

THE EFFECT OF SPATIAL ATTENTION ON PUPIL DYNAMICS

by

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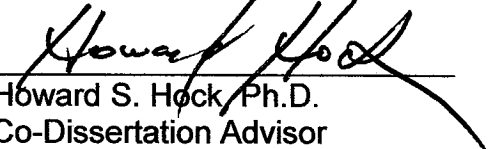
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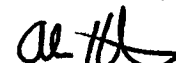
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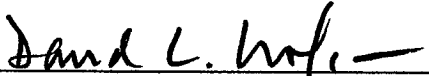
  
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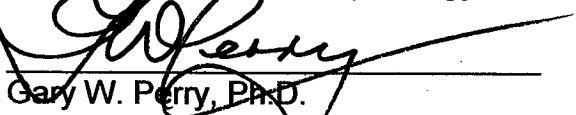
  
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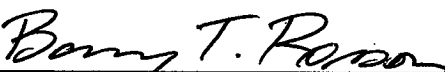
  
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## ABSTRACT

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Although it is well known that the pupil responds dynamically to changes in ambient light levels, the results from this dissertation show for the first time that the pupil also responds dynamically to changes in spatially distributed attention. Using a variety of orientating tasks, subjects alternated between focusing attention on a central stimulus and spreading attention over a larger area. Fourier analysis of the fluctuating pupil diameter indicated that: 1) pupil diameter changed at the rate of attention variation, dilating with broadly spread attention and contracting with narrowly focused attention, and 2) pupillary differences required changes in attentional spread; there were no differences in pupil diameter between sustained broad and sustained spread attention. Given that broadly spread attention increases the relative activation of large receptive fields and narrowly focused attention increases the relative

activation of small receptive fields (Balz & Hock, 1997), the results of this study indicate that these attentional effects on receptive field activation can be mediated by changes in pupil diameter. That is, under broad attention, the corresponding pupillary dilation observed would increase spherical aberration, blurring the image thereby reducing high spatial frequency information and decreasing the activation of relatively small cortical receptive fields compared to relatively large receptive fields. This increased perception of low spatial frequencies would be beneficial in cases where attention is spread over a large area. Alternatively, under narrow attention the resulting pupillary constriction reduces spherical aberration sharpening the image and preserving high spatial frequency information resulting in a relatively increased response of small receptive fields.

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## INTRODUCTION

The pupil and its primary response to light have been known for many years with the earliest research found in the 18<sup>th</sup> century (Janisse, 1977). Only in latter years has it been found that the pupil reacts to more than just light; it also responds to stimuli involving spatial structure (Barbur & Thompson, 1987; Slooter & van Norren, 1980; Ukai, 1985), motion (Sahraie & Barbur, 1997), color (Gamlin, Zhang, & Clarke, 1995; Tsujimura, Wolffsohn, & Gilmartin, 2003; Young & Alpern, 1980), and depth (Li, Liang, & Sun, 2006). The focus of this dissertation is to investigate the pupil's responses to these lesser-known stimuli, in particular the effect of spatial attention.

Spatial attention refers to the allocation of mental resources toward an object or area in the visual field. Attention is thought to serve as a type of signal enhancement allowing for the perception of stimuli that would otherwise be barely detectable to rise above threshold levels (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Cameron, Tai, & Carrasco, 2002). Along with improved detectability, spatial attention aids in the discrimination of fine details (Balz & Hock, 1997; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 1999). This 'resolution hypothesis' of attention is thought to occur through modulation of neural responses (Carrasco & Yeshurun, 2009). Specifically, Balz & Hock (1997) have proposed that under focused attention small receptive fields

sensitive to detailed visual information have greater activation compared to large receptive fields therefore increasing spatial resolution. While most current explanations indicate a cortical mechanism mediating such attentional effects, subcortical areas, such as the superior colliculus and pulvinar, have been indicated in attentional pathways (Ignashchenkova, Dicke, Haarmeier, & Their, 2004 ; Shipp, 2004). In line with these studies, a central question of this dissertation is whether the pupil, which is controlled subcortically, can mediate attentional effects. That is, by controlling the amount of blur (spherical aberration), the pupil may be able to mediate receptive field activation.

In the first section, the known pathways of the classic light reflex, and the effect of sympathetic and parasympathetic innervations on the pupil response will be reviewed. Furthermore, other non-classical pupil responses will be explored with emphasis on implications for cortical pathways. In the second section, the differences between endogenous and exogenous attention will be reviewed. In addition to the distinctions and characteristics of the two types of attention, the effects of attention on visual attributes, such as contrast sensitivity and spatial resolution, will be examined including the involvement of neural mechanisms for both types of attention.

## The Pupil

### *Pupil Pathways*

The iris contains two antagonistic muscles responsible for pupillary movement: the sphincter, which runs circularly around the inner iris, and the dilator muscle, which is positioned radially throughout the iris. While there are

inputs from the sympathetic and parasympathetic systems to both muscles, each system operates primarily on one muscle (Alexandridis, 1985). The sphincter muscle is mostly innervated by parasympathetic fibers and excitation of these fibers leads to a pupillary constriction, while inhibition of this pathway will produce a dilation of the pupil. As depicted in Figure 1, control of the sphincter muscle begins with parasympathetic neurons in the midbrain at the Edinger-Westphal (EW) nucleus (Kardon, 1998). From here, pupillary fibers travel through the oculomotor nerve and synapse at the ciliary ganglion, exiting through short ciliary nerves that innervate the sphincter muscle.

Efferent pathways to the dilator muscle originate in the hypothalamus (see Figure 2). This sympathetic pathway continues downward through the brainstem and synapses in the ciliospinal center of the spinal cord (Alexandridis, 1985). After leaving the spinal cord a second synapse occurs in the superior cervical ganglion of the neck, which then proceeds up with the carotid artery and through the long ciliary nerve, thus reaching the iris (Adler, 1975). Sympathetic outflow is thought to begin in the hypothalamus and be mediated in part by the cerebral cortex. For example, pupil dilation can be elicited through electrical stimulation of frontal cortex, motor cortex, and occipital cortex (Kardon, 1998). Due primarily to these impulses arising in the cerebral cortex, any sensory stimulus will evoke a pupillary dilation, a phenomena known as reflex dilation. During increasing sympathetic tone, the pupil dilates as the hypothalamus integrates autonomic nervous system inputs and correspondingly reduces activation of the EW neurons. Pupillary dilation

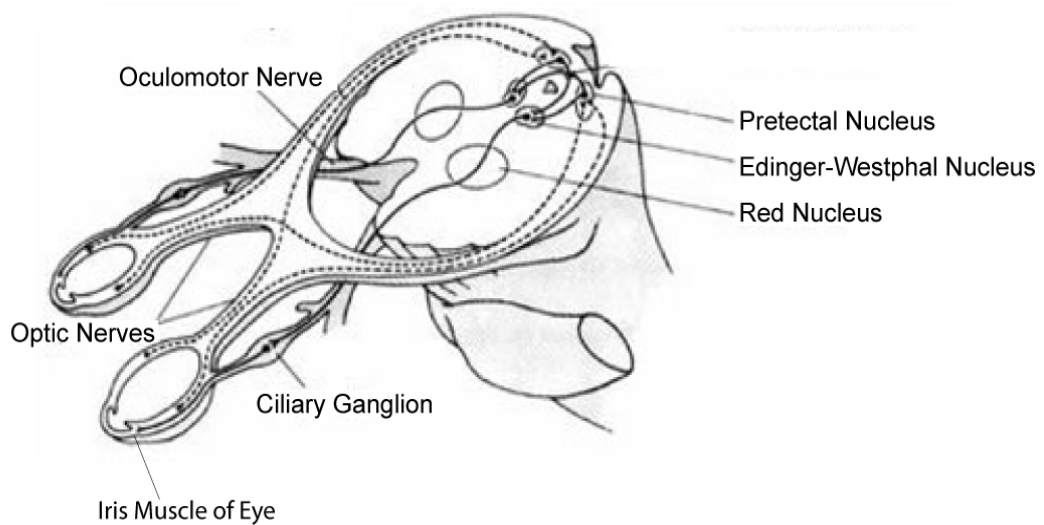


Figure 1. Parasympathetic pathways for pupillary constriction. The solid black line depicts the control pathway for pupillary constriction beginning in the Edinger- Westphal (EW) nucleus. From the EW nucleus the pupillary fibers travel through the oculomotor nerve and synapse at the ciliary ganglion before innervating the sphincter muscle of the iris. Adapted from Kardon (1998).

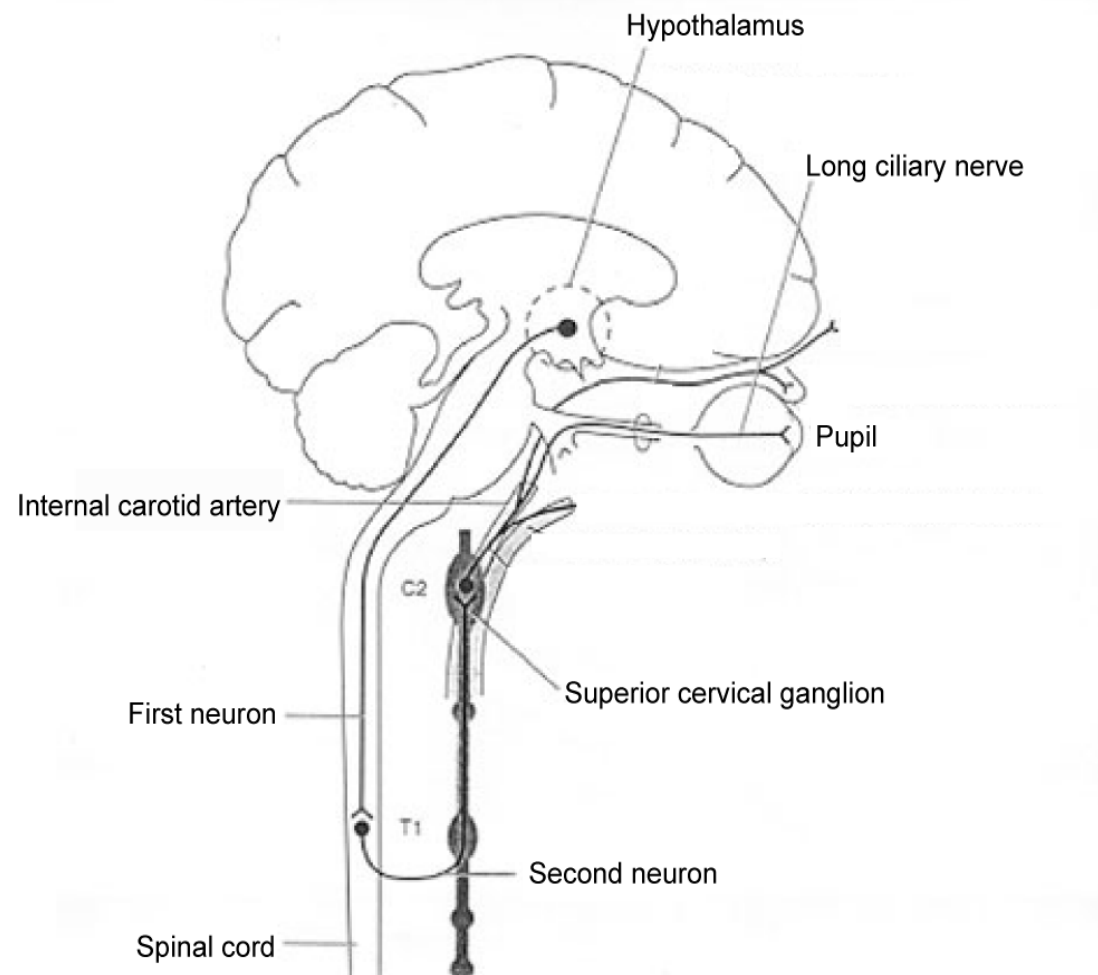


Figure 2. Sympathetic pathways for pupillary dilation. The solid black line depicts efferent control of the dilator muscle originating in the hypothalamus. From the hypothalamus, the pupillary fibers travel through the brainstem and synapse in the spinal cord. Leaving the spinal cord, a second synapse occurs in the superior cervical ganglion of the neck, which then reaches the pupil by proceeding up the carotid artery and through the long ciliary nerve.



therefore is both a combination of sympathetic outflow to the dilator muscle and inhibition of parasympathetic pathways to the sphincter muscle.

The afferent pathway for the pupil in response to light begins in the photoreceptors of the retina. Since the photoreceptors are responsible for conducting pupillary inputs, pupil responses to visual stimuli are similar to visual thresholds (Loewenfeld, 1999). Rod and cone properties are evident; pupil responses from rods have lower luminance thresholds but in general are less reactive to stimuli. Pupil responses from cones are less sensitive to low threshold stimuli but when the cone threshold is reached are larger and more extensive. Properties of adaptation are reflected in the pupil (Kardon, 1998). Under photopic conditions, the pupil has the greatest reaction from foveal stimulation and is less reactive for peripheral stimuli. Similar to dark-adaptation, the pupil when dominated by rod input has an increased sensitivity to lower wavelengths and increased thresholds for foveal stimuli. Also present in the pupil response is the Purkinje shift. Under scotopic conditions, the pupil's peak sensitivity is shifted and is most responsive to green-blue wavelengths. The pupil does, however, differ from visual perception in that spatial summation is greater for the pupil response. The rod and cone inputs are additively combined, and therefore large stimuli will evoke pupillary constrictions whereas small stimuli, though sufficient for visual detection, may produce little or no pupil response (Loewenfeld, 1999).

In addition to classical photoreceptors, a third type of photoreceptor, an intrinsically photosensitive retinal ganglion cell (ipRGC) containing the

photopigment melanopsin is integral in the pupillary light response. As ipRGCs contribute to pupil response alone but also receive converged rod and cone input, all three types of photoreceptors are necessary for the pupillary light response. Responses of melanopsin ganglion cells are typically slow, so the main contribution of ipRGCs is to the sustained component of the pupillary light response (Gamblin et al., 2007).

The pupillary pathway continues on through the optic nerve, crosses the optic chiasm and leaves the optic tract immediately before the lateral geniculate nucleus, instead entering the pretectal olivary nucleus. The extensive crossing which occurs between the right and left pretectal olivary nuclei integrates the afferents from the right and left eyes so that the input into the EW nucleus is evenly distributed and is responsible for the consensual light reflex seen in humans. Two separate classes of pretectal neurons exist based on the response to stimuli presented in the visual field (Kardon, 1998). The first type responds to stimuli presented in the center or foveal region of the visual field. The second type of pretectal neuron, however, will respond to stimuli in all parts of the visual field. In the monkey, Gamlin, Zhang, and Clarke (1995) found that in response to a light stimulus the firing pattern of the pretectal neurons was a phasic high frequency response followed by a lower frequency tonic response. As the light intensity of the stimulus was reduced the firing amplitude of the neuron reduced accordingly. The firing of a single pretectal neuron resulted in measurable changes in pupillary constriction. However, Gamlin et al. noted this mainly for neurons at high firing frequency

whereas low intensity firing had no direct effect on the pupil. Therefore, the response of the pupil at low stimulus intensities may involve a temporal summation of many neurons. Temporal summation is also evident in the latency of the pupil response. The time of onset for a pupil constriction is longer for low intensity stimuli, perhaps associated with the longer time it takes to summate the response of many neurons (Loewenfeld, 1999).

