The Number of Cortical Neurons Used to See

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Abstract:

A neuron's *receptive field* is the area in the visual field in which it responds to light. A neuron has one cell body and many dendrites. Physiologically, the integration occurs as the signals from the many dendrites converge on the cell body. The integrated input signals cause the cell to fire, i.e. produce an action potential. The cell firing stimulates the dendrites of other neurons. The integration is linear (weighted averaging) even though the cell firing depends nonlinearly on that weighted average. The main nonlinearity is a threshold. The cell does not fire if the weighted average is less than the neuron's threshold. Thus, although a complete mathematical model of the neuron would include the nonlinearity of the cell's response, the spatial integration by the cell's receptive field (or dendrites) is a simple sum, a linear weighted average. That weighted average is a *sample* of the image in the visual field of the observer. The weighting functions that produce these samples have been extensively studied in individual neurons in fish, cats, and monkeys, but very little is known about how these animals and people use multiple neurons to see. There are hundreds of millions of neurons in the visual cortex, but so little is known that previously studied performance of human observers might be accounted for by using a single cortical neuron. Here a new technique, based on a new mathematical theorem, allows non-invasive visual tests to demonstrate that people use a large number of neurons. More specifically, I find that people take 100 samples to perform my tasks. Each neuron takes one or two samples, so the observers must be using at least fifty neurons to do my visual tasks. Saying how many neurons are used is a significant step towards the ultimate goal of explaining how these neurons do the visual computation that is seeing.

Introduction:

A neuron's receptive field is the area in the visual field within which the presentation or removal of visual stimuli affects the activity of the neuron. The neuron integrates all the information within the receptive field. Anatomically, a typical neuron has hundreds of dendrites, one cell body, and one axon. The neuron continuously receives messages through ten thousand synapses on its dendrites. The many dendrites all converge on the cell body, where the incoming signals are all combined to one, which is sent out through the axon. The combining is linear integrations (weighted averaging). The cell firing depends nonlinearly on that weighted average. The main nonlinearity is a threshold. The cell does not fire if the weighted average is less than the neuron's threshold. Thus, although a complete mathematical model of the neuron would include the nonlinearity of the cell's response, the spatial integration by the cell's receptive field is linear integration, a weighted average. That weighted average is a *sample* of the image in the visual field of the observer. The equation describing how the receptive field computes a sample is

$$r = w_1 s_1 + w_2 s_2 + \ldots + w_{100000} s_{100000},$$

where s represents the strength of the stimulus image at 10,000 points and w represents the weight of the corresponding synapse transferring the information (Hubel 1968).

The operation of the receptive field reduces the pattern of stimulation on our sensory surface (e.g. the retina) into one number, a sample (Green 1974). Neural receptive fields are present in the auditory system, the somatosensory system, and the visual system. Every visually responsive neuron in the brain has a receptive field over which it is sensitive. Typically that receptive field computes one sample. Simples cells in the primary visual cortex (area V1) each compute one sample, but some neurons, like the complex cells in area V1, compute two samples (Spitzer and Hochstein 1985).

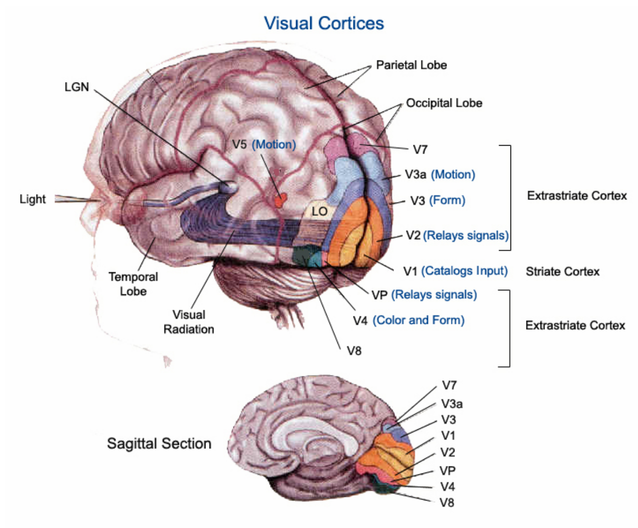

Figure 1. This image shows the divisions of the visual cortex at the back of the brain, in the occipital love. The neurons being studied in this experiment are located in area V1, the primary visual cortex.

This research paper uses a new perceptual test and a new mathematical theorem that allow direct measurement of how many samples the observer is using to do the task. There has been much study of individual neurons by microelectrode recordings in animals, and gross activation of brain areas by brain scans in man, and psychophysical investigation of limits to human perception (Marcelia 1980). However, it has been very difficult to make specific links between human perception and particular neurons.

