

Attentional Effects on Motion Processing

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Abstract

In the last decade, much has been learned about the influence of attention on visual motion processing. Many studies have shown that directing spatial attention to a motion stimulus or attending to a particular feature of a motion stimulus significantly alters the processing of that stimulus. In this review, we begin by discussing results from human psychophysical experiments investigating the effects of attention on motion perception. This is followed by a summary of single-unit neurophysiological experiments in monkeys and functional magnetic resonance imaging (fMRI) studies in humans investigating the effects of attention on neural motion responses. In the last section, we discuss the results of experiments that have attempted to establish links between psychophysical and neural effects of attention.

Introduction

The ability to detect and discriminate visual motion has played a critical role in evolutionary survival, for example, by allowing for the detection of prey/predators and by providing information essential in guiding self-locomotion. Over the last several decades, a wealth of studies has elucidated the mechanisms underlying different aspects of motion processing, ranging from low-level to high-level motion phenomena. In the last several years, researchers have begun to ask how attention influences motion processing. Below, we review this literature by summarizing results from psychophysical studies (in humans and monkeys), neurophysiological studies (single-unit recordings in monkeys and fMRI in humans), and the efforts that have been made to establish links between the two.

I) Psychophysical Studies

Psychophysical studies of attentional influences on motion processing have focused on the effects of *selective spatial* attention, *divided spatial* attention, and *feature-based* attention, which are addressed in turn below.

A) Selective Spatial Attention

One clear example of the effects of spatial attention on perceptual motion processing comes from a study by Chaudhuri (1990), demonstrating that diverting attention away from a motion stimulus (by requiring subjects to perform a difficult letter task at the center of gaze) significantly diminishes the motion after-effect resulting from that stimulus. This finding suggests that attention serves to enhance the sensory processing of motion signals at a relatively early level in visual processing. More recently, Dobkins & Bosworth (2001) used a spatial pre-cueing paradigm to investigate the effects of spatial attention on coherent motion thresholds. In these studies, visual performance was compared under conditions in which a spatial pre-cue directed subjects' attention to the location of a to-be-presented motion stimulus versus when no pre-cue was provided. Here, a small but significant benefit of pre-cueing was found for short stimulus durations (<150 ms). In line with the previously-mentioned effect of attention on the motion after-effect, this result suggests that directing attention to a motion stimulus may enhance the sensory processing of that stimulus (but see Lu, Liu & Doshier, 2000 for results suggesting minimal effects of attention on *contrast sensitivity* for moving stimuli).

The above-mentioned studies all employed stimuli defined by luminance motion. More recently, the effects of spatial attention have been investigated for chromatic (red/green, isoluminant) motion (Thiele, Rezec, and Dobkins, 2001). Results from these experiments show that removing spatial attention from a moving stimulus (by requiring subjects to perform a difficult letter task at the center of gaze) affects luminance and chromatic motion processing equally. Although these findings suggest no greater effect of *spatial* attention on chromatic motion, other studies have argued that *feature-based* attention plays a special role in mediating chromatic versus luminance motion processing (see Thiele, Rezec, and Dobkins, 2001 for discussion).

B) Divided Spatial Attention

In contrast to *selective spatial* attention studies, *divided* attention studies address how dividing attention across multiple stimuli in a display affects stimulus processing. Dobkins and Bosworth (2001) investigated divided attention effects on motion processing by employing a "set-size effects" paradigm (see Figure 1A). In this study, subjects' coherent motion thresholds

obtained for a “target” motion stimulus presented amongst three confusable noise “distractors” (set-size = 4) were compared to thresholds obtained for a target motion stimulus presented alone (set-size = 1). Although the addition of distractors was found to impair motion performance significantly, these set-size effects could be accounted for by a simple model based on signal detection theory, which assumes *unlimited* attentional capacity such that the quality of sensory processing does not decline as the number of items in the visual scene increases (see Figure 1B). Rather, this model demonstrates that visual performance worsens with increasing set-size because the presence of distractors increases the probability of an error occurring at the *decision level* (see Palmer, 1994, for similar effects of divided attention in other domains of vision, e.g., orientation and color). In sum, these results suggest that attention can be divided across multiple moving stimuli simultaneously without any limitations on sensory processing, *per se*.

