets of X of length m-1 is less than r then the difference between two subsets of X of length m will be less than r as well. The larger the value of this output, the more entropic the set X can be said to be. (The equations and descriptions included in this Appendix above this point are adapted from Richman & Moorman, 2000).

From this information about how entropy equations work, a prediction that is important in the studies of the present paper can be made. This prediction is that reducing the correlation between the members of each vector of length m taken from X above will increase the value of the entropy function's output by reducing how predictive the maximum difference between corresponding members of vector pairs of length m-1 is of the maximum difference between corresponding members of vector pairs of length m. One way that this reduction in correlation can be accomplished by adding random noise to time series X. Therefore, the amount of entropy in a time series will vary with the amount of noise in that time series. This fact, which is demonstrated in Figure A1 below, is what makes entropy equations an appropriate measure of the amount of noise in a time series.



*Figure A1*. This figure demonstrates how a popular entropy measurement, Sample Entropy (SampEn), can be used to measure the amount of random noise present in a signal. The graph at the top right of this figure shows a signal with no noise present. Note that the SampEn value for this signal (at far right in blue) is zero, which is consistent with its lack of contamination by noise. The graph at the bottom right of this figure shows the same signal modulated by the distribution of Gaussian noise depicted at the left. The SampEn value for this modulated signal (in black at the far right) is significantly higher than that for the original signal, suggesting that measures of entropy are effective in detecting the amount of noise in a signal. Equations for both the original and modulated signal are listed at the far right in the same color as their corresponding graph for reference.