My results set a substantial lower bound (50) on the number of cortical cells contributing to seeing. The results of this study are an important step toward unraveling how we use neurons to see.

1.1 Primary Visual Cortex: simple and complex cells

The retina is sensitive to light. It sends signals, by the optic nerve, to the lateral geniculate nucleus, which relays the information to the cortex (Marcelja 1980). The visual input for cortical processing arrives at the primary visual cortex, V1 for short. Hubel and Wiesel discovered in 1959 that V1 consists of two types of cells, simple and complex (Hubel *et. al.* 1962). Both these types of neurons respond selectively to stimuli with particular orientation, direction of motion and spatial frequency. The behavior of simple cells is easy to model, as a nonlinear function of a single image sample. The behavior of complex cells is harder to model. Spitzer and Hochstein (1985) modeled it as a nonlinear combination of two samples. Receptive fields of simple cells have a circular exhibitory region surrounded by a rectangular inhibitory region. Thus simple cells have distinct exhibitory and inhibitory regions, and respond to temporal modulation of grating patterns, at the same frequency (Tao *et. al.,* 2003). Thus they have a greater sensitivity to location, orientation and spatial frequency than complex cells. Graham and Wandell used psychophysical methods and quantitative models to test the linearity, showing that they use just one sample (Brainard 1997). Simple cells have a single "receptive field subunit," i.e. they take one sample (Movshon *et. al.* 1978). Complex cells take two samples and combine in a nonlinear way (Spitzer and Hochstein 1985). Complex cells are less spatial phase oriented and more directionally selective in terms of their firing. They do not have clearly divided exhibitory and inhibitory regions, thus complex cells respond regardless of position. However the firing of the neural complex cell is modulated by the direction the stimulus is travelling in (Hubel *et. al.* 1962). Complex cells are the nonlinear combinations of two receptive field subunits, and thus take two samples from the image (Spitzer and Hochstein 1985). Despite a great deal of study of V1, there is no good account for how people use those neurons to see (Barlow 2010).

There has been thorough investigation of how the receptive fields work in individual cells, including both simple and complex cells of the primary visual cortex. However very little is known about how what computation those neurons perform to allow us to see. Does vision require more than one neuron? The answer would be a useful step toward discovering the whole story of how we use neurons to see.

1.2 Receptive fields as detectors

Signal detection theory states that the optimal detector for a known signal, in a given noise, is a matched receptive field. Thus the neurons in the human visual system are optimal detectors of patterns that match their receptive fields (Green *et al.,* 1974).

1.3 How many samples?

Thus we know that neurons use their receptive fields to sample the image. We devised a task that benefits from taking more samples. A basic problem in statistics is to estimate the variance of a population from a set of samples. One calculates the variance of the samples and uses that to estimate the variance of the population. If the number of samples is large then the estimate can be very accurate. To make this a visual task, we present four sets of "checks": tiny uniform squares, each a different gray level. The observer is asked to report which set has highest variance. In our terminology, the observer sees four large squares, each consisting of many small checks. The observer is asked to say which of the four checks has highest variance, or seems to have the highest contrast or “roughness”. It is easy to calculate the best possible performance, sampling each check and computing the variance, and choose the highest-variance square. Humans, of course cannot be better than ideal, and may be much worse. It’s easy to calculate how many checks would need to be sampled to account for the accuracy of human performance. The power of our conclusions is greatly increased by a theorem, proven for this project, by Professor Martin Barlow in the Mathematics Department at University of British Columbia. He showed that any set of image samples that is not redundant, in the sense that one could be predicted from the rest, is equally informative as that number of checks for the purpose of doing this task. Thus, when we compute the minimum number of checks required to attain the human-achieved level of performance, this is also the minimum number of samples the human must be using. Since V1 neurons take only one or two samples, then the number of neurons used by the observer must be at least half the number of samples required to do the task.

With this approach we then set out to measure this required number of samples, and to study how it depends on the test conditions: the size of the square, the size of the check, and the number of checks in the square.

One hypothesis is that as the number of checks present increases, the visual system uses more samples. A second hypothesis is that the size of the check or the square might hit resolution limits and thus affect the number of samples used. A third hypothesis is that distance will have no effect, since even though the sizes (expressed as visual angle subtended) change, the number of checks is independent of distance. Alternatively, as the distance decreases and more of the display is pushed into the periphery, the observer would use fewer samples.

The purpose is to discover how many samples observers use to do this visual task, and how it depends on the parameters of the experiment.

Materials and Methods:

Participants:

10 participants took the required tests in the two tasks for this study. All participants were aged 16 to 17 years old. They and their parents gave informed written consent, as approved by the New York University review board. They all had 20/20 vision or altered to 20/20 vision and were fluent in English. What to do for each task was explained to each participant: 1) choose which of four squares has the greatest visual noise (variability of the gray checks), or 2) identify the letter present in the noise. They were not told the purpose of the experiment.