Pupillary dynamics are complicated by multiple inputs. The afferent pathway of the pupillary light response is modulated at the level of the pretectum and EW nucleus by cortical and subcortical feedback. The pretectum receives significant cortical input from V1, V4, and IT, but also from the LGN and superior colliculus (Gamlin, 2006). The pretectum then sends efferents to both the hypothalamus and the pupilloconstrictor neurons of the EW nucleus. Inhibition of this afferent pathway, by decreasing parasympathetic activity at the EW nucleus, causes the sphincter muscle to relax and contributes to the dilation response. This inhibition occurs through inputs from the cortex and the locus coeruleus. The end result is a dynamic network in which sympathetic and parasympathetic systems are integrated.

#### *Pupil and Visual Resolution*

Under photopic viewing conditions, the major limiting factor for visual acuity results from loss of image contrast due to optical aberrations (Schwiegerling, 2000). In addition to modulating retinal luminance levels, pupillary movements sharpen visual acuity by reducing glare and decreasing spherical aberrations. Due to blurring caused by the optics of the eye, changes

in pupil diameter are extensive enough to affect contrast sensitivity, which is especially relevant at high spatial frequencies (Campbell & Green, 1965; Campbell & Gubish, 1966). Therefore, over a range of photopic luminances, the pupil size adjusts to optimize the quality of the retinal image (Campbell & Gregory, 1960; Hirata, Yamaji, Sakai, & Usui, 2003; Laughlin, 1992).

### *Pupillary Unrest and Fatigue Waves*

The constant change in size of the pupil under steady illumination is called pupillary unrest or hippus. The pupillary oscillations are thought to be due to regulation of inputs from the parasympathetic and sympathetic systems. While it was believed that hippus was correlated with respiration and heart rate this observation has been disputed (Kardon, 1998; Loewenfeld, 1999). The rate and magnitude of hippus is primarily dependent on light intensity. Hippus during bright light consists of large, fast fluctuations while a dim setting produces smaller and less frequent waves. Pupillary unrest is characterized by irregular pupillary movements. For example, slow oscillations can be interrupted by random intervals of faster frequencies. These pupillary noise fluctuations have oscillations in frequency spectrum range of 0.05-0.3 Hz (Stark, Campbell, & Atwood, 1958).

In addition to light level and hippus, the level of alertness also influences pupillary unrest, seen as “fatigue waves”. Fatigue waves differ from hippus since they are larger and slower, occur in darkness as well as light and are not found in alert individuals. The overall random fluctuations of the pupil

contribute to the noise levels in pupil studies and require summation over many trials.

### *Pupil Responses*

The pupil's response to light depends on a multitude of factors, including the location of the light stimulus, with more response for center foveal stimuli, and overall adaptation of the retina, such that in dark adaptation the pupil response sensitivity shifts to peripheral stimuli. The intensity and duration of the stimulus also influence pupillary response (Lowenstein & Loewenfeld, 1959). Under scotopic conditions, it is possible to get very small pupil constrictions to near threshold level stimuli. Responses to these dim stimuli have long latency times and do not appear to be affected by stimulus duration. For instance, the amount of constriction is the same for a weak stimulus if presented for 100 milliseconds or 1000 milliseconds. In general, near threshold stimuli will evoke a transient response in the pupil characterized by a brief constriction, which quickly returns to baseline. At longer durations with dim stimuli, the return to baseline will occur even when the light stimulus is still present, known as pupillary escape (Loewenfeld, 1999). Brighter suprathreshold stimuli have much shorter latencies and greater constriction amplitudes. The pupil responds in a sustained fashion, the constriction is longer and remains below baseline for an extended period of time. These brighter stimuli do have an effect of duration with stimuli of longer duration invoking greater constriction amplitude.

The pupil light response can be separated into a sustained component and a transient component (Barbur, 2004; Young, Han, & Wu, 1993). Different pathways may mediate these components because of their distinct characteristics. Young et al. (1993) investigated whether these pathways may be comparable to the magnocellular and parvocellular pathways projecting to LGN. Using chromatic and achromatic stimuli, they measured pupil responses to luminance increments. Their results, analyzed with principal component analysis to find the portions of the pupil response that linearly covaried, contained two major components. The first component (sustained) had properties similar to tonic visual neurons, low contrast gain and a linear response to increasing luminance. The second component (transient), however, had high contrast gain properties, reacting to low light increments and saturating at higher luminances. While the pupil has phasic and tonic response components, there is no evidence that this corresponds to M and P pathways since pupil response components to achromatic and chromatic stimuli were virtually identical.

Evidence for separate pupil components has been investigated using background perturbation techniques. Barbur (2004) used a checkerboard background varying the luminance of the individual checks over the stimulus trial. Each check luminance was randomly assigned to be a percentage of the background luminance with the overall mean luminance of the checkerboard display remaining the same throughout the trial. This design was meant to selectively habituate or adapt the transient response since this component is

thought to react only to local luminance changes and not overall ambient light levels. Supporting this hypothesis, Barbur found that the constriction amplitude of the transient response *decreased* to a flash of light presented on the checkerboard as the amount of luminance contrast noise increased. However, the effect was not found for identical static stimuli pointing to the need for flux changes as a property of the transient component. This transient component may require cortical input, as dynamic low contrast stimuli have no effect on the constriction amplitude of the pupil in the blind hemifield of patients with V1 damage.

#### *Pupil Responses to Sinusoidal Light Fluctuations*

Pupillary responses are most effective to light flashes or step changes in luminance. Sinusoidal changes with low frequencies, therefore, evoke very small changes in the pupil. However, as the frequency increases the pupil responses become larger until the limit of the iris muscle's contraction time is reached and the response is sustained contraction. Due to lag in response time, pupillary reactions are normally out of phase with the sinusoidal stimulus. For example, one cycle per second modulation roughly corresponds to 180 degree phase difference (Loewenfeld, 1999).

#### *Pupil Cycling Time*

When a narrow beam of light is directed at the edge of the iris, the pupil correspondingly contracts. The contraction, however, moves the iris margin away from the light and prevents the light from entering the eye, and in turn the pupil redilates. This leads to an endless feedback loop of constriction and

dilation (Stern, 1944). The amount of time needed to complete one cycle is referred to as pupil cycling time and reflects conduction speed of afferent and efferent pupillary pathways. Since the measurement of pupillary cycling time highlights underlying pupillary movement mechanisms, several studies (Ellis, 1981; Heller, Perry, Jewett, & Levine, 1990; Howarth, Heron, & Whittaker, 2000; Lowenstein & Loewenfeld, 1950) have investigated the time course. A consistent finding that has emerged from the research is that the velocity of pupillary constriction and dilation are asymmetrical. That is, even for the same luminance intensity, the maximum constriction velocity is always larger than the maximum dilation velocity. This asymmetry is directly related to the observation that unlike constriction, pupillary dilation appears to have two phases. The primary redilation is thought to reflect the relatively quick inhibition of parasympathetic system, whereas secondary redilation results from a slower decrease in sympathetic inhibition and an eventual increase in parasympathetic tone.

#### *Pupil Responses to Spatial Stimuli*

In addition to the pupil light response, it has been found that the pupil is sensitive to spatial patterns. Some of the earliest research, using checkerboard-patterns, discovered with the appearance of the stimuli a small but reliable constriction occurred (Slooter & van Norren, 1980; Ukai, 1985). The amplitude of constriction varied with check size and had band pass properties; medium size checks gave the greatest constriction followed by a decreased response for larger and smaller check sizes. This finding was



linked to visual acuity with a high correlation between the pupil response and subjective acuity for the same check sizes. Using checkerboard stimuli that reverse contrast, Ukai (1985) found that pupil constriction amplitude increases for bigger differences in contrast change even though the average luminance of the display remained constant. Both researchers attributed their findings to local luminance changes or the near reflex (a constriction known to occur when the eyes shift fixation from a far away object towards a close object). Barbur and Thompson (1987) were among the first to consider that pupil responses to spatial patterns may not be an artifact of the light response but an entirely different response perhaps mediated by different pathways than those associated with the light reflex. Using sinusoidal wave gratings, their main finding was obtaining a curve of pupillary responses over different spatial frequencies which are comparable to the contrast sensitivity function. This finding prompted the suggestion that central visual pathways may modulate the pupil grating response.

This idea that pupillary responses to spatial patterns may involve pathways to the visual cortex was further investigated by extracting the pupillary response components. In this design, pupil responses were recorded over an extended duration as a square wave grating with different frequencies and contrasts appeared and disappeared (Young & Kennish, 1993). The influence of potential local luminance increments was controlled by using gratings composed of only luminance decrements. The pupil response was found to consist of an initial constriction with presentation of grating, a

sustained constriction response, and a second constriction when the grating disappeared. Principal component analysis of the waveforms revealed that the first constriction peak contained both transient and sustained components, while the second constriction peak could be described almost entirely by the transient component. Comparison of the pupillary response amplitude at different contrast levels and spatial frequencies indicated that the sustained response increased linearly with contrast and had a band-pass response to spatial frequency gratings. However, the second transient constriction response had high contrast gain properties, the response quickly leveling off with higher grating contrasts and responding maximally to low spatial frequencies. Interestingly, the first constriction, which is the same response investigated in earlier studies, had both an initial quick rise and then a linear response to contrast perhaps revealing a mixed component response. Considering that the pupil has sustained and transient responses, a comparison to the properties of magnocellular and parvocellular cells was advanced. It was hypothesized that the transient component, with high contrast gain and low spatial frequency peak responses, may be processed by M cells, whereas the sustained component, with low contrast gain and band-pass properties, is processed by P cells. Neurophysiological research has not been performed with spatial frequency gratings, so whether these M and P connections would be processed cortically or if these connections are a product of collaterals branching off into the pretectum (as in the minor projections of X and Y cells) remains to be seen. It is important to note that a

previous study involving the pupillary components to light and color (Young et al., 1993) concluded that, at least for the pupillary light response, evidence could not be found implicating the magnocellular and parvocellular pathways. This conclusion was reached based on the lack of difference in the pupillary response components when chromatic and achromatic stimuli were compared. However, the results did indicate that phasic and transient type properties were present.

The idea that cortical areas may influence pupil responses has received support from research involving patients with damage to the visual cortex, such as blindsight patients. These studies have found that while the pupillary response to luminance was normal, pupil responses to gratings were reduced in the blind hemifield (Barbur & Forsyth, 1986; Sahraie, Weiskrantz, Trevelyan, Cruce, & Murray, 2002; Weiskrantz, Cowey, & LeMare, 1998). In comparison, patients with damage to the dorsal midbrain including the olivary pretectal nucleus (Parinaud's syndrome) were found to have a reduced pupillary response to light which required large light fluxes to induce a response. However, pupil grating responses in these cases were normal. These findings indicate that cortical input is necessary for the pupil grating response, and that this response is controlled by different pathways than the normal light response (Barbur, 2004; Wilhelm, Wilhelm, Moro, & Barbur, 2002). The particular explanation put forth by Barbur (2004) is dependent on the fact that without any inputs EW neurons are in a constant excitatory state which would result in a constant steady constriction of the pupil. However, a normal state is

maintained by inputs which regulate the hyper-excitation of the EW neurons through inhibition. Barbur postulates this regulatory inhibition is significantly controlled by cortical areas. This normal inhibition is interrupted when a stimulus is processed in these areas (striate and potentially extrastriate), and the resultant weakening of parasympathetic inhibition leads to a constriction of the pupil. This pathway may be different than the normal light reflex pathway, which is thought to have the majority of efferent control in the midbrain.

Extrastriate connections are also considered to be involved in pupillary responses due to findings that the pupil responds to attributes such as color, motion, and depth. Experiments involving equiluminant color exchanges have found constriction responses with around 40-50 msec longer latencies than the pupil light response, perhaps reflecting longer processing from cortex (Gamlin, Zhang, & Clarke, 1995; Young & Alpern, 1980). The pupil responds to color changes in isoluminant stimuli by constricting to both the presentation of the test stimuli and its subsequent removal (Tsuji-mura, Wolffsohn, & Gilmartin, 2003). The second constriction is thought to be modulated by the magnocellular pathway since removing high temporal frequencies by gradual stimulus onset and offsets and luminance masking results in decreased amplitude of the second peak while having little to no effect on the first constriction. Similar research using chromatic flashes (Kimura & Young, 1995) reduced the waveforms into transient and sustained components. In line with Tsuji-mura et al. (2003), it was found that the second constriction peak was primarily from transient components, and this component's sensitivity was

similar to psychophysically determined chromatic sensitivity. These studies can be compared to the response components found in Young and Kennish (1993) where, using spatial gratings, they found a similar response; a constriction to the onset and offset of the stimuli. In their study, they looked at the effect of contrast and spatial frequency on the two constriction peaks. Based on the similarity to magnocellular neurons, they also concluded that the second peak was most likely modulated by the M pathway. For the first peak, they found a mixed component response which would explain why Tsujimura et al. found that their first constriction was not significantly influenced by manipulations affecting high temporal frequency components.

Pupil responses to motion and depth have additionally added support to the cortical pathway hypothesis (Li, Liang, & Sun, 2006; Sahraie & Barbur, 1997). For instance, a change from random motion to coherent motion will produce a small pupillary constriction as will a sudden change in the direction and speed of motion. Comparatively, patients with blindsight were found to have greatly reduced pupillary responses in their blind hemifield, indicating that while this response is primarily mediated by the striate cortex some components are processed through subcortical inputs to V5/MT (Sahraie & Barbur, 1997).

Pupil responses to stereo gratings yielded similar pupil constrictions, which could not be attributed to the normally constricting near reflex. In general, greater constrictions were found for higher disparity amplitudes. This

effect was thought to involve the activity of disparity sensitive neurons in V1 (Li et al., 2006).

### *Tasked Evoked Pupillary Responses*

While certain types of visual stimuli are known to produce pupillary constrictions, other types of cognitive stimuli (attention, memory, language) produce pupil dilations. One of the main findings from this research is that pupillary dilations are correlated with the amount of cognitive effort or processing load associated with the task (Beatty, 1982). During a simple short-term memory digit span task, the pupil will increase in dilation with each digit presented, and then subsequently relax from dilation as the digits are recalled. As the number of digits expands beyond classical short-term memory capacity the pupil response levels off, perhaps indicating a maximum amount of processing capacity available (Kahneman & Beatty, 1966; Peavler, 1974). Similar effects are seen in language. Using three types of processing loads by manipulating sentence structure, such as sentences containing acceptable syntax but incoherent semantics, scrambled sentences lacking both syntax and semantics, and the control sentences, the most amount of pupil dilation occurs with the scrambled sentences both in the hearing phase and with recall (Beatty, 1982). This finding again indicates that pupil dilation is linked to the degree of cognitively taxing information. Pupillary responses in perception research also corroborate the “mental effort” hypothesis. In pitch discrimination tasks, researchers have found more dilation when discriminating between sounds closer in pitch than sounds that differed greatly

in pitch (Kahneman & Beatty, 1967), indicating that the pupillary response can be used to measure perceptual difficulty of a task.