Interestingly, results from a recent psychophysical study have suggested that attention to multiple motion stimuli may not be *evenly* divided across space; there appears to be a greater weighting of attention in the inferior, as compared to the superior, visual field (Rezec & Dobkins, 2004).

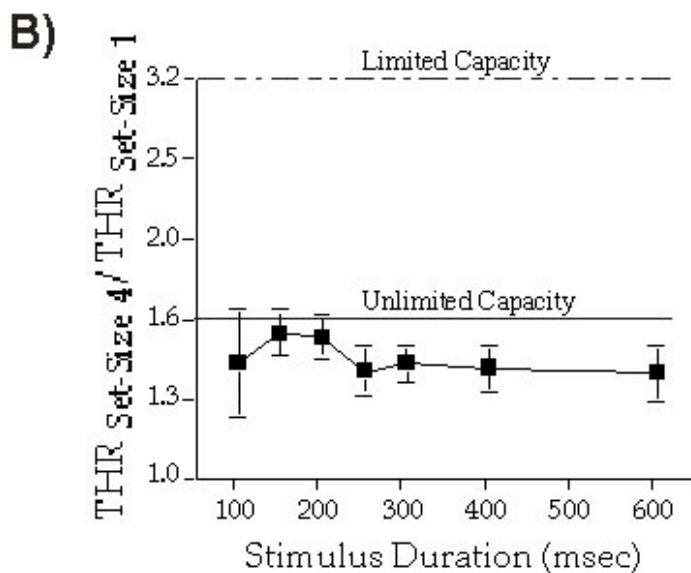
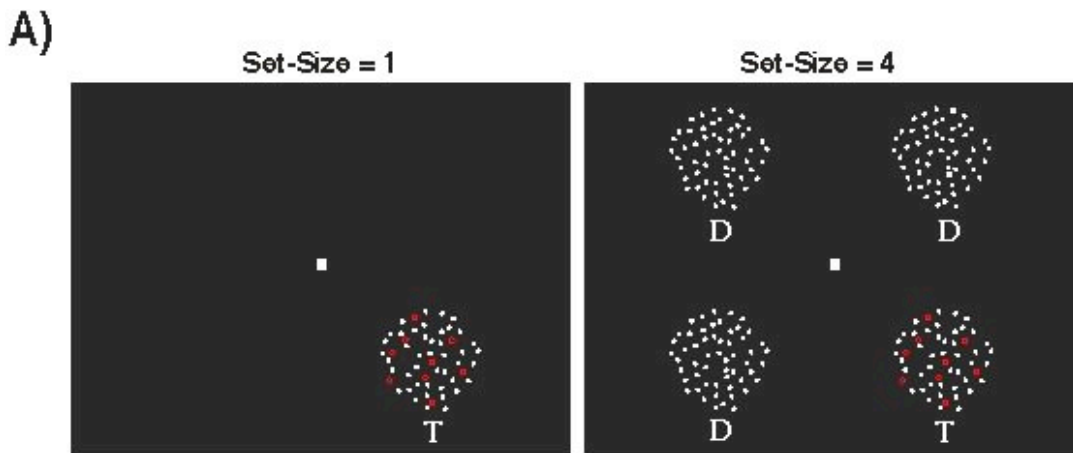


Figure 1. Effects of Divided Attention on Motion Processing (A) **Set-Size Stimuli and Design** (Dobkins & Bosworth, 2001). A proportion of dots (i.e., “signal” dots, shown here in *red*) move in a coherent direction (“leftward” or “rightward”) while the others (i.e., “noise” dots, shown here in *white*) move in a random fashion (note, all dots were white in the actual display). The signal proportion is varied across trials to obtain a *coherent motion threshold* (i.e., the percentage of signal dots required to yield 75% correct discrimination). Thresholds are obtained for set-size = 1, where a “target” motion stimulus (T) is presented alone (*left panel*) and set-size = 4, where the motion stimulus is presented amongst three “distractors” (D) containing no motion signal (*right panel*). The motion target appears randomly in one of four regions of visual space (superior left, superior right, inferior left, inferior right). (B) **Set-Size Data**. Group mean threshold ratios (THR set-size1/THR set-size4) are plotted as a function of stimulus duration. Error bars denote standard errors of the means across subjects (n = 9). Threshold ratios are greater than 1.0, indicating better performance in the set-size 1 condition. Across all durations, threshold ratios fall extremely close to the predictions for an Unlimited Capacity model (solid line), yet far from the predictions for a Limited Capacity model, which assumes that the quality of sensory processing declines as the number of items in the display increases (dashed line).