Description of Stimuli:

Method 1-

In the first method, the stimuli were 16 slides with four squares on each slide. Each slide was an individual puzzle of the same task. The task for the observer was to find the square with the greatest noise on each slide. The slides were made in such a way that the puzzle got harder as the next slide was approached. Each slide consisted of squares, each with a different noise level. The noise for each individual square was calculated by using all the values of the pixels to find the variance. Variances for all four squares are predetermined before the test is administered. The square with the greatest variance was the square with the greatest noise.

Method 2-

A program in MATLAB named "noise discrimination" was created to automate the generation of stimuli, which allowed me to run more trials and estimate each observer's threshold more precisely. However, despite the fancy software, the task presented to the observer was the same: which of four squares is noiser than the rest. Each observer had to go through three tests. Each test consisted of 2 runs of 100 trials each. One individual trial consisted of a slide consisting of four squares. Each slide consisted of squares, each with a different noise level. The noise for each individual square was calculated by using all the values of the pixels to find the variance. Variances for all four squares are predetermined before the test is administered. The square with the greatest variance was the square with the greatest noise. In each test, the viewing distance and the height of the square remained the same. The independent variable was the width of the pixels (check size) or the number of pixels present per square. The checkPix options were 1, 2, 4, 8, 32, and 64. After each test, the checkPix value was changed and the next test was given. After each test the results were recorded the observer was told to move on to the next text with the changed check size.

Along with the variance, the number of receptive fields the brain would use to solve each slide was calculated. This specific calculation was done using Barlow's theorem. A value that can achieve performance as good a performance with all the data is called a sufficient statistic. The sufficient statistic for this test for discriminating noise is the sum of squares of the luminance deviations at all n pixels. Thus Barlow's theorem states that if a large number of pixels are displayed and ideal human performance is achieved then the human mind is using at least n pixels to achieve that performance. Barlow's theorem went further to state that if the human mind uses at least n pixels to achieve ideal performance, it uses at least n receptive fields as well. By using his theorem, the number of receptive fields the ideal observer uses was determined.

Each slide had a square with the greatest noise. If the observer was able to determine which square had the greatest noise, then they used a specific number of pixels present in the square and thus the same number of receptive fields to discriminate the noise. This is a sample of the stimuli.

Figure 2. This figure shows the stimuli the squares had 10000 checks. The right answer is square number 2. In order to solve this task, one uses 97 receptive fields.

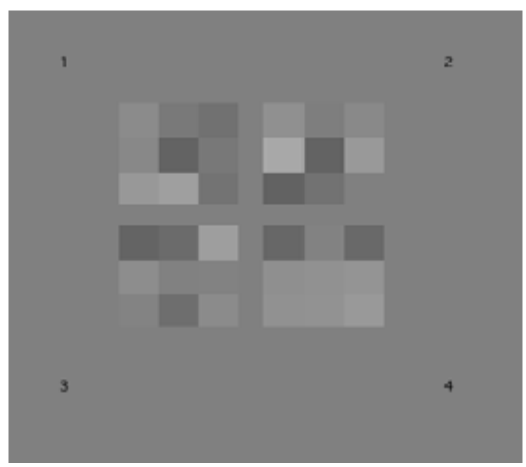

Figure 3. This figure shows the stimuli when the squares had 9 checks. The right answer is square number 2. In order to solve this task, one uses 6 receptive fields.

Method 1-

The observer was gently made to stand 110 cm away from the computer slide consisting of the four squares. The observer was then told to discriminate the noise and determine which square had the greatest noise. If the observer discriminated the noise correctly, then the next slide was placed on the computer and the task was repeated until the observer determined which square had the greatest noise incorrectly. This slide was then used to determine the minimum threshold of the observer and the number of receptive fields the observer uses to discriminate noise.

Then the observer was made to stand 222 cm away from the computer slide consisting of the squares. The same procedure was repeated. The observer was asked to discriminate the noise and determine which square had the greatest noise on each slide. After each correct answer, the next slide was placed on the screen. When the observer answered incorrectly, the slide was used to determine threshold and number of receptive fields. The observer was then made to stand 378.5 cm away from the computer and the entire process was repeated then the number of receptive field the observer uses was determined.

This test was the repeated on all ten observers.