The mechanism behind the pupillary response to mental effort has been investigated by looking at the relative contributions of the parasympathetic and sympathetic systems during a cognitive task (Steinhauer, Siegle, Condray, & Pless, 2004). Sympathetic and parasympathetic systems can be isolated by pharmacologically blocking the action of the iris muscles or by taking advantage of the normal contribution each system has in darkness and light. For example, in the dark a normal dilation occurs, and therefore parasympathetic (constricting) input would be minimal. If further task-related dilation occurred it would indicate the sympathetic system. However, in light a normal constriction occurs mainly due to the activity of the parasympathetic system, any subsequent task dilation would therefore reflect an inhibition of this system. Using these methods, it has been found that inhibition of the parasympathetic system has the greatest effect on the pupil dilation during a difficult task, indicating that inhibition of the parasympathetic system perhaps mediated by the frontal lobe is the main contributor to the pupillary dilations observed in cognitive tasks.

### *Summary*

Reaction to light is only one aspect of the range of stimuli the pupil will respond to. Pupillary constrictions to visual stimuli such as gratings, color, and motion have implicated another pathway involving cortical regions. Blindsight studies have found deficits in grating responses but preserved light responses

indicating that these non-traditional stimuli are distinct from the classical pupillary pathways to light. Task evoked pupillary dilations have also indicated cortical origins- in this case, the frontal cortex. The extent to which these systems may work in parallel and the exact pathways have yet to be discovered.

### Spatial Attention

Selective visual attention operates not only to filter out irrelevant stimuli but also to enhance features of attended stimuli. While an attentional benefit on performance has been found for a wide range of detection and discrimination tasks, it is the discovery that attention can affect perception of stimuli that has generated the most research. Whether automatically driven by the stimulus “exogenous” or voluntarily controlled “endogenous”, attention has been linked to an increase in spatial resolution (Balz & Hock, 1997; Yeshurun & Carrasco, 1999), contrast sensitivity (Goto, Toriu, & Tanahashi, 2001) and perceived spatial frequency (Carrasco, Ling, & Read, 2004; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Doshier & Lu, 2000a; Gobell & Carrasco, 2005; Huang & Dobkins, 2005).

### *Endogenous Attention*

The primary distinguishing factor of endogenous attention involves the effortful placement of attention in the visual field. This can occur with an eye movement toward a point of fixation (overtly) or at a position separate from fixation without a corresponding eye movement (covertly). Endogenous attention is considered to be influenced by “top-down” control, such that the



knowledge or expectation of where a stimulus will occur (even in the absence of a visual cue) is enough to increase detection rates in a visual search conjunctive task where a combination of features (e.g. color and orientation) must be integrated in order to distinguish the target from distractors (Nakayama & Mackenben, 1989). This type of attention can be summoned by central cues, which do not indicate the precise location of the stimulus target but instead a general area, such as a central arrow pointing to left or right of the screen. Reflecting higher order control mechanisms, endogenous attention is relatively slow requiring around 300 msec of cue presentation for the maximum effect to be achieved (Cheal & Lyon, 1991).

#### *Effects of Attentional Spread*

The perceiver's spatial scale of endogenous attention can be controlled, such that it can be narrowed to include only a limited area or broadened to encompass a wider visual field. By manipulating the size of the attended area, for instance with different size boxes, narrowing attention (smaller boxes) improves detection time relative to a larger area after a critical duration needed to summon the endogenous attention (Castiello & Umiltà, 1990). This increased improvement is however not contained within a set area but is dispersed, such that areas immediately outside of the attended area also experience the improvement in detection. Detection of a target stimulus is complicated by interference from surrounding distractors. Therefore, one benefit of narrowing attentional focus may be through the reduction of distracting information. To investigate whether attention can be focused

enough to eliminate interference from nearby distractors, LaBerge, Brown, Carter, Bash, and Hartley (1991) manipulated the size of attended area. In the narrowing task, participants were first instructed to attend to a target digit surrounded by distractors. Immediately after the first presentation, a second target appeared in the same position as the first target. The duration of the first task was varied as a manipulation of attentional area with the hypothesis that at shorter durations, attention must be focused over a smaller area for successful detection. This effect demonstrated that when attention was narrow (for short first displays) the response time was decreased.

While the previous experiments have shown that attentional narrowing can increase detection of a stimulus, other experiments have gone a step further to show that attention can increase spatial resolution and contrast sensitivity. Using a row of dots stimulus to control narrow (attention is limited to center dot) and broad (attention is maintained over entire row of dots) attention, a Vernier acuity task was simultaneously performed by participants (Balz & Hock, 1997). Under narrow attention spatial resolution was increased as less misalignment was needed for detection compared to the broad attention condition. However, this effect was not limited to the acuity task. In a subsequent experiment, a detection task for the distance of separated lines demonstrated that under narrow attention detection was increased. These results indicate that narrowing attention increases spatial resolution by selectively enhancing the sensitivity of small receptive fields near the focused area. Indeed, the benefit of attentional narrowing was limited to focal areas

and as the separations increased outside the range of narrow attention, this effect disappeared. These results were corroborated in a separate experiment involving attention and self-organized motion patterns (Hock, Balz, & Smollen, 1998). The motion pattern used in this experiment involved a row of evenly spaced line segments, when the row was displaced by one half of the inter-element distance, the line segments were perceived to move in one direction (most often occurring when line segment separations were small) or have an oscillatory motion (perceived for larger separations). Based on previous experiments, Hock and Balz (1994) hypothesized that unidirectional motion was the result of cooperative interactions between detectors with similar directional selectivity, while oscillatory motion reflected inhibitory connections between these detectors over larger distances. When the attentional manipulation of broad versus narrow attention was added to this motion pattern, it was found that broad attention increased the perception of unidirectional motion at line separation distances where oscillatory motion normally occurs. Since it is thought that unidirectional motion reflects facilitating interactions, this experiment supports the idea that broad attention can increase the area over which these interactions occur. Specifically, Hock et al. (1998) proposed that foveal receptive fields are composed of different size subunits, each unit containing facilitatory and inhibitory connections, with inhibitory connections dominating in the periphery of the subunit. Broadly spread attention activates larger receptive fields, which due to their size have facilitating interactions at larger distances. Therefore, broad attention by

activating larger subunits will decrease spatial resolution but increase the area over which facilitating interactions can occur.

The effect of attentional spread was further analyzed in a study involving contrast sensitivity (Goto, Toriu, & Tanahashi, 2001). In this study, attentional spread was manipulated by the size of a disk pattern while a centrally placed Gabor patch was increased in contrast until it was perceived by the participant. This study found, as in previous studies, a benefit of narrowing attention, this time as an increase in contrast sensitivity in all but the lowest spatial frequencies. This experiment along with Balz and Hock (1997) provide evidence that attention, in particular narrow or focused attention, can enhance spatial resolution.

### *Exogenous Attention*

In contrast to “top-down” endogenous attention, transient or exogenous attention is characterized by its reflexive, stimulus driven qualities. Using cues with sudden onsets, Nakayama and Mackeben (1989) found that exogenous attention can boost detection in conjunction tasks, more rapidly than endogenous attention. In their conjunction task, exogenous attention was manipulated using a cue marking the upcoming target. Varying the amount of time the cue was present before the target (cue lead time) revealed that exogenous attention boosts detection within 50 to 100 msec. Yet these effects also quickly disappear since detection is reduced if cue lead time is extended past 200 msec, leading Nakayama and Mackeben to the conclusion that exogenous attention is quickly captured but cannot be maintained for

extended periods of time. In accordance with this finding, Cheal and Lyon (1991) demonstrated that exogenous attention was summoned by peripheral cues, and that these cues had the greatest benefit at short intervals. In line with “bottom-up” processes exogenous attention is not influenced by expectations, that is even when participants know where a target will occur (the cue and target position never change), there is no additional benefit for detection (Nakayama & Mackeben, 1989). This type of attention can be thought of as involuntary (Jonides, 1981). For instance, manipulating visual search tasks so that peripheral cues are unreliable as to the target’s location, and additional instructions to ignore the cues, still results in attentional benefits during the trials that the cue and target matched.

#### *Effects of Exogenous Attention*

As in endogenous attention, exogenous attention serves to increase spatial resolution. Using a variety of stimuli (Landolt-square, gap detection and Vernier acuity) to measure spatial resolution, Yeshurun and Carrasco (1999) established that peripheral cuing of the stimulus resulted in better detection rates than neutral cues for all gap sizes, with the greatest overall effect at larger eccentricities. This increase in spatial resolution lead to the conclusion that exogenous attention reduces the size of receptive fields, which will be exemplified where it is most needed- at larger peripheral receptive fields. Additional evidence that attention operates by decreasing spatial filters was investigated by using a stimulus for which the best detection occurs not with foveal processing but at a location mid-peripheral (Yeshurun & Carrasco,

1998). In this experiment, participants were to detect a “patch” of lines in a background of lines oriented in a different direction (texture segregation). This stimulus has been found to elicit the best detection at mid-peripheral locations perhaps because foveal spatial filters are too small, and therefore the patch falls outside the range of such filters. Indeed, Yeshurun and Carrasco found that exogenous cues decreased detection of the “patch” at fixation compared to neutral cues but increased detection at mid-periphery and farther eccentricities. In the fovea, the authors hypothesized that the receptive fields were already too small for the stimulus, and that attention increased this difference therefore decreasing detection further. However, locations where the spatial filters were around optimal or too large, attention aided in detection by reducing the size, therefore they became closer to the optimal receptive field size needed for detection. In addition to spatial resolution, other experiments have found that exogenous attention can increase performance in tasks involving contrast sensitivity and spatial frequency (Carrasco, Ling, & Read, 2004; Carrasco, Penpeci-Talgar, & Cameron, 2001; Doshier & Lu, 2000a, 2000b; Gobell & Carrasco, 2005; Huang & Dobkins, 2005). This research provided evidence that in addition to better performance on detection and discrimination tasks, attention can alter the appearance of stimuli. In this experimental paradigm, subjective appearances are determined indirectly as the participants view two Gabor patches of the same spatial frequency, and report the orientation of tilt (left or right) of the patch with the highest contrast (Carrasco et al., 2004). Attention is manipulated by presenting a peripheral or

neutral pre-cue before the stimuli appeared and to minimize the effect of response bias the peripheral cue is assigned to the Gabor patches randomly and therefore not a reliable cue or indicator of contrast. While neutrally cued conditions produced perceptual contrast comparisons equal to physical equalities, peripherally cued conditions do not. For example, in the neutral condition the point of subjective equality (PSE) for the two Gabors occurred when the gratings were physically of the same contrast, but when attention was directed toward one Gabor the PSE occurred for gratings at different contrasts. In particular, the cued Gabor was of lower physical contrast, yet participants rated it the same to a higher contrast uncued Gabor. Ruling out a response bias toward selecting cued stimuli, participants were able to reverse their criteria and select the Gabor of lower contrast instead therefore choosing the uncued stimuli more often. Additionally, when cue length duration was lengthened outside of the optimal duration for exogenous attention, the attentional effects disappeared. These results lead Carrasco et al. (2004) to the conclusion that attention not only benefits task performance but also alters the appearance of stimuli in this case by increasing the apparent contrast.

Additional studies have found support for this effect in other domains such as spatial frequency (Gobell & Carrasco, 2005). Using the same methodology as the experiment mentioned above, Gobell and Carrasco found that attention can increase spatial frequency appearance, such that participants report stimuli to be higher in spatial frequency when it was cued in comparison to physically identical uncued stimuli. This effect was found to

apply also to acuity, that is, gap size appeared larger with attention. These studies and others have led to the 'resolution hypothesis' emphasizing the effect of attention is to increase spatial resolution by fine tuning neural responses (Carrasco & Yeshurun, 2009). For instance, in the case of spatial frequency, attention can increase the sensitivity of high spatial frequency channels therefore making the stimulus appear to be of higher spatial frequency. Psychophysical evidence indicates that attentional effects are mediated cortically, as early as V1 (Yeshurun & Carrasco, 2000). This is corroborated by neuropsychological findings that attention causes receptive fields to respond by shrinking to attended stimulus (Luck, Chelazzi, Hillyard, & Desimone, 1997).

In addition, attentional modulation of neural responses is not limited to spatial stimulus properties. Studies with flicker stimuli have found that attention can increase the overall rate of perceived flicker suggesting an increase in neuronal firing resulting in increased sensitivity of high temporal frequency filters (Montagna & Carrasco, 2006). Further support for this hypothesis comes from the finding that attention increases coherence of random dot patterns, reflecting the effects of attention perhaps by increasing neuronal firing rates in MT/MST (Liu, Fuller, & Carrasco, 2006).

### Research Plan

While previous research has predominantly focused on a cortical pathway, such as areas V1 and V4, for attentional effects, the intent of this dissertation is to investigate a subcortical mechanism mediated through the



pupil. This question will be addressed by manipulating participants' attentional spread while recording pupil responses. However, unlike traditional studies in which attention is oriented discretely for a detection or discrimination task, this research paradigm employs rhythmic shifts in attentional spread (attentional oscillations). The general stimulus consists of four square elements, forming a diamond, which are placed over a small area near the center of the screen or over a larger area extending into the periphery of the screen. Participants are instructed to simultaneously attend to all the central elements, then all the peripheral elements, without moving their eyes from the central fixation point. The size of attentional spread is then dictated by the placement of the elements i.e. narrow attention while the central elements are displayed and broad attention while the peripheral elements are displayed. Considering that the spherical aberration present when the pupil dilates is pronounced enough for the resulting blur to reduce contrast sensitivity (Campbell & Green, 1965; Campbell & Gubish, 1966), pupillary changes, by reducing high spatial frequency information, can mediate changes in receptive field sensitivity. During narrow attention (attending to central elements), a decrease in pupil diameter reduces blur caused by spherical aberration and by preserving high spatial frequency information results in greater activation of small receptive fields relative to large receptive fields. Whereas under broad attention (attending to peripheral elements), an increase in pupil diameter increases blur due to spherical aberration, and by eliminating detailed information in the retinal image, reduces the activation of small receptive fields relative to large

receptive fields. Recruitment of large receptive fields would be beneficial in cases where attention is spread over a large area, causing blur through spherical aberration and thereby decreasing perception of high spatial frequencies. The pupil, therefore, may be one of the means through which attentional effects are implemented.

