**First Year Project**

**Covert Attention Introduces Hierarchical Interference in the Neural Representations of Contrast and Motion Coherence.**

**Or**

**Neural Substrates of Attention and Awareness.**

Dan Birman, PI: Justin Gardner

**Abstract**

How does a prior expectation about

**Introduction**

In everyday life we feel a direct and undeniable connection between attending to something and our clear awareness of it. Despite this there exist a variety of laboratory situations in which attention and awareness appear to diverge. This apparent disconnect between experience and experimental findings has fueled a debate about whether *selective attention* and *awareness* are dissociable (Koch & Tsuchiya, 2007). In scene recognition experiments participants are able to identify the content of peripheral stimuli despite attending to a demanding fixation task (Li, VanRullen, Koch, & Perona, 2002). In contrast, many studies have found that participants are unable to respond about unattended stimuli, in particular for simple features such as shapes and colors (Mack, Arien & Rock, Irvin, 1998). One possible interpretation for the variability in results in these tasks is that stimulus features may be interacting in unexpected ways. The neural activity responsible for scene recognition may be modified only by certain types of attentional modulations. For example, attending to motion appears to result in diminished awareness of scene gist (Cohen, Alvarez, & Nakayama, 2011), while attending to other features may not cause in-attentional blindness. We propose that this feature-specific hypothesis may depend crucially on the layout of visual cortex. Our hypothesis is that modifying a neural representation through spatial or feature-based attention is only detrimental to awareness when there are direct connections between the relevant neural representations. Contrast is known to be well specified by neural activity in the earliest cortical visual area: V1. The human MT+ complex on the other hand is less sensitive to contrast, but considerably more sensitive to the presence or absence of motion in a stimulus. We propose to test our hypothesis by measuring behavioral and neural activity related to the representations of contrast and motion when participants are cued to one feature. Behaviorally we expect to see that performance on a motion task will suffer more when participants are cued to contrast compared to when participants are cued to motion and asked about contrast.

We propose to test the prediction that attention and awareness will interact only when their neural substrates interfere. One way to assess this is to use a dual task paradigm in which one task’s neural substrate has a variable overlap with the neural substrate of the other task. In vision, tasks that rely on assessing different perceptual features are thought to engage different neural substrates. For example, contrast is represented by early visual cortex (CITE) while the signal to noise ratio of an objects in a scene are represented by later visual areas (Tjan, Lestou, & Kourtzi, 2006). One object feature, the gender of faces, has shown a dissociation of attention and awareness in dual task paradigms (Reddy, Wilken, & Koch, 2004). Gender is known to be represented by cortical regions that overlap with the signal to noise ratio response, but not the contrast response (Freeman, Rule, Adams, & Ambady, 2010). By varying a main task between contrast and noise discrimination we can therefore adjust the overlap of neural responses with gender categorization. We predict that when both the attentional task and categorization task require similar neural substrates they will interfere with each other. But when the neural substrates diverge we expect to find results similar to previous work on recognition in dual-task settings (Li et al., 2002; Reddy et al., 2004).

To quantify how the neural substrates of attention and awareness overlap and diverge we will expand on previous work for contrast discrimination (Pestilli, Carrasco, Heeger, & Gardner, 2011). The authors of this study used computational modeling to show that a downstream mechanism pooling the neural responses in early visual cortex can account for the behavioral effect of selective spatial attention. We will replicate this result but also extend similar computational models to account attentional modulation in the noise discrimination task. Our prediction, based on evidence dissociating the neural substrates of contrast and noise, is that that performance on the noise discrimination task is best modeled from neural responses in late visual cortex. These computational models can then be used to investigate how awareness depends on neural responses. If the same neural activity can explain how focal attention modulates both behavioral performance and awareness, then this is evidence that attention and awareness are not dissociable processes. On the other hand if the impact of attention on discrimination performance and awareness can only be explained using different models, this is evidence that the underlying computational processes, at the neural level, also diverge.

**Methods**

**Subjects**

Four human subjects (all male, ages 24-34) participated in the experiment. All subjects performed the behavioral experiment and one participant performed the functional MRI experiment. Subjects in the behavioral experiment performed one training session to become accustomed to the task, four to eight control runs (65 trials each), and between 12 and 24 task runs (100 trials each, 15% miscued). Subjects in the functional experiment performed a retinotopic mapping (1 hr, consisting of ten 4 minute scans) and four to five sessions of the main experiment (2 hrs each, consisting of ten 7 minute scans).