Method 2-

For the first trial, the checkPix value was set to one. The observer was then asked to identify the letter in the square. The observer was then told to discriminate the noise and determine which square had the greatest noise. If the observer thought that square three had the greatest noise level then the observer would click the mouse three times. This was repeated for 100 trials and then a new run started on the program with another 100 trials. After the two runs were completed, the value of checkPix was changed to two and the test was repeated. After these two runes, once again the value of checkPix was changed to four. After these two runes, once again the value of checkPix was changed to eight. After these two runes, once again the value of checkPix was changed to thirtytwo. After these two runs, once again the value of checkPix was changed to sixty four. This was done with each observer. After completing this test at the distance of 50 cm, the entire procedure is repeated at a distance 200 cm.

Results:

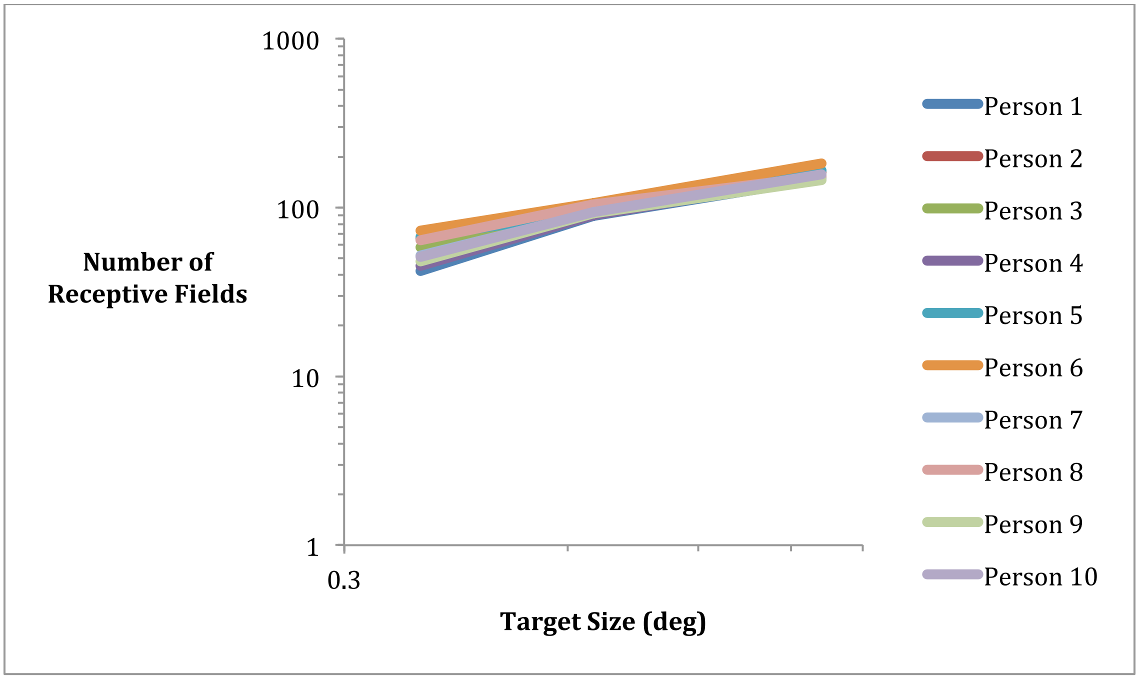

Figure 4. The effect of target size on number of receptive fields.

The horizontal axis represents the target size in degrees and vertical axis represents the number of receptive fields. The 10 individual lines show the different number of receptive fields of the 10 subjects across three different target sizes. All 10 lines follow a general trend of increased number of receptive fields as target size increased. The two variables follow a direct and linear relationship across all the subjects. Individually however, the number of receptive fields is more variable at a lower target size and begin to saturate at a larger target size. Even though the target size increases by a factor of three, the number of receptive fields, used by the subjects in order to complete the given task, come closer together and began less variable.