The research plan consists of testing the conditions under which the pupil is influenced by attention. Experiment 1A investigates exogenous attention, considered to be involuntary and quick acting, by using an apparent motion stimulus. In Experiment 1B, the necessity of a consistent and predictable temporal structure of attentional oscillations on pupil diameter is determined by randomly varying the duration of successive frames within each trial. A third manipulation, Experiment 1C, investigates if other transient stimuli affect the pupil's response, such as flicker. Additionally, in Experiment 1D, the slower, more voluntary endogenous attention is used to determine if the pupil's responses are mediated by this component.

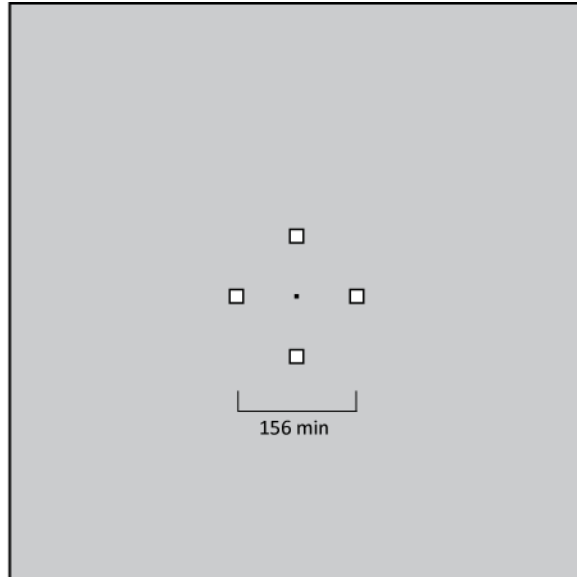
## GENERAL METHOD

### *Stimuli*

The general stimulus, displayed in Figure 3, consists of four square elements arranged in a diamond configuration. These elements, centered around a central fixation point, were used to manipulate the perceiver's attentional scale between narrow attention (elements placed over a small area near the center of the screen) and broad attention (elements spread out over a larger area extending into the periphery of the screen). The stimulus presentation began with the appearance of the central elements, signaling narrow attention, which remained visible for a duration of 2.5 seconds after which the peripheral elements, signaling broad attention, appeared for a duration of 2.5 seconds. The elements and therefore type of attentional spread cycled every 5 seconds corresponding to a frequency of 0.2 Hz.

The stimuli were presented on a FlexScan T566 with a Dell Precision 360. Participants viewed the stimuli while their pupillary responses were recorded by an eye tracking device. The chin rest was 38.1 cm from the screen, with small adjustments in order to accommodate individual differences in eye location (i.e. deep set eyes). Based on this viewing distance, the central elements were 156 min apart (from center to center), and the peripheral elements were separated by 1562 min. The elements were centered around a

Frame 1  
2.5 seconds



Frame 2  
2.5 seconds

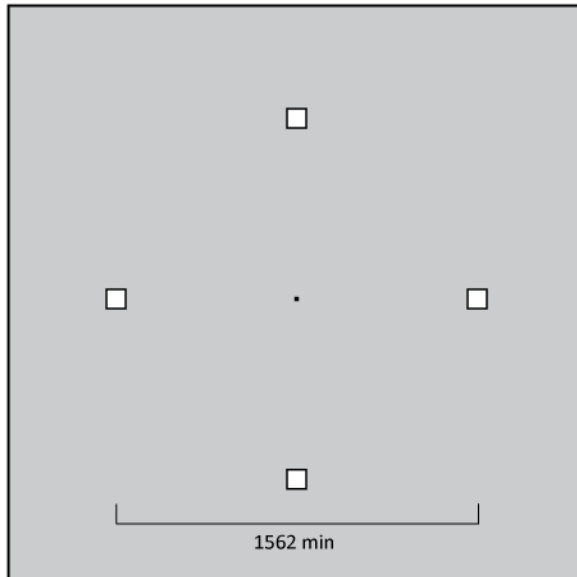


Figure 3. General stimulus. The spatial distribution of elements signals narrow (Frame 1) versus broad (Frame 2) attention. The elements cycled every 5 seconds corresponding to a frequency of 0.2 Hz. The central elements were 156 min apart (from center to center), and the peripheral elements were separated by 1562 min.

central fixation point with a luminance of  $0 \text{ cd/m}^2$  and a visual angle of  $5.2 \text{ min}$ .

In order to control for the known effects of luminance on pupillary reactions, each element is locally balanced so that the local average luminance of the element is equivalent to the background luminance. As shown in Figure 4, these balanced elements consist of a bright inner square (luminance =  $109 \text{ cd/m}^2$ ) surrounded by a dark border (luminance =  $0 \text{ cd/m}^2$ ) and were displayed on a background luminance of  $46 \text{ cd/m}^2$ . The size of elements and background luminance was adjusted so that the local luminance of each element was equivalent to the background luminance, and therefore do not add to the overall luminance at their locations. The inner bright squares subtended a visual angle of  $10.4 \times 10.4 \text{ min}$ , and the surrounding black border consisted of  $15.6 \times 15.6 \text{ min}$ . The outer bright squares subtended a visual angle of  $15.6 \times 15.6 \text{ min}$ , and the surrounding black border consisted of  $26 \times 26 \text{ min}$ .

### *Conditions*

Four different conditions were utilized within each of the experiments. The first experimental condition was the attentional oscillation paradigm. That is, participants were asked to shift their attention from the set of inner elements (narrow attention) to the outer elements (broad attention). The importance of attentional oscillations was validated by two additional conditions in which the participants held their attention constant by either maintaining a narrowly focused attention (narrow-sustained) or a broadly spread attention (broad-sustained). Since pupillary noise fluctuations (hippus)

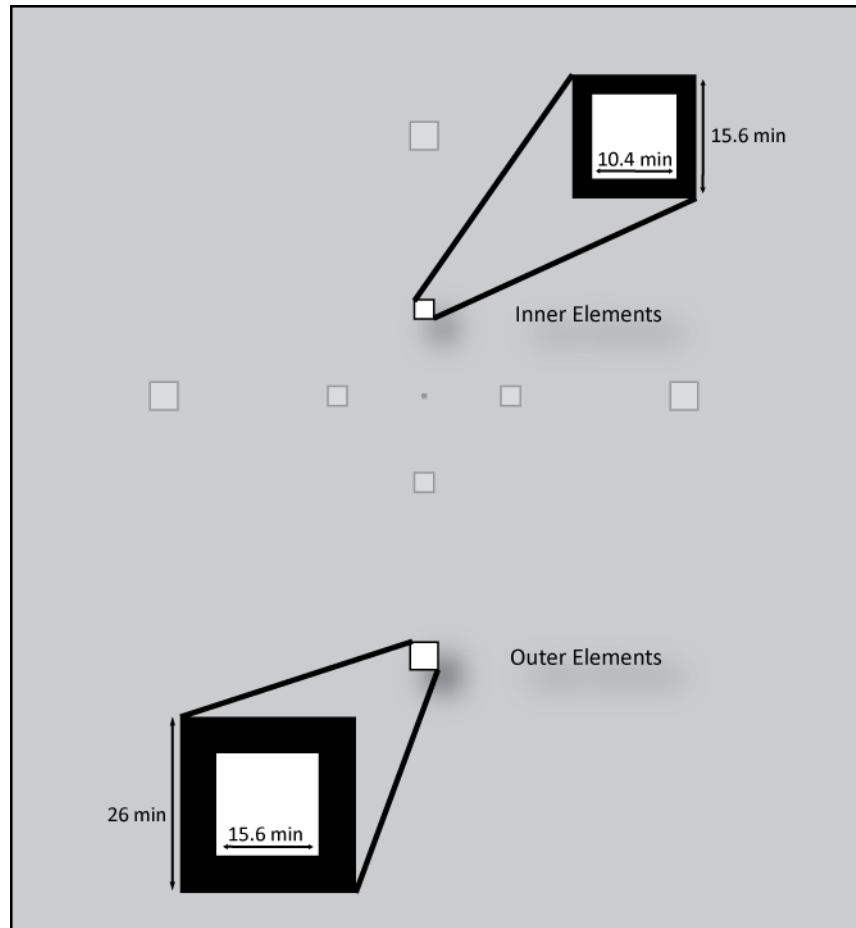


Figure 4. Luminance and size of balanced elements. The inner and outer elements were composed of a bright square (luminance =  $109 \text{ cd/m}^2$ ) surrounded by a dark border (luminance =  $0 \text{ cd/m}^2$ ) presented on a background luminance of  $46 \text{ cd/m}^2$ . The size of the elements and background luminance was adjusted so that each element is locally balanced in luminance (the average luminance of each element is equivalent to the background luminance).

are known to naturally occur even in the absence of stimuli and have oscillations in frequency spectrum range of 0.05-0.3 Hz (Stark, Campbell, & Atwood, 1958), a control consisting of only a central fixation element was utilized to measure baseline pupillary responses and to rule out the existence of a characteristic frequency near the stimulus frequency.

### *Eye Tracker and Data Analysis*

Data was collected using the View Point PC60 EyeTracker from Arrington Research. The View Point PC60 uses an infrared light source to illuminate the eye and for the video signal from the camera to be analyzed by the computer. A stimulus window allows for a real time video of the pupil, which is visible on the experimenter's console for the duration of the experiment. The software locates the pupil in the stimulus window by probing for dark regions within a defined search area. The search area can be manually adjusted by the experimenter, and a successful capture of the pupil is indicated by a yellow oval which traces the outline of the pupil. Insurance that the pupil is accurately locked on by the software is available during the duration of testing by the yellow tracing and marked in the data output. For these experiments, the EyeTracker software was interfaced with a MatLab computer program. MatLab controlled the timing and display of stimuli; whereas the EyeTracker collected the data output and controlled the sample rate of 16 milliseconds.

Since a large amount of data is collected, a data analysis tool was used to aid in data manageability. This tool consists of program written in PHP

code and run on a local web server. The analysis tool was designed to allow for flexibility in combining and viewing data. The EyeTracker output, for example, includes multiple measurements such as the pupil width, pupil aspect ratio, total time, delta time (amount of time since last collected sample), fixation duration, X and Y position, and the quality of the pupil measurement (if the pupil was captured by EyeTracker). Combining EyeTracker and MatLab output, the data analysis tool marks the start of each trial in the pupil data stream and sets exclusion criteria before averaging across trials, such as marking data that occurred following a blink or during an eye movement. The specific exclusion criteria used in all experiments was one sample preceding and five following a poor quality sample, and any data samples which fell one standard deviation away from the average X and Y gaze positions. Following processing, data points marked for exclusion were replaced by the average of the minimum and maximum for that particular trial. The percent of samples that were excluded and replaced was 3.2% for Experiment 1A, with similar estimates for additional experiments.

Of particular interest for data analysis was to determine the rhythmicity of pupillary responses under the influence of attentional oscillations; that is to detect the frequency at which pupil diameter changes. If the pupil is responding to changes in attention then the expectation is that the pupil diameter would cycle at the same rate as the narrow / broad variation in attention. The pupillary time series therefore was converted into a frequency spectrum using a Fast Fourier Transform.



The Fourier transform decomposes a waveform into sinusoids of different frequencies, amplitudes and phases that sum to the original waveform. A Fast Fourier Transform (FFT) is a computationally efficient version of a Fourier transform which was used to fit the pupillary time series into sine waves that best describe the amplitudes of each frequency component. The FFT results can be presented using the amplitudes or squared amplitudes (power spectrum) for each frequency band. For these experiments, FFT data is displayed using amplitudes.

To determine if the pupil was responding to changes in attention, the time series was transformed into a frequency spectrum using a Fast Fourier Transform. For the FFT to be computationally efficient, it is necessary that the number of points be a power of two. The data was limited to 2048 points in the time series for a total time of 34 seconds (about 7 cycles) entered into the FFT. The first second was removed from the time series (allowing for participants to prepare their attentional spread), excluded data (due to blinking, eye movements, etc.) were replaced, and the time series was shortened to 2048 points. The nine trials for each participant in each condition were then averaged and transformed into the frequency spectrum.

### *Procedure*

Before beginning the experiments, each participant was tested for eye-dominance, and the EyeTracker camera was positioned to record from the dominant eye. The non-dominant eye was covered by an eye patch. In order to achieve accurate eye positioning, each participant performed a calibration

check, which allowed the EyeTracker to match screen locations with participants gaze locations. Lights in the experimental room were dimmed and resulted in an ambient room illumination of  $1.9 \text{ cd/m}^2$  measured by wall reflectance near the EyeTracker. Upon presentation of stimuli, participants were instructed to maintain fixation on the center element, which was visible for the duration of the trial, and to avoid eye movements.

### *Participants*

Seven participants were included in Experiment 1A and five of those participants also volunteered for Experiments 1B-1D. All except the author LD and HH were naïve to the purpose of the experiment. The remaining participants were undergraduate students at Florida Atlantic University.

### Experiment 1A

The purpose of the first experiment is to investigate the effect of exogenous attention on pupil dynamics using a transient cue. Since exogenous attention is known to be reflexive and stimulus driven, an apparent motion stimulus was used to capture attention. The stimulus elicits changes in attentional spread by first appearing in the center of the screen (narrow attention) and after a set duration the stimulus extends into the periphery of the screen (broad attention), creating the appearance of apparent motion. Moreover, the importance of attentional oscillations is tested by conditions in which the participant views the stimuli while maintaining a fixed attentional spread. The participant's pupillary light reflex to flashes of light of the same temporal structure of the experimental stimulus is measured as a means to

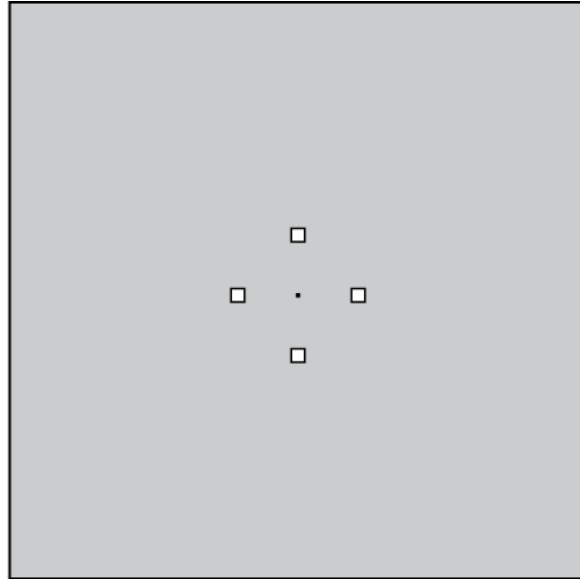
check normal pupil reactions in participants and accurate data measurement of the EyeTracker.