C) Feature-Based Attention

In addition to the effects of spatial attention, other studies have investigated the effects of *feature-based* attention on motion processing. One way this has been addressed has been to present two moving stimuli superimposed (which controls for the effects of spatial attention), and require subjects to attend to one or the other. For example, Lankheet and VerStraten (1995) asked subjects to attend to one of two oppositely-moving (and superimposed) dot fields, and found that the motion after-effect produced by a subsequently-presented dynamic motion stimulus was in the direction opposite to the attended motion field (and see Alais and Blake, 1999 for a similar finding). This result demonstrates that simply shifting attention to a particular feature (*direction of motion*, in this experiment) within a given region of space can enhance the processing of that feature. More evidence for feature-based attention effects on motion processing comes from a recent study measuring speed discrimination (Saenz, Buracas, and Boynton, 2003). In this study, subjects were required to make concurrent speed discrimination judgments for two different motion stimuli presented at spatially separate locations. Performance on this task was significantly better when the two stimuli moved in the *same* versus *different* directions. These findings suggest that attending to a particular feature-- direction of motion-- facilitates the processing of other stimuli in the visual field containing the same feature (and see section IIB, *below*, for a neural correlate of these perceptual findings).

II) Neurophysiological Studies

Several studies have investigated the *neural* effects of attention on motion processing, both in macaque monkeys and humans, with the main focus on motion areas MT and MST. Complementing the psychophysical studies described above, these neural studies address the

effects of *selective spatial* attention and *feature-based* attention, which are addressed in turn below.

A) Selective Spatial Attention

1) Attentional Modulation of Neural Responses

The effects of spatial attention on neural motion processing have been addressed in several single-unit neurophysiological studies in macaque monkeys, which compare neural responses to a moving stimulus when spatial attention is directed to, versus away, from that stimulus. In these experiments, two spatially segregated moving stimuli are presented; one that the monkey is instructed (via a pre-cue) to respond to (and thus, by definition, *attend* to) and one that the monkey ignores. Using this paradigm, Seidemann and Newsome (1999) found that when both moving stimuli fell within a neuron's receptive field (one in the neuron's preferred, and one in the null, direction), attending to the preferred motion stimulus increased the responses of MT/MST neurons by approximately 9%. The magnitude of the attention effect was roughly the same when one stimulus was placed inside, and the other outside, the receptive field. Using a similar paradigm, Treue & Maunsell (1996,1999) found much larger attentional effects. When one moving stimulus was inside the neuron's receptive field, attention was found to increase responses by 20% in MT and 40% in MST. When both moving stimuli were within an MT neuron's receptive field (one in the preferred, and one in the null, direction), attention increased responses by 70% in MT and 100% in MST. The discrepancy in magnitude of attentional effects between the Treue & Maunsell and Seidemann & Newsome studies may be due to stimulus or task differences between the two. For example, the task used in the Treue & Maunsell studies may have involved the additional recruitment of *feature-based* attention, thereby resulting in greater overall attentional effects (see Treue & Maunsell, 1999 for discussion).

These effects of selective spatial attention revealed in single-unit studies are supported by results from fMRI experiments conducted in human subjects. For example, Rees et al., (1997) demonstrated that responses in area MT+ to a peripherally presented motion stimulus varied depending on how much attention was diverted away from the that stimulus.