**Experimental Task**

Subjects performed a two-alternative forced choice discrimination task. On each trial participants were shown two patches of dots and asked to report which had a higher apparent contrast or motion coherence. Each dot patch was shown for 750 ms and followed by a 250 ms mask, generated by flashing random checkerboards at 55% contrast at 40hz. A random inter stimulus interval followed for between 200 and 500 ms after which the fixation cross turned white, indicating that the response period was starting. Participants had 1 second to respond. Each trial was followed by a random inter-trial-interval of 300 to 500 ms. Participants fixated a central cross (1 deg x 1 deg visual angle, 1 pixel wide, luminance ?!). During control runs participants were cued to attend to either motion or contrast and responded about the cued feature. On task runs participants responded about the miscued feature on 15% of trials. The trial timing was modified during scanning to improve estimation of the hemodynamic response, stimulus: 750 ms, mask: 250 ms, ISI: 200-1000 ms, resp: 1000 ms, ITI: 2000-10000 ms. During the behavioral experiment the screen updated at 100 hz and at 60 hz during scanning.

The dot patches appeared left and right of fixation, extending from 3.5 to 11 degrees horizontally and from -5 to 5 degrees vertically. The patches were displayed on a gray background (50% luminance) on a monitor with a linearized luminance scale. Each patch contained 1000 dots, half of which were darker than the background and half of which were equally brighter. The luminance difference between the dots and the background was defined as C / 2, where C is the contrast (0 to 1) on the current trial. A percentage of the dots, M, moved horizontally either right or left (randomly chosen on each trial) while the remaining 1 – M dots had random angles. M therefore reflects the motion coherence of the dot patch. All dots moved at a consistent speed of 3.25 degrees / s.

Contrast and motion discrimination performance was tested at a single pedestal intensity. Contrast was tested at 60% and motion coherence was tested at 10%. Both features were crossed such that neither feature was informative about the strength of the other feature on any given trial. For each feature a 1-up-3-down staircase (??) was used to set the increments in contrast or motion coherence that was added to the pedestal contrast on the target side. The independent staircases balanced task difficulty across the features so that subjects were always performing the task at a near-threshold level, eliminating any potential confound with task difficulty between conditions. During control runs pedestal values of 20/40/60/80% contrast and 0/10/20/40% coherence were used to allow estimation of the BOLD response across a larger range of feature intensities. For each pedestal an independent staircase was computed to maintain task difficulty near threshold. Pedestals were pseudo-randomly interleaved across trials.

**Stimulus Presentation**

Outside the scanner the visual stimuli were presented on a ViewPixx 22.5” LCD (VPixx Technologies) with a resolution of 1920 x 1200 pixels and a 100 Hz refresh rate at a distance of (?) cm from the subject’s eyes to obtain a field of view of ? x ?. Inside the scanner subjects used an adjustable mirror system to view an image that was rear-projected onto a fiberglass screen using an Eiki LC-WUL100L projector operating at 1920x1200, 5000 lumens, projected through a neutral density filter. The projector and LCD screen were calibrated to have linearized gamma scales using a PR650 Spectroradiometer (Photo Research Inc., Chatsworth, CA.). We dynamically adjusted the 10-bit gamma table to achieve the best luminance resolution possible (maintaining the linearized output) for displaying each dot patch. All stimuli were produced using MATLAB (The Mathworks Inc., Natick, MA, USA) and MGL (<http://gru.stanford.edu/doku.php/mgl/overview>).

**Eye Position Measurements**

An Eyelink 1000 eye tracking system (SR Research Ltd., Mississauga, ON, Canada) was used outside the scanner to confirm that subjects maintained fixation throughout the task. Eye tracking was not performed inside the scanner. The Eyelink system recorded corneal reflections of an external infrared light source and tracked the center of the pupil. A brief calibration was performed before each 5-minute run. Eye tracking setup was successful for all sessions. The calibration data was used to perform an affine transformation of the acquired eye tracking data to the position of the eye in degrees of visual angle.