## Method

### *Stimuli*

Five separate conditions were used in Experiment 1A. Figure 5 displays the temporal and spatial characteristics of three conditions, attentional oscillations, broad-sustained, and narrow-sustained. The stimuli consisted of four square elements, themselves forming a diamond configuration, which alternate between the center of the screen (inner squares) and the periphery of the screen (outer squares). As shown in Figure 5, each set of squares appeared for a duration of 2.5 seconds, and upon their disappearance the alternate squares appeared and remained on for 2.5 seconds. This sequence was repeated eight times, and the entire trial lasted 42 seconds with the addition of a one second delay before and after presentation of stimuli. The fixation-only condition was identical in length of trial and frame structure to the experimental condition, however in this condition only the central square was present. For the luminance changing condition only a fixation point was present. The luminance of the screen alternated from  $150 \text{ cd/m}^2$  to  $0 \text{ cd/m}^2$  while the fixation point luminance alternated from  $0 \text{ cd/m}^2$  to  $150 \text{ cd/m}^2$ .

Frame 1  
2.5 seconds



Frame 2  
2.5 seconds

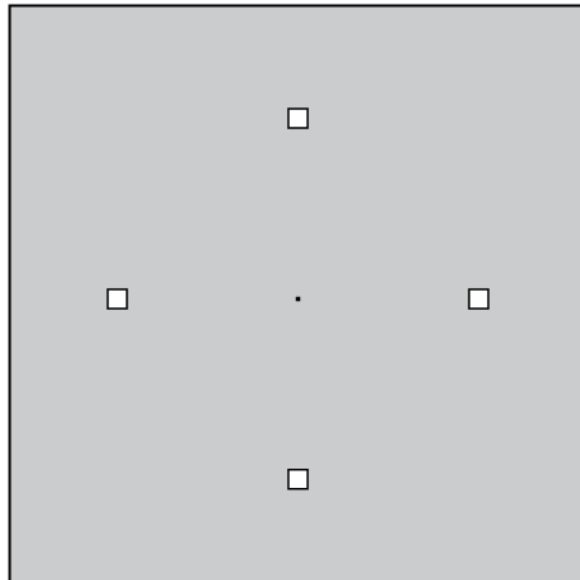


Figure 5. Stimuli used in Experiment 1A: Movement. The spatial distribution of elements signals narrow (Frame 1) versus broad (Frame 2) attention. Each trial is composed of eight repetitions of the two frames.

## *Design*

Each testing session included all five conditions, approximately order balanced over 3 days. Within each condition, three trials were presented resulting in 9 trials for each condition.

## *Procedure*

*Attentional Oscillations.* The stimuli always began with the four inner squares present, and participants were instructed to fixate on the central element and simultaneously attend to all four squares while maintaining their attention for the duration of presentation. As the stimuli changed to the outer elements, participants spread their attention to simultaneously include all four elements. This sequence was then repeated 8 times. It was emphasized to participants to maintain their eye position on the center fixation element and avoid eye movements.

*Fixation-Only.* In this condition, only the fixation element was present, and participants were instructed to maintain their fixation for the duration of the trial.

*Narrow-Sustained.* In this condition, participants were asked to attend only to the inner elements for the entire duration of the trial. Therefore, when the inner elements disappeared and the outer elements appeared participants were asked to continue to sustain narrow attention.

*Broad-Sustained.* Conversely, in this condition participants were asked to maintain a spread attention of the outer elements for the entire trial.

Therefore, when the outer elements disappeared and the inner elements appeared participants were asked to continue to sustain broad attention.

*Luminance Change.* Participants were instructed to maintain central fixation while the overall luminance changed.

### Experiment 1B

The first experiment tested if the pupil is mediated by attentional effects using an exogenous cue. However, since there was a constant, and therefore predictable frame duration it is conceivable that pupil changes were not driven entirely by the stimuli, since cue predictability may add an endogenous aspect. Whether the pupil is only entrained by the consistent and predictable stimulus change duration will be addressed in this experiment by varying the temporal structure of the attentional change.

### Method

#### *Stimuli*

The stimuli were identical to those in Experiment 1A, except that the temporal dimension was changed, such that the frame durations were not equal in length, and therefore did not follow a predictable pattern. Each set of squares appeared for a duration of either 2 or 3 seconds with each cycle equaling 5 seconds. Consistent with Experiment 1A, the cycle of inner and outer elements was repeated for a total of 8 cycles and had a total time of 42 seconds with the addition of a one second before and after the trial. Two conditions, attentional oscillations and fixation-only were used in this experiment.

## *Design*

Each testing session consisted of both conditions presented twice using an ABBA design. Within each condition, 2 trials were presented resulting in 12 trials per each condition over 3 days.

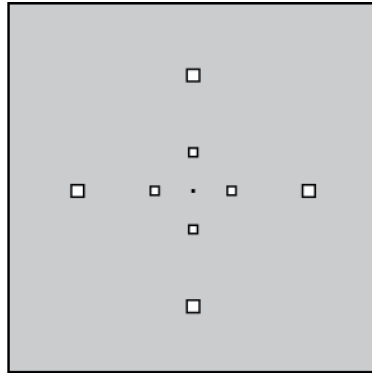
### Experiment 1C

The effect of transient cueing stimuli on the pupil in the form of an apparent motion stimulus was used in Experiments 1A and 1B. However, other transients that induce exogenous attention may also elicit changes in pupil diameter. This experiment investigates a different transient, flicker, to determine if this transient mediates pupil responses. The flickering of the elements is used as a peripheral cue which is thought to activate more automatic components of attention (Jonides, 1981). This experiment tests the generalizability of exogenous attention affecting the pupillary response by testing a different transient stimulus.

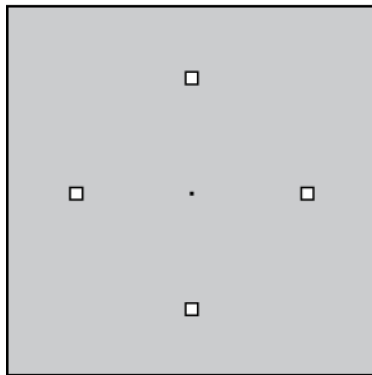
### Method

#### *Stimuli*

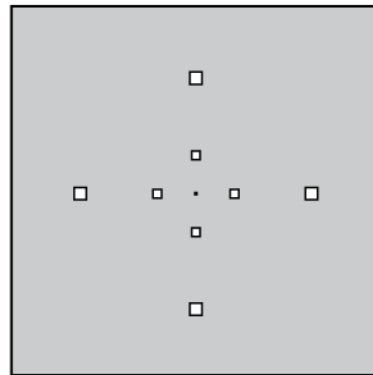
The stimuli described in General Methods were modified so that all eight balanced elements were visible at the beginning of the trial. Displayed in Figure 6, the elements remained present for a one second frame to allow the participants to prepare and set their fixation. After the one second preparation, the inner elements were removed for 100 milliseconds and reappeared in the next frame, resulting in the perception of flicker. After flickering, the inner elements remained visible and stationary for 2400 msec.



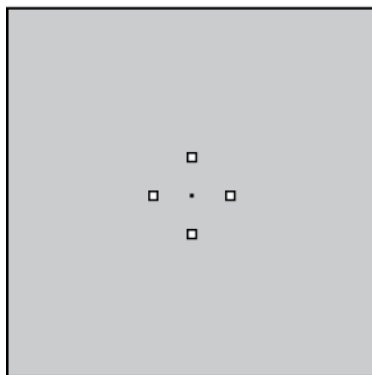
Lead In:  
1.0 second



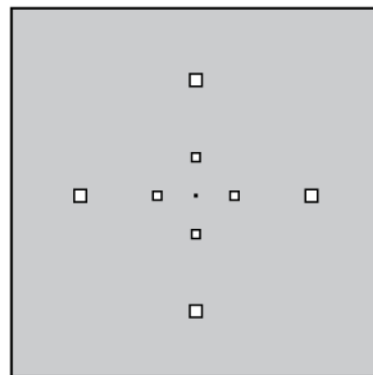
Frame 1: 100 msec  
inner elements removed



Frame 2: 2400 msec  
attention to inner elements



Frame 3: 100 msec  
outer elements removed



Frame 4: 2400 msec  
attention to outer elements

Figure 6. Stimuli used in Experiment 1C: Flicker. Elements were removed for 100 milliseconds (Frame 1 and Frame 3) resulting in flicker which signaled narrow (Frames 1 & 2) versus broad (Frames 3 & 4) attention. Each trial is composed of 8 repetitions of the 4 frames.



Four conditions, attentional oscillations, broad-sustained, narrow-sustained, and fixation-only were included in this experiment. All conditions followed the same specifications of Experiment 1A but were modified to match the changes for the flicker cue.

### *Design*

Each testing session included all four conditions, approximately order balanced over 3 days. Within each condition, three trials were presented resulting in 9 trials for each condition.

### Experiment 1D

Whereas in Experiments 1A, 1B & 1C pupillary responses to exogenous attention were measured, the purpose of this experiment is to determine the effect of endogenous attention on pupillary movements. Endogenous or sustained attention is considered a top-down process, such that attention is guided and voluntary. Reflecting its effortful nature, sustained attention is slow relative to transient attention, involves different brain areas and is optimized by different cues (Corbetta & Shulman, 2002; Nakayama & Mackenben, 1989). Experiment 1D is designed to tap into this voluntary component by having all eight of the balanced elements visible for the entire trial and remain stationary upon presentation, therefore removing the transient cue. Attention is instead cued by a change in luminance of the central fixation element since central cues are known to aid in endogenous attention (Cheal & Lyon, 1991). In light of the numerous differences found in the literature between sustained and transient attention, this experiment investigates

whether pupillary responses can be evoked by endogenously cued attentional oscillations and if so whether they differ from the responses obtained with exogenously cued attentional oscillations.

## Method

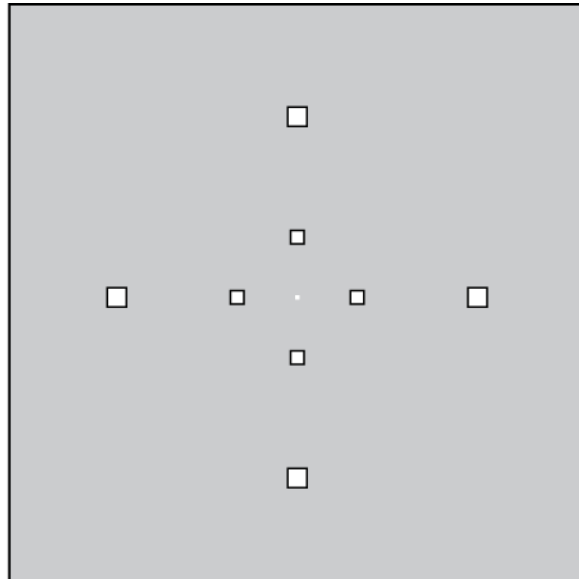
### *Stimuli*

The stimuli described in General Method, the two sets of four balanced elements, were utilized for this experiment. However, the presentation was modified, such that all eight balanced elements remained stationary and visible for the duration of the trial. Participants were cued to shift their attention by the central fixation element, which changed in luminance from 250 cd/m<sup>2</sup> signaling narrow attention to 0 cd/m<sup>2</sup> signaling broad attention (see Figure 7). As in Experiment 1A, the narrow attention condition was cued first and was maintained for 2.5 seconds. Four conditions, attentional oscillations, broad-sustained, narrow-sustained, and fixation-only were included in this experiment. All conditions were as described in Experiment 1A but were modified to match the endogenous cues, such that the narrow-sustained and broad-sustained conditions had all eight elements present and a central fixation element that alternated in luminance. The fixation-only condition contained only the central fixation element which alternated in luminance.

### *Design*

Each testing session included all four conditions, approximately order balanced over 3 days. Within each condition, three trials were presented resulting in 9 trials for each condition.

Frame 1  
2.5 seconds



Frame 2  
2.5 seconds

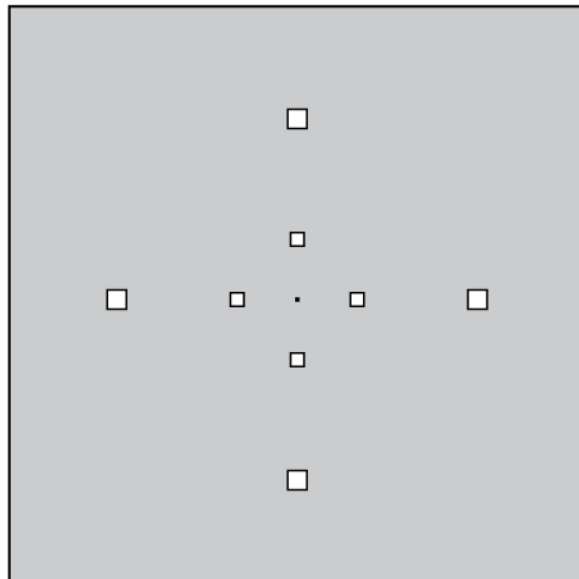


Figure 7. Stimuli used in Experiment 1D: Central Cue. Luminance change of the fixation point signaled narrow (luminance increment; Frame 1) versus broad (luminance decrement; Frame 2) attention. Each trial is composed of eight repetitions of the two frames.

## RESULTS

### Data Analysis

#### *Peak Analysis*

If pupillary movements are reflecting attentional oscillations, then there should be an increase in Fourier energy at the temporal frequency with which the stimulus changes. Based on the experimental frame duration, this would correspond to a frequency of 0.2 Hz. The analysis of the FFT consists of 1) determining whether there was more Fourier energy at 0.2 Hz relative to the adjacent flanking frequencies in the attention and fixation-only conditions (the “peak analysis”), and 2) comparing the Fourier energy for the attention and the fixation conditions at 0.2 Hz. The statistical comparison was based on the Wilcoxon Matched-Pairs Signed Ranks Test, which is a nonparametric equivalent of the t-test for matched scores and takes into account the magnitude and direction of differences between matched pairs (Howell, 1982). The test is based on the logic that if the difference scores were drawn from the same population they would be symmetrical around the median; half would be positive and half would be negative. The null is rejected when the difference scores are in the predicted direction and any scores in the opposite direction are small in size. The absolute values of the differences scores are therefore ranked, and the test score is the smaller of the sum of the positive and

negative ranks. The score is then compared to a standardized signed ranks difference Z.

### *Pupil Response to Light*

The pupil response to light is known to behave like a sawtooth pattern, such that the velocity of pupillary constrictions is up to three times quicker than dilations (Ellis, 1981). Figure 8 displays the pupillary response to cycles in luminance (panel A) compared to a sawtooth waveform alternating at the same frequency (panel B). This asymmetry in the pupil response reflects differences in conduction speed of afferent and efferent pupillary pathways. That is, whereas pupillary constriction is predominately the result of quick parasympathetic inputs, pupillary dilation has two distinct phases. The first phase, primary redilation, reflects the relatively quick inhibition of parasympathetic system, followed by a slower phase, secondary redilation, resulting from a decrease in sympathetic inhibition and an eventual increase in parasympathetic tone (Lowenstein & Loewenfeld, 1950).