In a more recent study, Cook and Maunsell (2002) investigated the effects of spatial attention by employing a valid/invalid pre-cue paradigm while recording from neurons in areas MT and VIP. On each trial, two spatially segregated "noise" stimuli appeared, only one of which (the target) would subsequently contain a coherent motion signal (and only one of which was presented in the neuron's receptive field). Monkeys were trained to detect, and respond to, the onset of coherent motion in the target. As a means of manipulating the amount of spatial attention placed on the motion target, the location of the target was validly cued 80% of the time. Thus, for the 20% invalidly-cued trials, the monkey's attention to the motion target was expected to be considerably less. In contrast to the aforementioned neurophysiological studies, the advantage of the valid/invalid pre-cue approach is that it allows behavioral performance to be measured for both well- and *poorly*-attended stimuli, and thus allows for direct comparisons between psychophysical and neural effects of attention. In area MT, neural responses were approximately 18% greater in the well-attended (i.e., valid pre-cue) than in the poorly-attended (i.e., invalid pre-cue) condition, demonstrating neural effects of attention that are on the order of those previously observed (Treue & Maunsell, 1996, 1999; Seidemann & Newsome, 1999). In addition to reporting the increase in neural response due to attention, Cook & Maunsell also measured the "effective" change in motion signal strength due to attention, by determining the change in signal strength (measured in "percent coherent motion") of a well-attended stimulus

required to yield the same response as a poorly-attended stimulus. Here, they found that for MT neurons, attention increased the effective signal strength by roughly 3%. In VIP, attention increased the effective signal strength by a larger amount, approximately 14%. In order to determine which brain area mediated the psychophysical effects, these values in MT and VIP neurons were compared to simultaneously-obtained psychophysical data (see section IIIA, *below*).

2) Attentional Effects on Direction Selectivity and Contrast Coding

In addition to studies measuring the overall effects of spatial attention on neural responses, others have investigated whether selective spatial attention acts to sharpen the direction selectivity of MT neurons and whether attention serves to alter the “effective” luminance contrast of a moving stimulus (see [ATTENTIONAL MODULATION OF APPARENT STIMULUS CONTRAST]). With respect to *directional tuning*, it has been shown that spatial attention increases responses by a constant factor across the entire direction tuning curve (i.e., attention acts as a “response gain”), thereby producing no change in the sharpness of tuning (as measured by the bandwidth of the tuning curve). These findings indicate that attention influences MT responses to a moving stimulus independently of the direction encoding of that stimulus, i.e., that attention and direction do not interact. The pattern of results is quite different for the encoding of stimulus *contrast*, however. Martinez-Trujillo and Treue (2002) addressed this issue by measuring the effect of spatial attention for different contrasts of a moving stimulus. If attention and contrast act independently on neural responses, attention should increase responses by a constant factor across stimulus contrasts (i.e., the “response gain model” of attention). Alternatively, if attention and contrast interact, the relationship between attention and contrast should not be constant. Specifically, attention might serve to shift the contrast response function leftward, which would result in the largest effects of attention occurring for stimuli of intermediate contrasts. In this scenario, attention can be described as altering the “effective” contrast of the stimulus (referred to as the “contrast gain model” of attention). The results from this MT study support the contrast gain model, indicating that bottom-up changes in contrast are, in essence, interchangeable with top-down influences of attention.

B) Feature-Based Attention

The neural effects of feature-based attention on motion processing have been addressed in a single-unit study by Treue and Martinez-Trujillo (1999). Similar to the *spatial* attention experiments described above, these experiments presented two moving stimuli, one inside, and one outside, the receptive field of an MT neuron, with the directions of these two stimuli being either the same or opposite from one another. The relevant results are for the situation in which the monkey was required to perform a motion task on (and thus attend to) the stimulus outside the receptive field, such that responses to an ignored motion stimulus in the receptive field were recorded. Here, the results revealed larger responses to the ignored motion stimulus when the direction of that stimulus was the *same* as that of the stimulus the monkey attended to outside the receptive field (average increase = 13%). This finding thus reflects a feature-based attentional mechanism for motion that can exert effects of roughly the same magnitude as shifting spatial-based attention. Results from human fMRI studies have also demonstrated neural effects of feature-based attention. Saenz, Buracas, and Boynton (2002) obtained fMRI responses while subjects performed a speed discrimination task on one of two oppositely-moving (and superimposed) dot fields in a given region of space. Simultaneously, in a separate region of

space, an ignored moving stimulus was presented, moving in either the same or opposite direction as the attended stimulus. In line with the single-unit data of Treue & Martinez-Trujillo, and mirroring the results from their psychophysical paradigm (described above), fMRI responses in MT+ were found to be larger when the ignored motion stimulus moved in the same direction as the attended motion stimulus. Evidence for feature-based attention has also been provided in fMRI studies by O'Craven et al. (1997). In these experiments, responses in area MT+ to the same stimulus were modulated solely by having subjects shift their attention between a moving set of dots and a stationary set of dots that were superimposed.