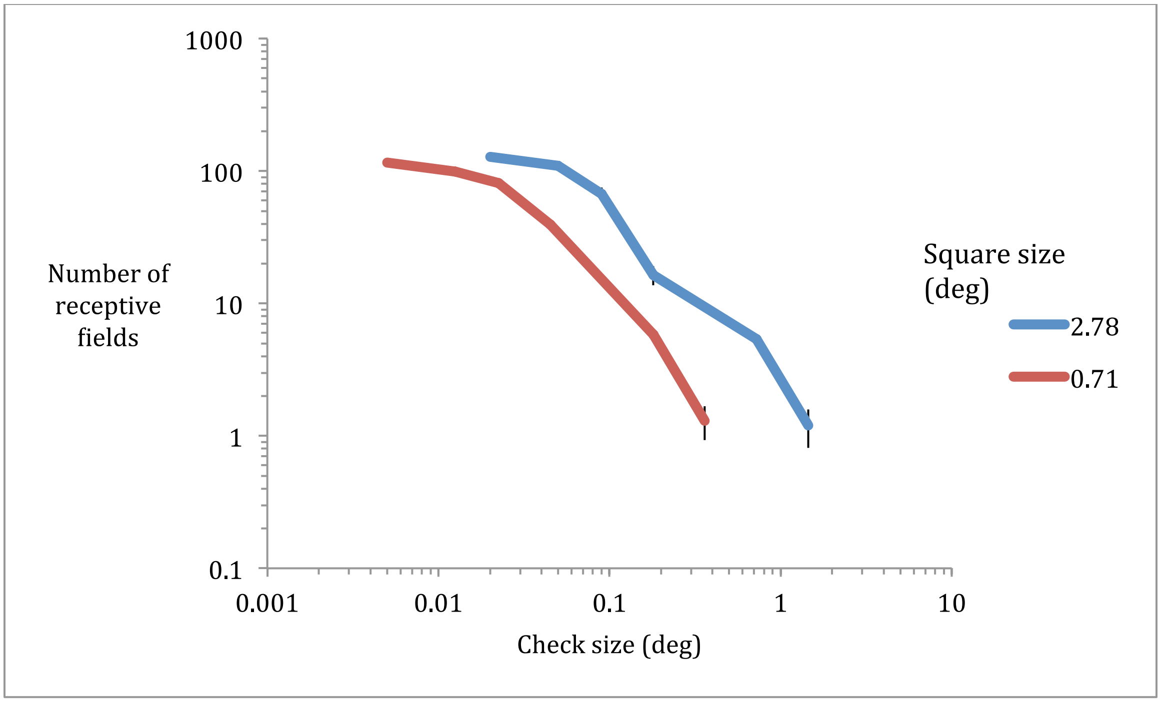

Figure 5. The effect of check size on number of receptive fields.

The horizontal axis represents the check size in degrees and the vertical axis represents the number of receptive fields. The square size of 0.71 deg is the line for the results at the distance of 200 cm and square size of 2.78 is the line for results at the distance of 50 cm. The general trend, shown by the averages of all 10 subjects, shows that as check size increase, the number of receptive fields used by the visual system decrease. Another pattern observed was saturation of the number of receptive fields used at about 100 receptive fields when the check size was reduced by a great factor of 5. At the larger square size (2.78 deg), the data was more variable than at the smaller square size (0.71 deg). For the smaller square size, the data points were closer together, thus showing less variability. The number of receptive fields also stayed fairly consistent despite the difference in square sizes. The lines for both the square sizes consist of values similar to one another and follow the same general pattern.

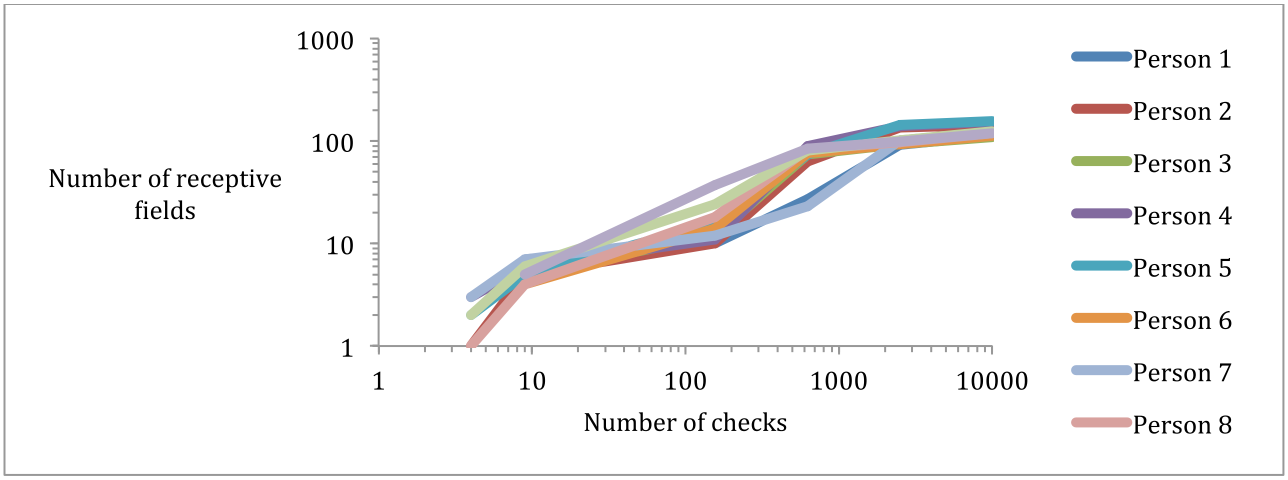

Figure 6. The effect of the number of checks on the number of receptive fields at a distance of 50 cm.

The 10 lines show the different number of receptive fields used due to the different number of checks given across the 10 subjects at a distance of 50 cm. The general trend was as number of checks increased, the number of receptive fields used increased.