### *1/f Noise*

Intrinsic in countless natural time series,  $1/f$  is defined as a type of noise in which a signal's power spectrum is proportional to the inverse of the frequency. A  $1/f$  signal is characteristically linear with a negative slope in a log-log scale, such that there is greater power in the low frequency components than high-frequency components. Figure 9 displays the log-log power spectrum for the average fixation data, where each point corresponds to the FFT magnitude for each temporal frequency. While the presence of  $1/f$

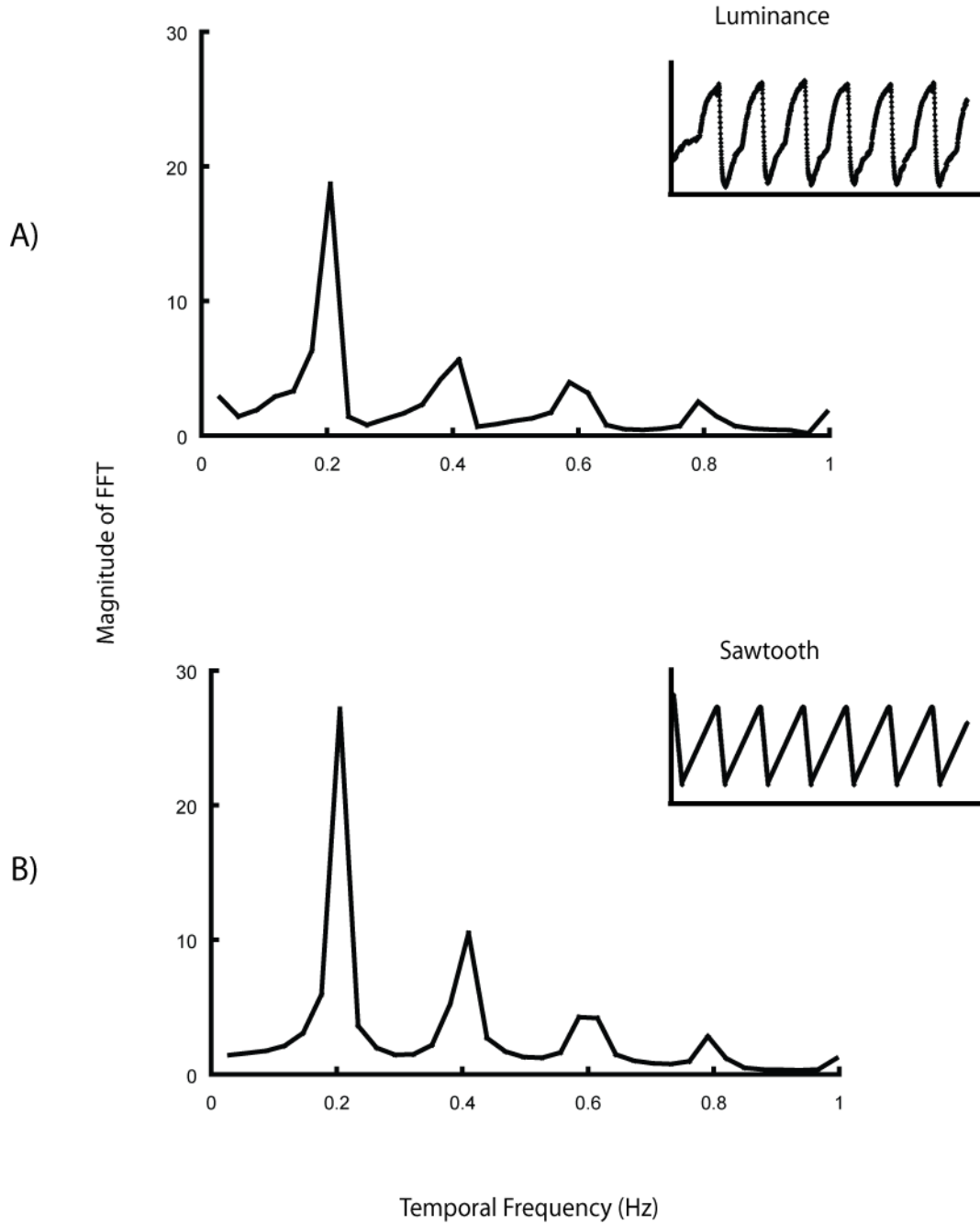


Figure 8. Comparison between FFT results for pupillary light response and sawtooth waveforms. A) FFT for pupil response to 2.5 second alternations in luminance. B) FFT results for a generated sawtooth waveform alternating every 2.5 seconds. The insets in each panel contain the time varying signal.

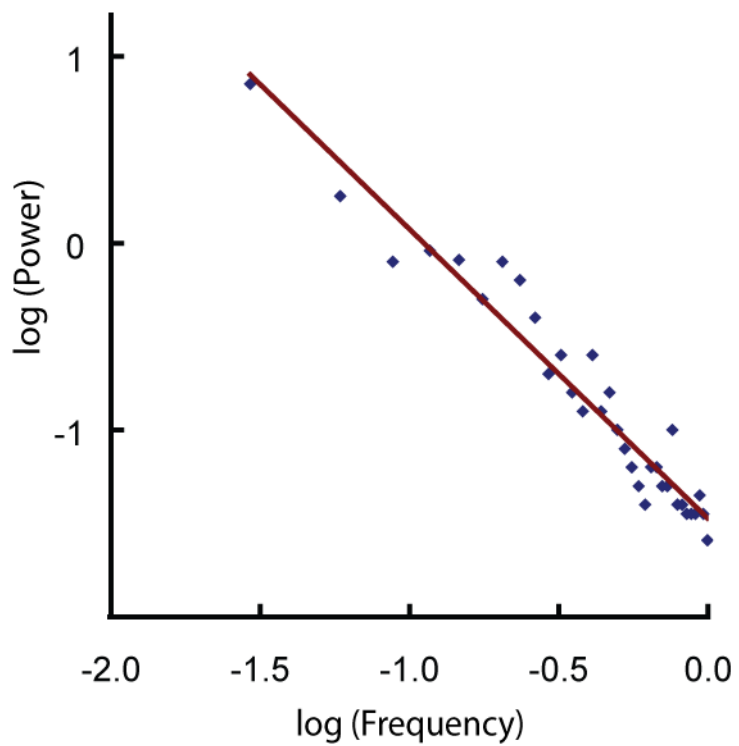


Figure 9. Log-log power spectrum obtained from FFT of averaged fixation data. Slope of best fit line is -1.5, consistent with 1/f noise.

noise indicates a slope of the best fit line equal to -1.0, in practice the accepted slope falls in the range of -0.5 to -1.5 (Wagenmakers, Farrell, & Ratcliff, 2004). The slope of the power spectrum for the average fixation data was -1.5, which was found to be similar across experiments. Therefore, the Fourier magnitudes in the fixation conditions can be considered an independent measure of 1/f noise.

### *Partial Correlations*

If pupillary movements to attentional oscillations follow the previously described sawtooth characteristics of pupillary luminance responses, then the magnitudes of the attention FFT should correlate with the magnitudes of the FFT found for luminance data alternating at the same frequency (see Figure 8). In particular, the attention FFT should contain both even and odd harmonics characteristic of a sawtooth waveform. A correlational analysis determined if the FFT found for attentional oscillations can be described as having sawtooth characteristics found in pupillary luminance cycles (Ellis, 1981; Heller, Perry, Jewett, & Levine, 1990; Howarth, Heron, & Whittaker, 2000; Lowenstein & Loewenfeld, 1950). Since the correlations between the attentional FFT and the luminance FFT are artificially increased by the presence of 1/f noise for both measures, the FFT magnitudes for the fixation condition, a pure indicator of 1/f noise, was partialled out of the attention/luminance correlations. The importance of attentional shifts was also validated by correlating the luminance FFT with the FFT's for two sustained attention conditions (narrow-sustained and broad-sustained), again partialling out the FFT for the fixation condition.



The correlations were calculated for 34 temporal frequencies ranging from 0.03 and 1.0 Hz.

### Results: Experiment 1A-1D

Figure 10 shows the average FFT results across participants for attentional oscillations in Experiments 1A-1D. The FFT data were analyzed to determine the significance of any peaks present at the 0.2 Hz frequency for the attentional oscillation conditions and fixation conditions. The presence of a peak was determined by comparing the magnitude at the frequency of 0.2 Hz to the average magnitude of the adjacent flankers (0.17 Hz and 0.23 Hz). The Wilcoxon Matched-Pairs Signed Ranks Test results are displayed in Table 1. A significant peak was obtained for all experiments at 0.2 Hz in the attentional oscillation condition, establishing that the pupil was responding to changes in attention. This is in contrast to the fixation condition for which no significant peaks were found. The lack of a significant peak in the fixation conditions therefore confirms that the pupil does not have a naturally occurring response present at 0.2 Hz. Additionally, if the pupil is responding to changes in attention it is expected that there will be a larger FFT magnitude at the 0.2 Hz frequency in the attention conditions than in the fixation conditions. The difference of FFT magnitudes for attention oscillations versus fixation at the 0.2 Hz temporal frequency indicated that the magnitudes were larger in the attention condition. A significant difference was found in all experiments with the exception of Experiment 1C (exogenous flicker), which was marginally insignificant due to a small reversal found in one participant.

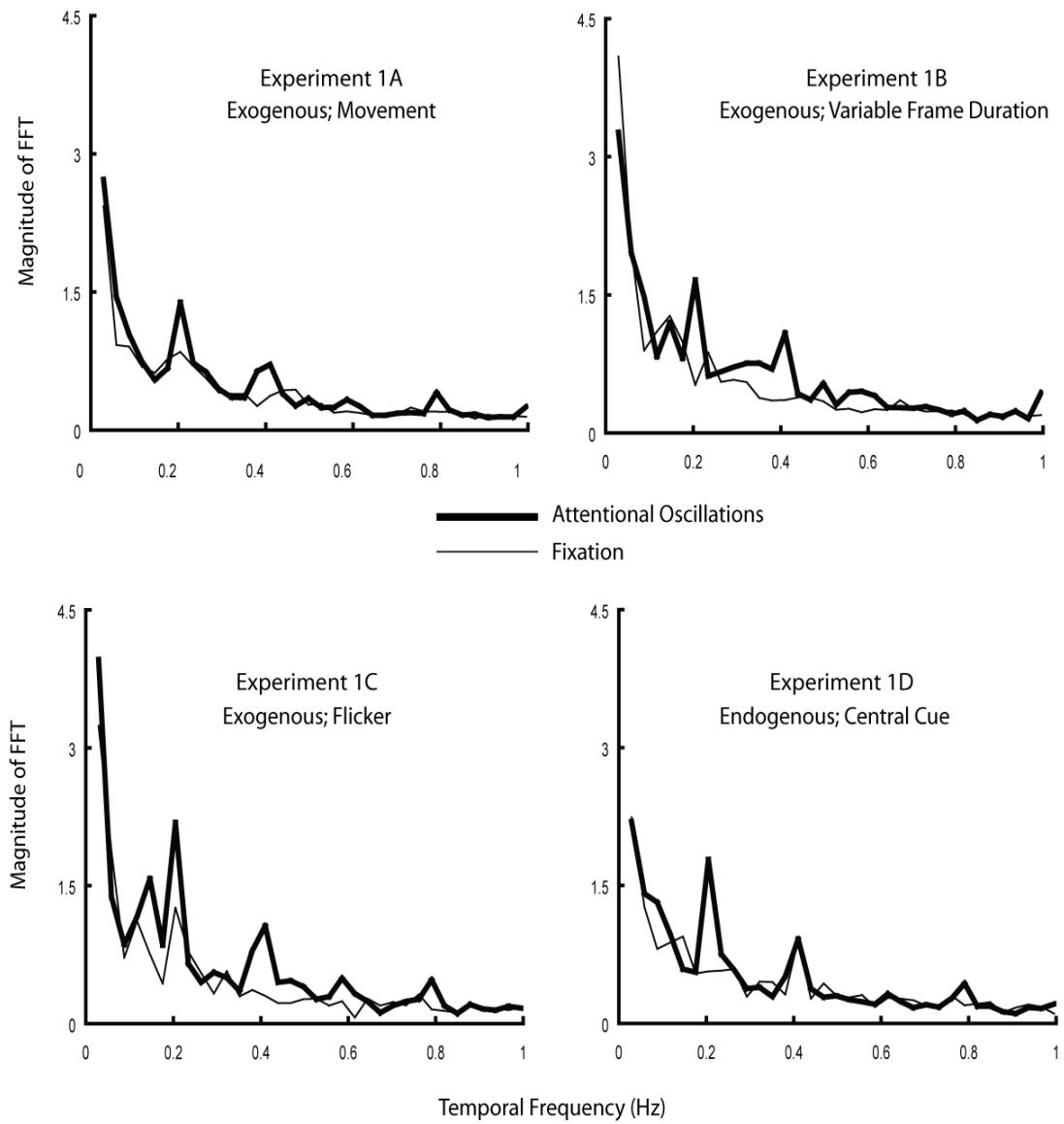


Figure 10. FFT results from Experiments 1A-1D for broad and narrow attentional oscillations and fixation conditions. For attentional oscillation conditions, stimulus cycled at a temporal frequency of 0.2 Hz.

	FFT Amplitude at 0.2 Hz versus FFT Amplitude at Flanking Frequencies (0.17 Hz & 0.23 Hz)		Difference of FFT Amplitude for Attention versus Fixation
	0.2 Hz Attention	0.2 Hz Fixation	at 0.2 Hz
Experiment 1A Exogenous; Motion	$z = -2.028, p = .02^*$	$z = -.676, p = .25$	$z = -1.859, p = .03^*$
Experiment 1B Exogenous; Variable Frame	$z = -2.023, p = .02^*$	$z = -.674, p = .25$	$z = -2.023, p = .02^*$
Experiment 1C Exogenous; Flicker	$z = -1.753, p = .04^*$	$z = -1.214, p = .11$	$z = -1.483, p = .07$
Experiment 1D Endogenous; Central Cue	$z = -2.023, p = .02^*$	$z = -.405, p = .34$	$z = -2.023, p = .02^*$

Table 1. Results from Wilcoxon Matched-Pairs Signed Rank Test for FFT data from Experiments 1A- 1D tested at fundamental temporal frequency of the stimulus/attentional change (0.2 Hz). Asterisk indicates statistical significance ( $p < .05$ ).

Analysis of the individual experiments establishes that a transient attentional cue is sufficient to entrain the pupillary response. However, motion is not necessary per se, as the flicker cue condition also elicited a pupil response, revealing that the pupil responds to exogenous attention regardless of the specific type of cue. The endogenous experiment (central cue) demonstrates that the pupil responds to endogenous as well as exogenous attentional shifts. Furthermore, since in the endogenous experiment the stimuli remained stationary, the results indicate that the change in stimulus does not in itself drive the pupillary movement but is instead dependent on attentional oscillations. This change in pupil response is not dependent on the rhythm of the frame duration as evidenced by the result from Experiment 1B, which utilizes an unpredictable sequence of frame durations.