Todo: eye position analysis

**Contrast and Motion Discrimination Functions**

Feature discrimination task performance was evaluated using feature-discrimination functions. A feature-discrimination function defined the relationship between the pedestal intensity (i) and the increment in intensity (deltai) required to obtain threshold-level performance. Feature-discrimination functions were computed separately for contrast and motion coherence. For each condition a maximum-likelihood procedure (Wichmann & Hill, 2001) was used to fit subject responses to a Weibull function (Weibull, 1951):

p (c ) = ….

Where p(delta i) is the probability of being correct given an intensity increment of delta I, lambda is the lapse rate, epsilon is the delta I for which the probability correct reaches 63% of the difference between chance and maximal performance, and m is the slope of the psychometric function. Subjects performed on average X psychometric functions with X trials each. A minimum of 50 trials were allowed per function, sufficient to estimate the discrimination threshold accurately (Kontsevich & Tyler, 1999). By running multiple staircases we were able to compute the variability of the threshold across runs

**MRI Acquisition and Preprocessing**

MRI data were acquired on a GE Discovery MR 750 on a Nova Medical 32ch head coil. Retinotopy experiments were collected on a Nova Medical 16ch visual array. For each subject we acquired a high-resolution 3D anatomical image (“canonical anatomy”) which was segmented via FREESURFER (http://surfer.nmr.mgh.harvard.edu) to generate white matter and gray matter segmentation (Dale, Fischl, & Sereno, 1999). We collected a single T1-weighted image (MPRAGE TR ??, TI ??, TE ??, FA ??, voxel size ??, matrix ??. Regions of interest were drawn on flattened representations of the cortical surface including the visual areas and the motion sensitive regions that defined hMT+. These regions of interest were constrained to voxels that intersected the gray matter. Analyses were conducted on original untransformed data while flattened representations were used for visualization.

Each functional experimental session consisted of a lower resolution T1-weighted image (“session anatomy”) (????) and multiple T2\*-weighted functional scans (multiband 8, TR 500 ms, TE 30 ms, flip angle ??, voxel size 2.5 x 2.5 x 2.5 mm, matrix 88 x 88). An automated procedure was used to find the best affine transform to align the session and canonical anatomy (Nestares & Heeger, 2000). The functional scans were aligned to the session anatomy directly using the coordinates measured by the scanner. Retinotopic mapping was performed using a T2\*-weighted functional scan (multiband 2, TR 1400 ms, TE 30 ms, flip angle ??, voxel size 2.5 x 2.5 x 2.5 mm, matrix size). Oblique slices were chosen to maximally cover the occipital visual areas, approximately perpendicular to the calcarine sulcus. For all subjects our functional sequences achieved full brain coverage.

fMRI images were analyzed through a pipeline using mrTools.

**Retinotopy**

Visual fields were determined based on a retinotopy performed in a separate scanning session. High-contrast radial checkerboard patterns were presented either as an expanding or contracting ring or a 90\* rotating wedge. Each scan consisted of 10.5 cycles (24 s per cycle) of the ring expanding/contracting or the wedge completing a full rotation with a sampling rate of 17 volumes per cycle (178 volumes per scan). In addition four presentations of a sweeping bar stimulus were made. Each session therefore consisted of two scans of the ring stimulus (one expanding, one contracting), four scans of the wedge stimulus (two each clockwise and counter-clockwise), and four scans of the bar stimulus. A generative model of voxel responses (the Population Receptive Field model, ??) was fit to each voxel, identifying the Gaussian response field parameters that best fit the recorded response data. Visual fields were then defined according to published criteria.

**Feature-response Functions**

To compute the feature-response functions, a deconvolution analysis (for details see: (Gardner et al., 2005)) was used to determine the mean hemodynamic response to each dot patch in the contralateral visual cortex. The average time-course in each visual area for each grating location was computed and the response following stimulus presentations for 20 s was calculated, assuming linear summation for responses that temporally overlapped. These responses were calculated separately for each combination of feature (contrast, motion coherence) and cueing condition (cued, miscued) at every intensity increment, rounded to the nearest 10%. This resulted in 36 total conditions (contrast: 8 intensities x 2 cueing + coherence: 10 intensities x 2 cueing). A gamma function was fit to this deconvolved response and the amplitude of this function determined the magnitude of response. These response magnitudes were then plotted as a function of stimulus intensity to yield the contrast-response function for each visual area and cue condition.