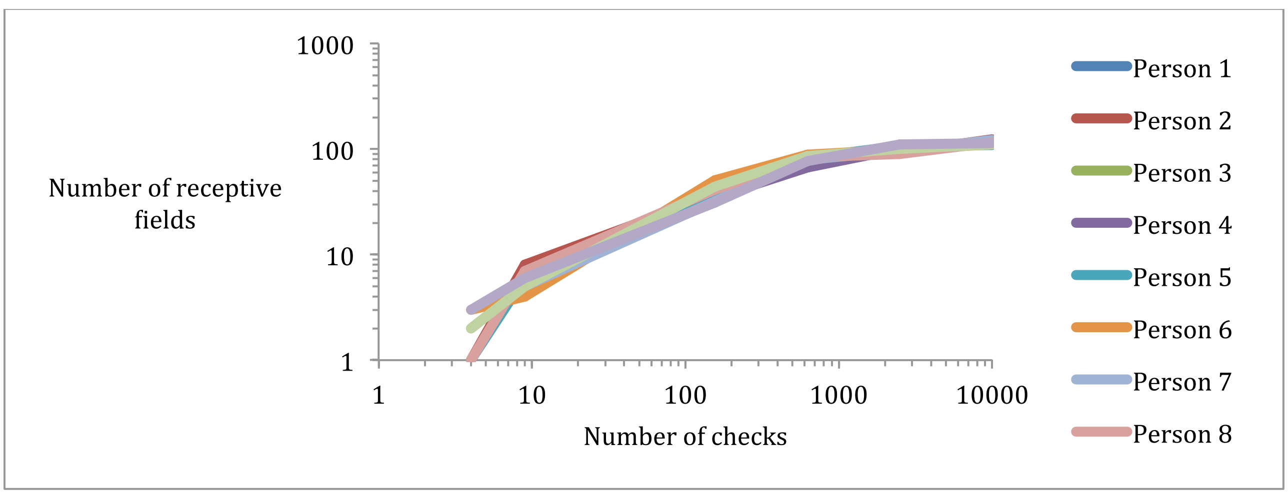

Figure 7. The effect of the number of checks on the number of receptive fields at a distance of 200 cm.

The 10 lines show the different number of receptive fields used due to the different number of checks given across the 10 subjects at a distance of 200 cm. The same trend was present was this data set that as the number of checks increased, the number of receptive fields increased as well. However , the data was less variable at a larger distance (200 cm) then at a shorter distance (50 cm).