*Partial Correlations: Attentional Change*

Since a significant peak was found for the attentional oscillations conditions, a correlational analysis between the FFT magnitudes for the attentional oscillations conditions and experimental luminance data partialling out the fixation magnitudes (representing  $1/f$  noise) was performed. The partial correlations were significant for all experiments (Table 2). That is, the attentional oscillations data follows the previously described sawtooth pattern of the pupillary luminance response.

A) Attentional Oscillations	
Experiment 1A Exogenous; Motion	$r(31) = .53, p = .001^*$
Experiment 1B Exogenous; Variable Frame Duration	$r(31) = .74, p = .0001^*$
Experiment 1C Exogenous; Flicker	$r(31) = .66, p = .0001^*$
Experiment 1D Endogenous; Central Cue	$r(31) = .77, p = .0001^*$

B) Sustained Attention		
	Broad	Narrow
Experiment 1A Exogenous; Motion	$r(31) = .26, p = .14$	$r(31) = -.06, p = .76$
Experiment 1B Exogenous; Variable Frame Duration	Not Tested	
Experiment 1C Exogenous; Flicker	$r(31) = -.12, p = .51$	$r(31) = -.10, p = .57$
Experiment 1D Endogenous; Central Cue	$r(31) = -.01, p = .96$	$r(31) = .34, p = .05^*$

Table 2. Correlational results calculated between the FFT amplitudes for luminance and attention, partialling out the FFT amplitudes for the fixation condition. A) Attention varies with stimulus at 0.2 Hz. B) Attention is sustained while stimuli vary at 0.2 Hz. The correlations were calculated for 34 temporal frequencies ranging from 0.03 and 1.0 Hz.

### *Partial Correlations: Narrow-Sustained and Broad-Sustained*

In contrast, the FFT results for the sustained attentional spread conditions are shown in Figure 11. The FFT magnitudes for the narrow-sustained and broad-sustained conditions were also partially correlated with the experimental luminance data. The results of the correlational analysis displayed in Table 2 validate the importance of attentional oscillations, as there were no systematic significant effects for narrow-sustained and broad-sustained conditions demonstrating that under conditions where there are no attentional changes, the pupillary response does not behave in the known sawtooth fashion.

### *Effort Effects*

Since it is known that pupillary dilations are correlated with the amount of cognitive effort or processing load associated with the task (Beatty, 1982), it could be argued that differences in pupillary size reflect a difference in task difficulty between broad and narrow conditions rather than changes in attentional spread. However, the mean pupil diameter between the broad-sustained and narrow-sustained conditions was not found to be significant for any experiment. The lack of difference in the mean diameter between the broad-sustained and narrow-sustained conditions indicates that differences in effort cannot explain the 0.2 Hz rhythmicity of the pupil. While the lack of difference in mean pupil diameter between broad-sustained and narrow-sustained conditions demonstrates that there are no pupillary effects of sustained attentional spread, such results do not indicate the absence of

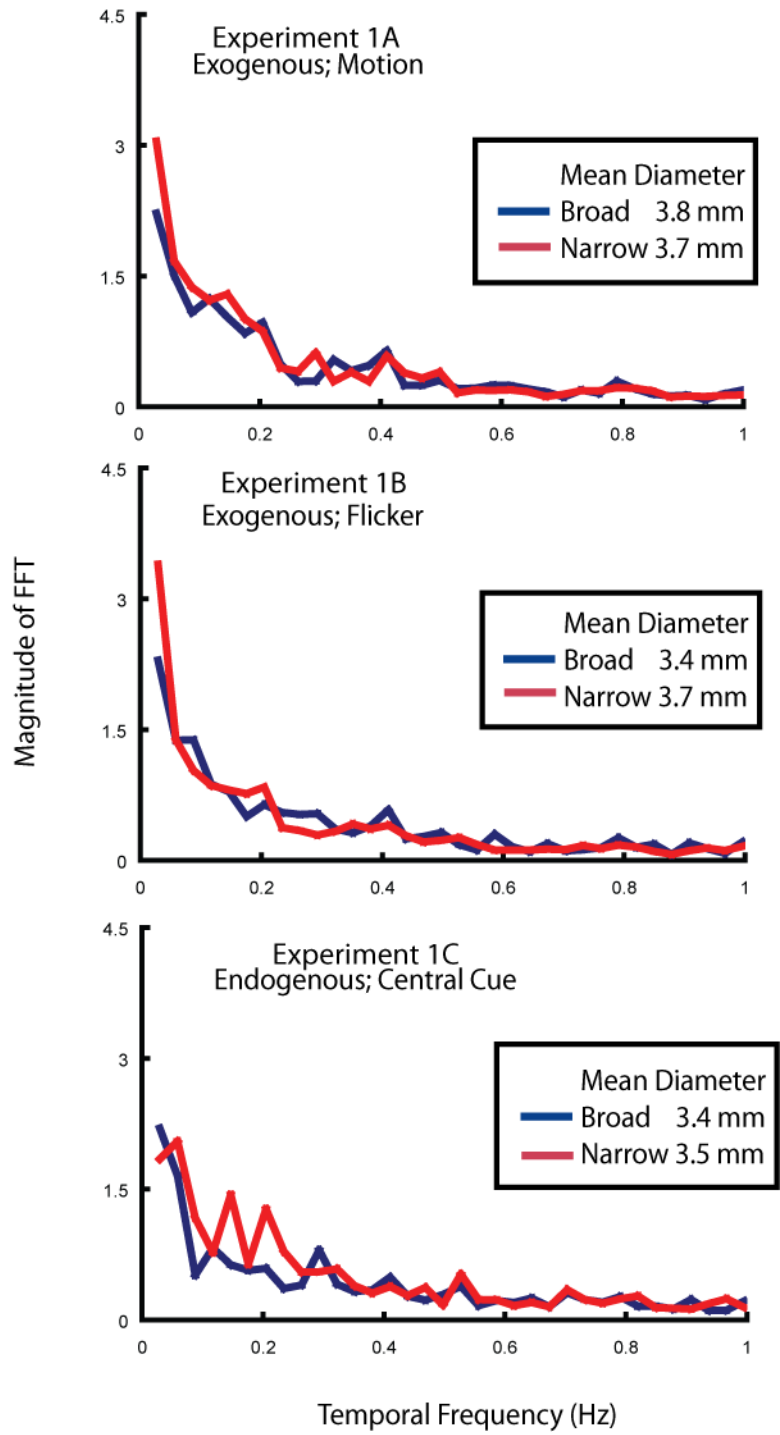


Figure 11. FFT results and mean diameter for sustained attentional spread conditions.

general sustained attention effects, which has been well documented (Balz & Hock, 1997; Castiello & Umilta, 1990; Goto, Toriu, & Tanahashi, 2001; Hock & Balz, 1994; Hock, Balz, & Smollen, 1994; LaBerge et al., 1991), but validates the role of dynamical changes mediated through the pupil.



## EXPERIMENT 2

That the pupil does not respond immediately to stimulus input but is delayed due to mechanical limitations of the iris muscle and integration of the signal in afferent pathways has been well documented (Loewenfeld, 1999). The amount of time that elapses between presentation of stimuli and pupil response (latent period) depends on a number of factors including strength and type of stimuli as well as individual difference factors such as fatigue and age. This corresponding lag in response time can result in pupillary reactions which are out of phase with the occurrence of the stimulus. For instance, pupillary responses to sinusoidal light fluctuations are often shifted in phase, particularly at higher frequencies where pupil response phase differences of 180 and 360 degrees has been found (Loewenfeld, 1999). Due to these known temporal delays, for relatively brief frame durations, it is difficult to match the pupil's response to the frames corresponding to broad and narrow attention. Using longer trials to compensate for delays, this experiment seeks to confirm if participants will have greater dilation during broad attention frames than narrow attention frames.

## Method

### *Stimuli*

The stimuli and procedure are the same as described in Experiment 1A. However, the frame duration was changed from 2.5 seconds to 4.5 seconds, the latter corresponding to a temporal frequency of 0.11 Hz. The alteration of inner and outer elements was repeated for a total of 4 cycles. With the addition of a one second before and after the trial, the total time was 38 seconds. One condition, attentional oscillations, was used in this experiment.

### *Design*

The experiment was performed over three days with each testing session consisting of three trials for a total of 9 trials.

### *Participants*

Three participants from the previous experiments were tested: HH, LB and AH.

## Results

Figure 12 shows the time series data for the participants. The average pupil diameter within each frame overlays the time series. Consistent across participants, the pupil was on average more constricted during narrowly focused frames and comparably more dilated during broadly spread frames, with the exception of the last two frames for participant LB. This experiment confirms that with enough time to allow for delays and anticipatory effects, the directional hypothesis that the pupil constricts under narrow conditions and dilates under broad attention.

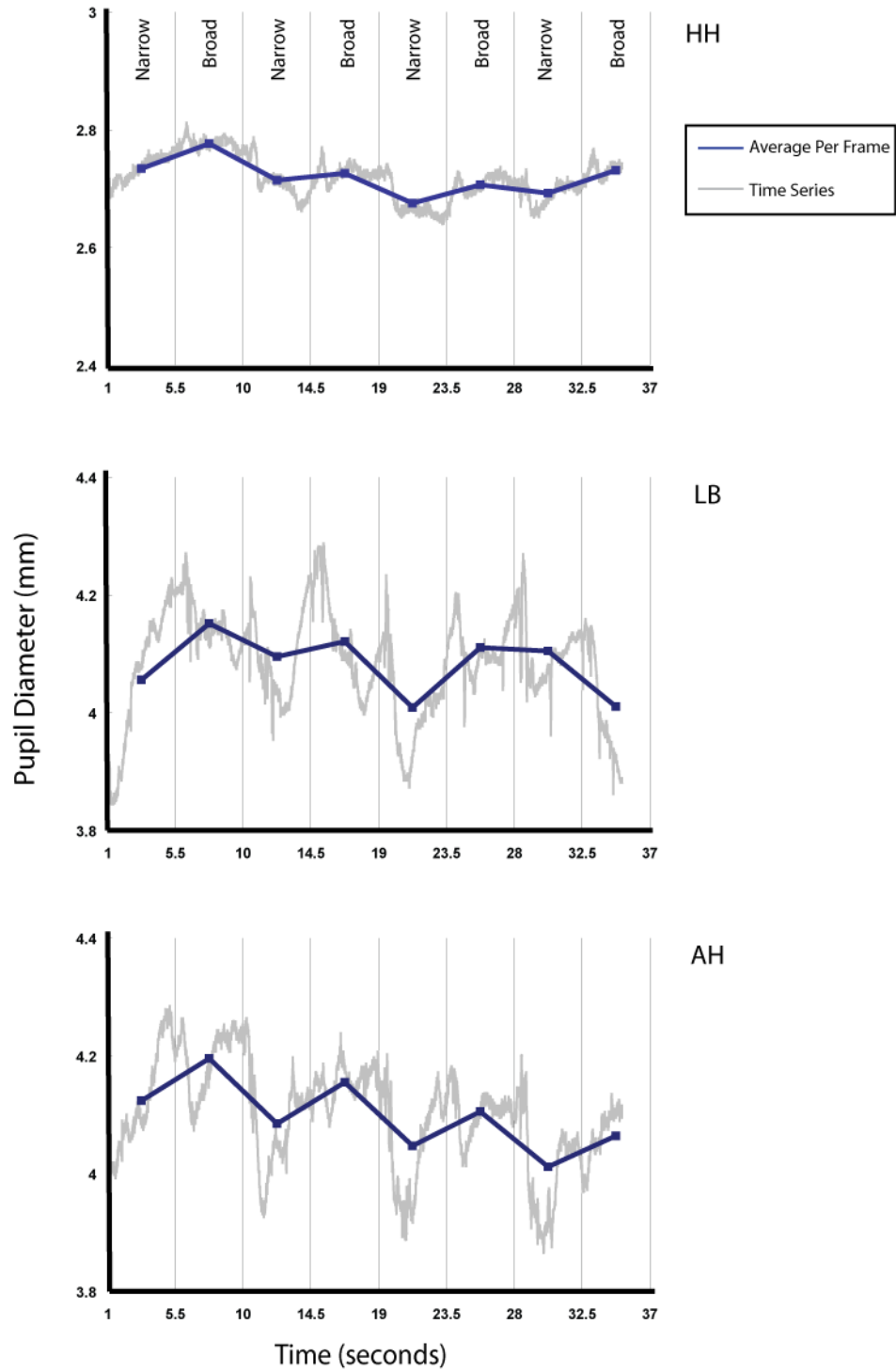


Figure 12. Results from Experiment 2. Pupillary responses (light grey lines) for 4.5 second frame durations (0.11 Hz) were averaged within each frame (black markers).

## EXPERIMENT 3

Previous studies (Balz & Hock, 1997) have shown, by varying a perceiver's spread of attention, differences in performance on detection tasks with broad and narrow attention. That is, participants can focus their attention sufficiently to reduce detection of peripheral luminance increments relative to broad attention conditions. This experiment was designed to confirm through a detection task that participants were following instructions and capable of broadening and narrowing attention sufficiently to alter detection rates for a peripheral luminance change. Therefore, it follows that during sustained attention trials participants will have increased detection rates for broad compared to narrow attention. An attention oscillation condition could not be used in this design since dynamic pupil changes alter sensitivity, such that when the pupil dilates to the change in broad attention this might decrease the ability to detect a luminance change due to spherical aberration. In order to optimize the ability to detect differences in broad and narrow attention this experiment contrasted broad-sustained and narrow-sustained attention.