**Dissociable Neural Substrates of Attention for Contrast and Noise Discrimination**

We will first replicate and extend previous findings on contrast discrimination (Hara, Pestilli, & Gardner, 2014; Pestilli et al., 2011). Hara et al. and Pestilli et al. showed that focal spatial attention modulates neural responses in early visual cortex and that downstream pooling of these responses is sufficient to explain changes in behavioral performance. We will use the same experimental structure as Pestilli et al., but grating stimuli will be replaced with faces that vary both in contrast and phase coherence. Participants will be presented with four face stimuli each at a random contrast and noise level. During a single block of trials participants will be asked to focus their attention on changes in contrast or noise. Within a single trial they will be asked to either distribute their attention across all four stimuli or to focus on a single stimulus. Participants will perform a change discrimination task, identifying which of two intervals had a higher contrast or noise level. The task will be performed inside of an fMRI scanner to acquire neural responses. In addition, retinotopic and functional localizers will be used to locate important visual regions (V1-V4, FFA).

The data from this experiment will be used to generate separate computational models for contrast discrimination and noise discrimination for each of the visual processing regions (V1->FFA). Each model will account for the role of attentional modulation in that range and characterize that region’s involvement in changes in behavioral performance. We expect to see a dissociation in which responses in early visual cortex are important for contrast discrimination (Pestilli et al., 2011) while responses in late visual cortex and FFA will be important for coherence discrimination (Tjan et al., 2006). This is based on evidence showing that the BOLD response in FFA is invariant to the level of contrast (Loffler, Yourganov, Wilkinson, & Wilson, 2005). These separate computational models will therefore characterize dissociable neural substrates responsible for behavioral performance in contrast and noise discrimination tasks.

*Details*

Participants will perform a change discrimination task (see Figure 1) while cortical responses are recorded from visual areas (V1-V4, FFA, ?). During a single scan session participants will perform several blocks of trials. During each block participants will perform either contrast discrimination or noise discrimination. On each individual trial a participant will be cued (1s) to attend to either one of four circular locations (focal) or to all four locations (distributed). Two stimulus presentations will follow the cue (1000 ms each) each followed by a short break (500 ms). At each of the four spatial locations a random face will be presented whose contrast and noise level vary randomly across several “pedestal” levels. During one of the two stimulus presentations one of the faces will have a small increase in its pedestal level. Participants will be given a short window at the end of the trial to report during which window the level was higher (1200 ms). Each participant will therefore experience four different trial types: noise vs. contrast combined with focal vs. distributed. To avoid any confound of difficulty we will adjust the size of the change in pedestal level to maintain 76% correct performance.

Using the data recorded from the scan sessions we will construct behavioral performance functions for each of the four trial types, plotting the discrimination threshold necessary to achieve 76% performance at each pedestal level. In addition we can use the localized ROIs to generate a neural response function for each region and trial type, at each of the pedestal levels. Using the same approach as in Pestilli et al. on contrast discrimination (Pestilli et al., 2011) we can then perform a model fit analysis to understand how focal attention modulates the neural response to either contrast or noise level to improve behavioral performance.

*Results*

Following on the work by Pestilli et al. we expect to find a neural response function and behavioral performance function for each task across the pedestal levels. We will use computational models to show that relative differences in neural response for different contrast or noise levels can be used to solve the task, and that the BOLD signal in specific brain regions is likely responsible for behavioral performance. For contrast discrimination we expect that early retinotopic regions will be involved, while for noise discrimination we expect later regions that represent faces as a whole will show increased activity (Figure 2). We also expect that a computational model of efficient selection (i.e. downstream weighted pooling of early visual activity) will best explain the behavioral performance during contrast discrimination (Pestilli et al., 2011). During noise discrimination we expect that multiplicative response gain, noise gain, efficient selection, or an alternative model will fit the results.

**Replicating the Dissociation of Attention and Awareness**

Although there is considerable evidence that awareness of natural scenes exists in the absence of “top-down attention” (Li et al., 2002) there is only limited evidence that face gender processing occurs in the absence of attention (Reddy et al., 2004). To replicate these results we will add an additional task to the main discrimination paradigm, to assess awareness of face stimuli in the periphery. This dual task design mimics the approach used in Li et al. and Reddy et al. In our experiment the peripheral task will be a gender categorization task. We will assess awareness by manipulating the performance of participants on each task independently. Our prediction is that the main task and peripheral task will have less interference when their neural substrates are dissociable. We will test this by asking participants to perform contrast discrimination as a main task while simultaneously performing gender categorization in the periphery. Our prediction is that there will not be a large change in performance when performing the tasks together or separately, replicating the result of Reddy et al.