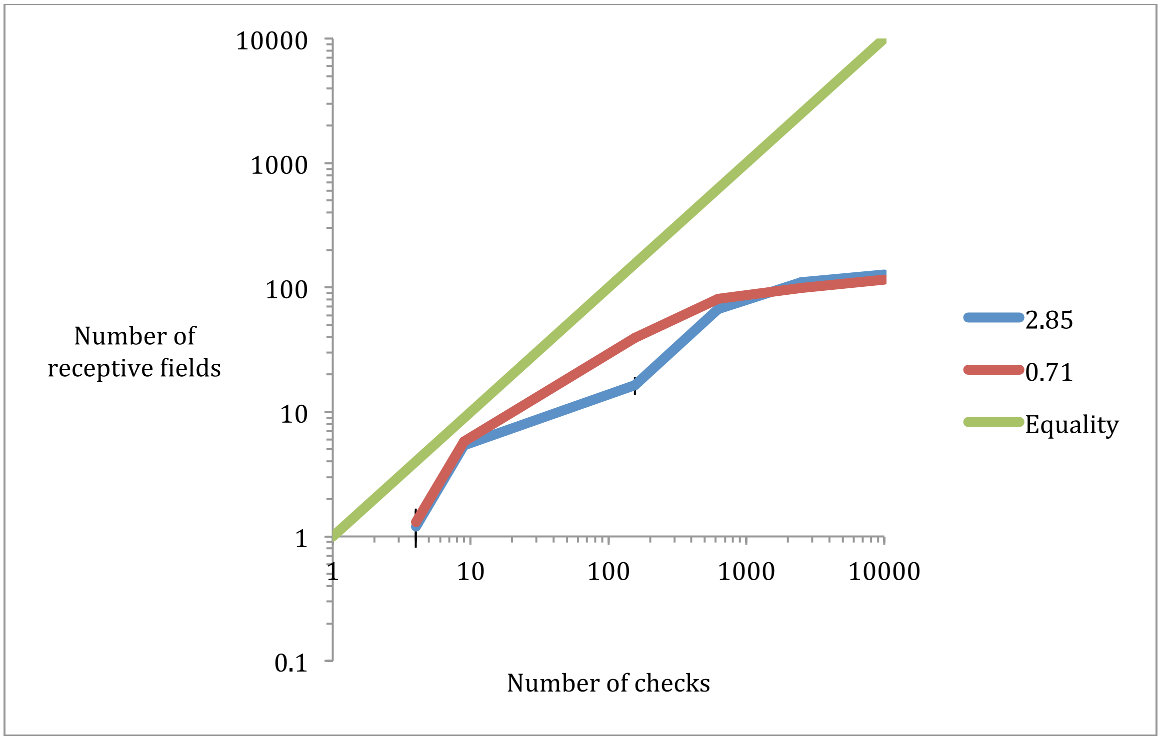

Figure 8. The effect of the number of checks on the number of receptive fields.

The lines show the averages of the data presented in the previous graphs. The shorter distance (50 cm) is represented by 2.78 degrees in terms of square size and the larger distance (200 cm) is represented by 0.71 degrees in terms of square size. The general trend of increasing number of receptive fields is found for both square sizes. The number of receptive fields used by the visual system overlap for both the square sizes at the minimum and maximum of number of checks. The variability between the two square sizes is present around 156 checks. Surprisingly, even thought the number of checks is increased by nearly a factor of 10000 the number of receptive fields being used begin to saturate at about 100 receptive fields, suggesting a maximum of fields that can be used by the visual system. The lines for both the square sizes consist of values similar to one another and follow the same general pattern.

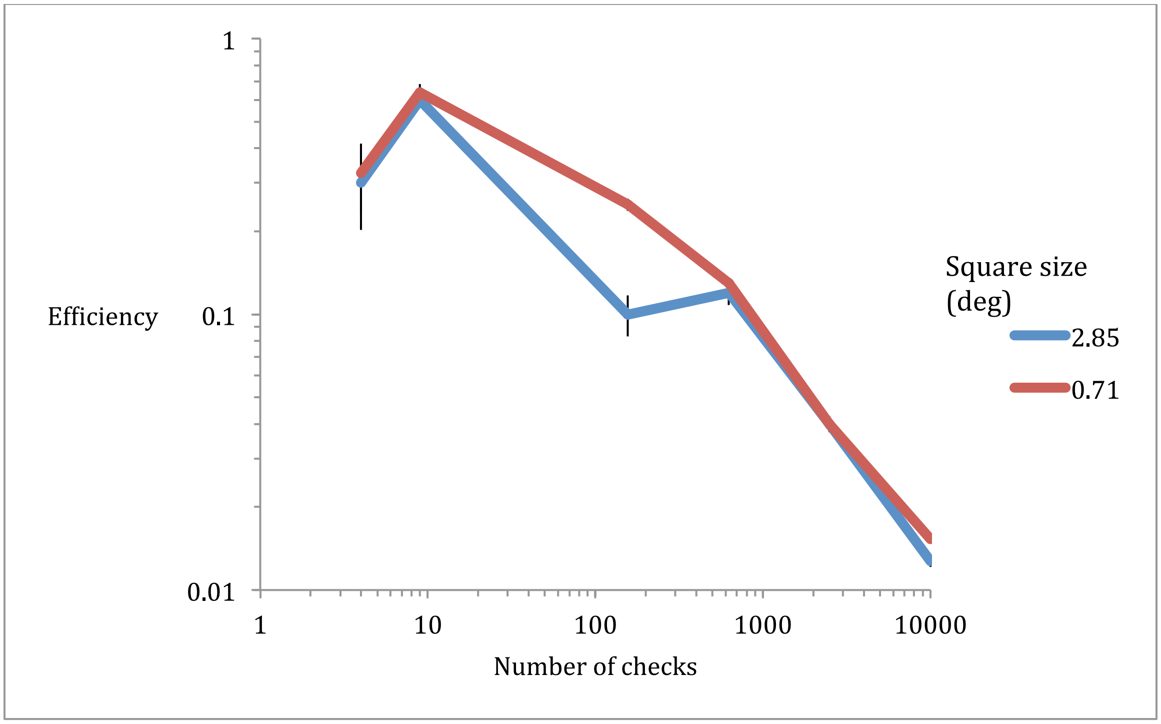

Figure 9. The effect of the number of checks on the efficiency of the observer.

The horizontal axis represents the number of checks and the vertical axis represents the efficiency of the observer. The efficiency is calculated by the amount of information used to the amount of information present or the number of receptive fields used to the number of checks present. The shorter distance (50 cm) is represented by 2.78 degrees in terms of square size and the larger distance (200 cm) is represented by 0.71 degrees in terms of square size. The pattern followed is as the number of checks increase, the efficiency generally decreases. The efficiency starts off at about 0.3 (30%) at four checks and peaks at about 0.64 (64%) at nine checks. From 9 checks to 10000 checks, the efficiency begins to decrease. The efficiency is variable, however begins to saturate at about 10000 checks, similar to the saturation of the number of receptive fields.