### Methods

#### *Stimuli*

The stimuli described in Experiment 1A, the two sets of four balanced elements, were utilized for this experiment. Displayed in Figure 13, each set

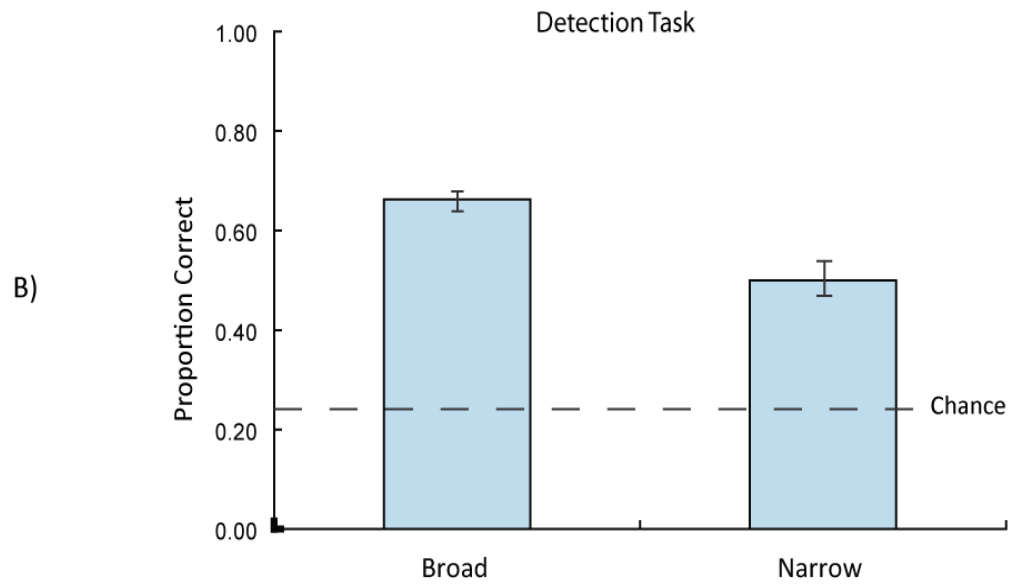
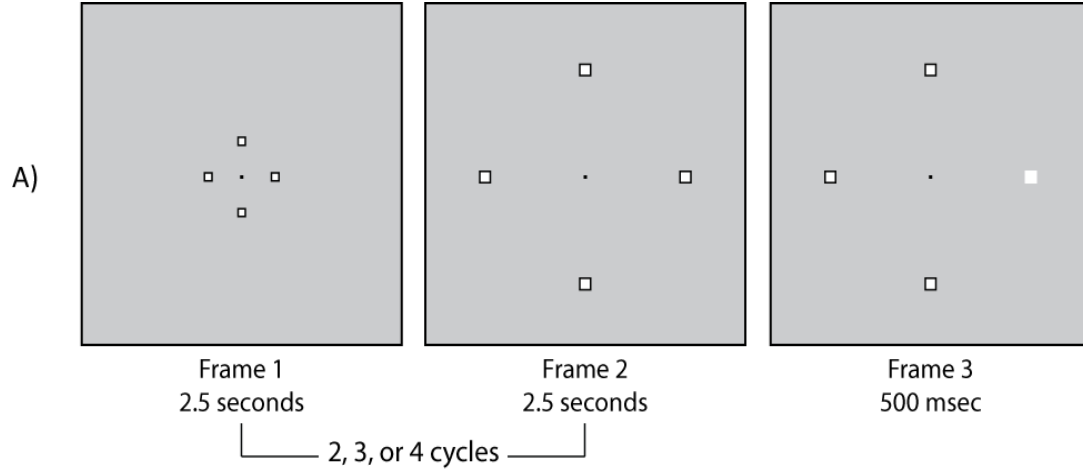


Figure 13. Stimuli and results for Experiment 3. A) The stimulus alternates between Frame 1 and 2 for either 2, 3 or 4 cycles before the annulus of one of the outer elements increases in luminance (the luminance increment was pre-calibrated for each subject. B) Proportion correct detection for a peripheral luminance change under broad and narrow attention.

of squares appeared for a duration of 2.5 seconds and upon their disappearance the alternate squares appeared and remained on for 2.5 seconds. To insure that participants were attending to the task, the number of repetitions was varied randomly from trial to trial and was repeated for either 2, 3 or 4 cycles. On the last cycle, the annulus of one of the outer elements increased to a luminance pre-calibrated for each participant to avoid ceiling and floor effects. The individual participant's luminance increment values were as follows: 98, 105 or 120  $\text{cd/m}^2$ . After the luminance increment occurred, the fixation element changed color indicating that the participant should respond. Including wait time for the participant's response after the fixation element color change, each trial lasted 23.5 seconds. Two conditions, broad-sustained and narrow-sustained were used in this experiment.

### *Design*

Each daily testing session included one presentation of the narrow-sustained and the broad-sustained condition. The order of condition presentation was reversed over successive days for 8 days. Each daily presentation consisted of twelve trials per condition with the luminance change occurring randomly at each of the four peripheral locations three times (25% of the trials).

### *Procedure*

The stimuli always began with the four inner squares present. Before the trial participants were instructed to maintain their attention depending on the condition (broad-sustained or narrow-sustained) for the duration of

presentation. When the fixation element turned blue to indicate the end of the trial, participants responded by tapping their finger to indicate which of the outer elements changed. In practice sessions, participants were given instructions to indicate the location of peripheral luminance change by tapping their finger according to the clockwise placement of the elements, that is, one tap if the luminance change occurs for the upper element, two taps if the luminance change occurs for the right element, three taps if the luminance change occurs for the lower element, and four taps if the luminance change occurs for the left element. It was emphasized for participants to maintain their eye position on the center fixation element.

### *Participants*

Four participants from the previous experiments were included: HH, LB, AH and KH.

### Results

The data for the behavioral task are displayed in Figure 13. During the broad-sustained condition the participants had significantly higher detection rates than during the narrow-sustained conditions,  $t(3) = 2.8$ ,  $p = .034$  (one-tailed). This data confirms that the participants were in fact able to alter their attentional spread sufficiently to increase detection under broadly spread conditions for a peripheral luminance increment and conversely narrowly focus their attention sufficiently to reduce detection of the peripheral luminance increment.

## GENERAL DISCUSSION

Although it is well known that the pupil responds dynamically to changes in ambient light, the results from this dissertation reveal for the first time that the pupil also responds dynamically to changes in spatially distributed attention. Experiments 1A-1D demonstrate, through a variety of orientating tasks, that the pupil responds to changes in attention. That is, the pupil was found to cycle at the rate of attentional oscillations. An additional goal of the first set of experiments was to determine the conditions under which the pupil response can be elicited. It was shown that a motion stimulus is sufficient to mediate the pupil response (Experiment 1A) and that these effects are not dependent on the type of transient, since a pupillary response was also found for a flickering stimulus (Experiment 1C). Additionally, the predictability of the stimulus does not matter (Experiment 1B).

Considering the differences for exogenous and endogenous attention observed in previous studies, it was of interest to determine if the pupillary response could be found with both types of attention. The results indicate that the pupillary response is elicited by both exogenous and endogenous stimuli with the critical factor being the alternation in attentional spread rather than the type of stimulus. The necessity of this attentional change is especially evident in the endogenous condition (Experiment 1D), where the stimuli itself never



changed, and therefore could not be driving the pupillary response. This is further supported by the results of the control conditions (broad-sustained and narrow-sustained) when participants were asked to maintain their attentional spread. Under these conditions, the pupil did not alternate in a way consistent with known pupillary responses (i.e. sawtooth pattern).

While Experiments 1A-1D demonstrated that pupil responses alternate with attentional oscillations for both endogenous and exogenous stimuli, Experiment 2 addressed the directional hypothesis. That is, if the pupil mediates receptive field activation by controlling the amount of blur present in the retinal image then a relative pupillary constriction should be observed under narrow attention and conversely a relative pupillary dilation under broad attention. The results from Experiment 2, which found that the average pupil diameter was greater during broad attention frames compared to narrow attention frames, support this hypothesis.

Additionally, a detection task was utilized in Experiment 3 in order to determine if participants were following instructions and capable of changing their attentional spread. By manipulating a peripheral luminance change, it was shown that detection rates were greater under broad attention conditions compared to narrow attention conditions. The results of the detection task replicate previous findings (Balz & Hock, 1997) that participants can sufficiently broaden and narrow their attention to alter detection rates for a peripheral luminance change. While this experiment manipulated a peripheral luminance increment, it should be noted that Balz and Hock (1997) have

shown, while a relatively small effect, decreased detection under broad attention to a central luminance change.

Pupillary size is a key determinate in the degree of visual resolution possible; as pupil diameter increases, the presence of spherical aberration degrades the image and reduces the amount of contrast detected by the retina. Since the loss of contrast tends to be more severe for high spatial frequencies, the degree of degradation will be dependent on the spatial frequency of the pattern (Campbell & Green, 1965; Campbell & Gubish, 1966). The magnitude of the pupil change in this study was relatively small, the mean diameter ranged from 3.2 mm to 3.5 mm with a average change of .07 mm to 0.1 mm for Experiments 1A-1D. Considering the stimulus predominantly consisted of Fourier energy at lower spatial frequencies (0.5 cycles / deg), it is unlikely that a change of 0.1 mm will have a measurable reduction on contrast sensitivity. Small changes are characteristic of pupillometry studies involving such non-traditional stimuli. Indeed, the percent change in pupil surface area (4.0% to 6.9%) found in this set of experiments was consistent with previous effect sizes reported in the literature (Conway, Jones, DeBruine, Little, & Sahraie, 2008; Fukuda, Stern, Brown, & Russo, 2005; Hupe, Lamirel, & Lorenceau, 2009). Additionally, it is likely that the magnitude of this effect is underestimated. The dynamical nature of the pupil results in an inherently noisy system. Consequently, this low signal to noise ratio requires the averaging of multiple trials. Since the time course required for the allocation of attentional resources will vary across trials, due to delays or anticipatory

effects, these resulting differences in phase will damp the signal and, therefore, magnitude effects will be reduced.

A consistent finding that has emerged from the literature is that attention can increase spatial resolution (Balz & Hock, 1997; Carrasco & Yeshurun, 2009; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 1999). While previous authors have described an increase in spatial resolution under focused attention, as mediated through cortical processing, this experiment introduces another means through which these attentional effects can be implemented--through the pupil. Subcortical areas, such as the superior colliculus and pulvinar, have been linked to the control of spatial attention, particularly for overt re-orientation tasks (Ignashchenkova, Dicke, Haarmeier, & Their, 2004; Shipp, 2004) but have not been implicated directly in spatial resolution. The results from this study therefore suggest a subcortical mechanism mediating attentional spatial resolution effects.

Given that broadly spread attention increases the relative sensitivity of large receptive fields and narrowly focused attention increases the relative sensitivity of small receptive fields (Balz & Hock, 1997), the results indicate that these attentional effects can be mediated by the spherical aberration produced by the pupil. In this hypothesized pathway, shown in Figure 14, parietal activity, which has been associated with endogenous and exogenous attentional processing, (Corbetta et al., 1993; Nobre et al., 1997) sends feedback projections to the subcortical nuclei of the pupil resulting in the observed pupillary changes. Under broad attention, the corresponding

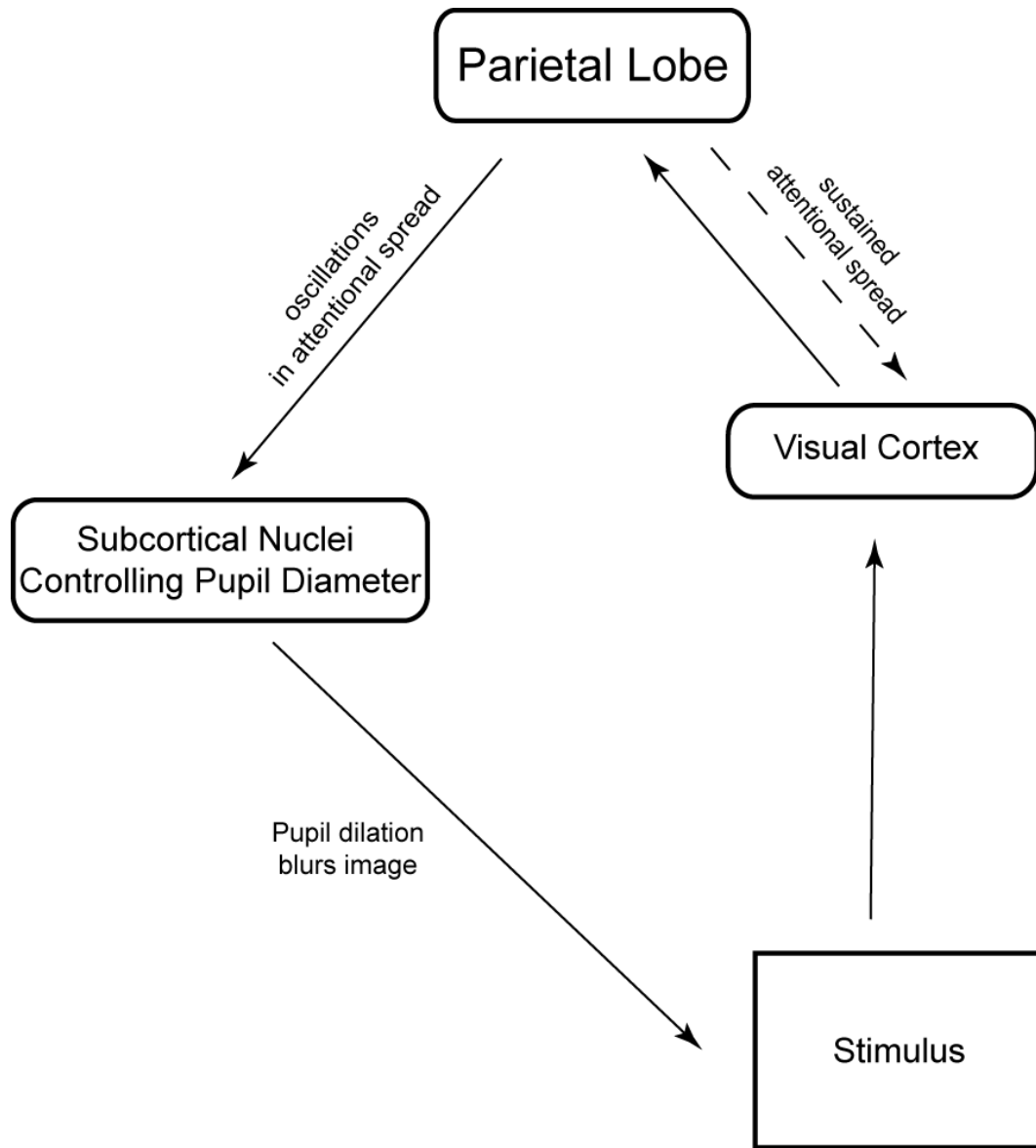


Figure 14. Pathways for oscillations in attentional spread versus sustained attention tasks. For attentional oscillations, parietal activity feeds back to the pupil potentially blurring the image and thereby reducing high spatial frequencies and decreasing the activation of small receptive fields in the visual cortex.

pupillary dilation observed would increase spherical aberration, blurring the image thereby reducing high spatial frequency information and decreasing the activation of relatively small cortical receptive fields compared to large receptive fields. This increased perception of low spatial frequencies would be beneficial in cases where attention is spread over a relatively large area. Alternatively, under narrow attention the resulting pupillary constriction reduces spherical aberration sharpening the image and preserving high spatial frequency information resulting in a relatively increased response of small receptive fields. That is, by controlling the amount of spherical aberration present in the retinal image the pupil is able to mediate receptive field activation.

The pupillary response found in this study does not indicate that a subcortical mechanism underlies all types of attentional tasks. Indeed, the methodology utilized in these experiments may be necessary to obtain pupillary oscillations. That is, attentional oscillations may invoke the pupil while the other attention tasks described in the literature (i.e. spatial precueing task for target detection) are not mediated subcortically, but entirely by V1. It is evident from the control conditions, where participants maintained sustained attention (broad-sustained or narrow-sustained), that at least for this type of task, subcortical mechanisms are not mediating attention. Further research will investigate the extent to which pupillary responses are specific to this form of methodology or generalize to other attentional tasks such as discrete detection and discrimination tasks.

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