*Details*

Participants will perform the contrast discrimination portion of the task outlined above with an additional secondary peripheral task. We use “main task” to refer to the attention task at fixation, and “peripheral task” to reference the new gender categorization task. During one, both, or neither, of the two stimulus presentations of the main task (Figure #) an additional stimulus face will appear in the periphery. The face presentation time will be short and subsequently masked. Participants will use one hand to perform the main task and their other hand to respond after seeing the peripheral face stimulus, identifying it as male or female. To control task difficulty between the main and peripheral tasks we will change the length of peripheral face presentations to maintain performance at 76%. To assess whether this dual task configuration impacts performance participants will perform blocks of the main task and peripheral tasks in isolation, as well as the dual task.

*Results*

Our hypothesis is that contrast discrimination and gender categorization rely on neural substrates that are largely held in different regions. This predicts that when a neural modulation, induced by focal attention to contrast level, occurs in early visual cortex, this will not have a major impact on gender representations held in the FFA. In turn, behavioral performance for both the main task and peripheral task will be similar during the dual task condition compared to the isolated tasks.

**Testing the Neural Substrates of Attention and Awareness**

Our hypothesis is that when the neural substrates of two tasks overlap, attending to one task will suppress performance on the other task. In our full experiment participants will perform either contrast or noise discrimination at fixation, at varying levels of attentional load (focal vs. distributed). Simultaneous to the fixation task participants will perform the peripheral gender categorization task designed to assess awareness.

*Details*

The experiment will be identical to that outlined above, but participants will perform both the gender and noise discrimination tasks during separate blocks. The experiment will be performed in the scanner. Anatomical and localizer scans will be recorded to identify visual cortex ROIs. The data will be analyzed in the same way as above by replicating the computational models linking neural response to behavioral performance. In addition, we will analyze whether awareness of gender in the peripheral task can be predicted as a function of the neural modulation, due to attention, occurring within different regions.

*Results*

We predict two effects on the awareness of the peripheral stimuli. First, we expect there to be a task specific effect. We do not expect contrast discrimination to disrupt attention to peripheral stimuli in either focal or distributed attention conditions (see previous results). In contrast, we expect that performing a noise discrimination task that requires the use of a neural population that is shared with the gender categorization task will cause a reduction in awareness. Furthermore, we predict that the neural modulation induced by attending to the level of noise will be sufficient to predict the level of awareness in the peripheral task. Specifically: the change in neural response due to focal attention will be sufficient to explain both the performance increase in the main task and the drop in awareness in the peripheral task.

**Discussion**

Our main manipulation will have tested whether the impact of focal attention on neural activity in task-relevant regions is sufficient to explain the reduction in awareness for a secondary task. Importantly we predict that the reduction in awareness will depend precisely on which specific regions were modulated by attention. During a contrast discrimination task where focal attention modulates early visual cortex we do not expect a parallel reduction in awareness for a task that relies on representations held in late visual areas such as FFA. In contrast, during a noise discrimination task where focal attention modulates cortical regions that are shared by both tasks we expect a reduction in awareness that will parallel the increase in noise discrimination performance. Our hypothesis states that this tradeoff is a fundamental property of local neural processing: as attention boosts the signal to noise ratio (SNR) for one representation this guarantees a decrease in the signal to noise ratio for other representations. If awareness is a process that relies on these SNRs then the impact on awareness will be a function of the change in SNR.

Observing a clear association between attention (the modulation of neural responses to specific features in specific cortical regions) and awareness (the ability to read-out information about a stimuli, e.g. verbal report) is essential to disambiguating the role of each of these processes. There is a considerable reliance in the literature on operational definitions that are not informed by the underlying neural processes. Our approach is one method to clarify whether attention and awareness can in fact be separated as two computational processes that solve distinct problems for organisms, as is speculated by other authors (Koch & Tsuchiya, 2007). We expect that this intuition is in fact a mistake and that attention and awareness cannot be clearly disambiguated at a neural level.