Discussion:

The purpose of this experiment was to identify the different factors that affect the number and function of receptive fields. By studying how different factors affect these receptive fields, an insight is provided into the brain and the processes and mechanisms it uses in order to complete second to second functions. Due the results provided conclusions can be drawn about the properties and features of the receptive fields.

Identical tests were given to observers at two different distances. All the figures show that even though variability existed between the two distances, the distance did not have a significant of the number of receptive fields used by the visual system. The visual system uses the same number of receptive fields in order to process information presented to the retinas, neglecting the distance to the necessary information. When the same task (same information) was presented at a distance increased by a factor of 4, on average the same number of receptive fields were used to process the information. Thus when focusing on a specific object in our visual surroundings, the visual system does not take into account distance and rather just focus on the intended object.

Another observation all the figures and graphs agree upon is the maximum number of receptive fields used. In Figure 2.1, the check size was decreased by a factor of 4, yet the number of receptive fields used began to saturate at about 100 fields at the smallest check (pixel) size. In Figures 3.1, 3.2 and 3.3, the number of checks was increased by a factor of 10000, yet the number of fields began to reach a constant value of about 100 receptive fields at the greatest number of checks. 100000 checks were present in front of the observers, yet the maximum the observer was able to use was 100 receptive fields. Compared to the amount of information given, the amount of information used was extremely small. For the first time, in neural studies history is an upper bound for the number of receptive fields used determined. Previous studies have shown a lower bound for the number of receptive fields that the visual system needs in order to process information. However never before has an upper bound or a maximum number of receptive fields been discovered. The results support the conclusion that no matter what factor, there is a certain limit of about 100 receptive fields that we can use.

Previously, in Horace Barlow's paper, it had been determined that a typical observer attains 50% efficiency or uses at the greatest 50% of the information provided to the visual system. Using the data presented in Figure 4.1, the efficiency is greatest at nine checks with 64%. The new finding conforms the previous one as the percentages are near to same. It has been concluded that when the number of receptive fields get too large, efficiency declines because the element is then picking up more noise from the background then necessary (Barlow 1978). New data also support the previous conclusion, however in a new approach. Since there is a maximum to the number of receptive fields that can be used, even though there is increasing amounts of information, a low efficiency will be present. The information present will be given at a ratio higher than the ability of the receptive fields to process, thus attaining low efficiency.

Significance of this experiment can be split into two categories, of research development and of practical application. For research development, these findings prose a great scientific advancement in testing neurons. Firstly because they conclude that there is an upper bound of receptive fields that can be used by a visual system in solving a task. This finding really gives insight into the brain and allows us to know how vision truly works in up in the control center. Secondly the results attained by use of this method prove that this method is indeed an advancement in how to test the function of the neurons of the brain. Past experiments have attempted to prove that specific neurons are used by the brain in conducting certain functions. However these experiments use assumptions rather than conformation. The Pixel to Receptive Field theorem, theorized by Martin Barlow, is used to find the exact number of neurons used by the brain in certain tasks. This method can be further applied to other studies of the brain. It can be used to study other functions and processes the brain carries out. If applied to further studies, this new method would have amazing outcomes and findings. Besides research implications, there are practical uses to these new findings. By understanding of vision works, the world can be manipulated in a way that brings out greater human efficiency. Furthermore, the world is now completely technology dominated. Knowing how different pixel sizes and number can help extrapolate conclusion about how our eyes see the world. Technology and the environment can be changed so that humans can understand the world better and can obtain greater efficiency in completing day to day activities. The brain is an amazing control center without which the human body would be mere material. The brain gives it life and allows it to perform needed functions. Knowing how the brain truly functions is an extremely significant piece of information for us, as human to know and understand.

Conclusion:

Here a new technique, based on a new mathematical theorem, allows non-invasive visual tests to demonstrate that people use a large number of neurons. More specifically, I find that people take 100 samples to perform my tasks. Each neuron takes one or two samples, so the observers must be using at least fifty neurons to do my visual tasks. Saying how many neurons are used is a significant step towards the ultimate goal of explaining how these neurons do the visual computation that is seeing.

The conditions of the experiment were varied in several ways, to determine how they affect the number of samples used by the observer. As the information given increases (number of checks), the number of samples used increases, up to 100. Viewing distance, another factor, does not have a significant effect on the number of samples used. Due to the 100-sample limit, the efficiency of the visual system decreases as the number of checks grows past 100, since the human is using a decreasing fraction of the given information. This is an important advance in understanding the role of cortical neurons in visual perception.

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