III) The Relationship between Neural and Psychophysical Effects of Attention

While the effects of attention on both motion perception and neural responses in MT/MST have been amply demonstrated, few studies have attempted to establish direct links between neural and psychophysical effects. The most useful approach has been to quantify and compare neural and psychophysical effects within the same monkey subject or to compare neural effects in monkeys with psychophysical effects in humans, which are addressed in turn below.

A) Neural and Psychophysical Data obtained from the Same Monkey Subjects

To date, a single study has compared neural and psychophysical effects of spatial attention in the same monkey subject. The dearth of studies of this sort can be attributed, in part, to the fact that attention studies require a comparison between responses to attended versus *ignored* stimuli. While obtaining neural responses to ignored stimuli is easily achieved, the same is not true for perceptual responses; asking a subject to behaviorally respond to an ignored stimulus will likely make that stimulus no longer ignored. For human psychophysical studies, this is less of an issue since experimenters can explain the subtleties of “ignoring yet responding” to a stimulus, which is very hard to actuate in monkey subjects. Cook & Maunsell, 2002 circumvented this problem by employing a valid/invalid pre-cueing paradigm, which allowed them to obtain perceptual responses to both a well- and poorly-attended moving stimulus (see description of paradigm, *above*). Using this method, they compared the neural effects of spatial attention (in areas MT and VIP) with psychophysical effects obtained from the same monkey subject. For both neural and psychophysical data, attending to a motion stimulus was found to be equivalent to increasing the motion signal strength of that stimulus by a given amount. However, the magnitude of the psychophysically-derived change in effective signal strength (approximately 6%) matched *neither* the neurally-derived estimate in area MT or in area VIP; psychophysical effects were *larger* than neural effects in MT (3%) and *smaller* than those in VIP (14%). This result led the authors to speculate that area MST (which is situated between areas MT and VIP) may be the brain area whose responses correlate with (and thus underlie) the psychophysical effect of attention. These results and conclusions should be viewed with some caution, however, since the estimated magnitude of attention effect is likely to be influenced by the particular analysis parameters employed (e.g., linear versus non-linear functions fit to the data sets, and/or which response epoch was chosen for the measurements, see Cook and Maunsell, 2002 for discussion). Small errors in deriving these estimates of attention effect could result in fallacious matches/mismatches between neural and psychophysical effects.

B) Psychophysical Data from Humans Compared to Neural Data from Monkeys

In a recent human psychophysical study, Rezec, Krekelberg, and Dobkins (2003) quantified the effects of spatial attention on motion processing as a function of luminance

contrast, with the goal of comparing their psychophysical data with the neural results of Martinez-Trujillo & Treue (2002) in area MT (described above). Like the psychophysical design employed by Chaudhuri, 1990 (see above), this study compared the duration of the motion after-effect produced by a moving grating stimulus that the subject was allowed to attend to versus one that the subject ignored (by requiring subjects to perform a difficult letter task at the center of gaze during the presentation of the motion stimulus).

As expected, diverting attention away from the motion stimulus significantly diminished the duration of the motion after-effect produced by that stimulus, indicating that attention serves to alter the sensory processing of motion signals at a relatively early level in visual processing. And, the effect of attention was found to be roughly *constant* (about 1.4-fold) across a wide range of stimulus contrasts (4 – 80%), which included contrasts where the duration effect had saturated (see Figure 2). At first glance, these psychophysical results might appear consistent with the “response gain model”. However, the authors instead showed that a *contrast gain model* of attention -- one which incorporated the effects of *adaptation* to motion, in addition to the effects of attention to motion, could easily account for their psychophysical findings. Specifically, the model assumes that adapting to a moving stimulus shifts the contrast response function *rightward* (as has been shown for area MT neurons, Kohn & Movshon, 2002), and that this shift is greater under attend vs. ignore conditions. These psychophysical findings are therefore in line with the contrast gain effects of attention observed in area MT.

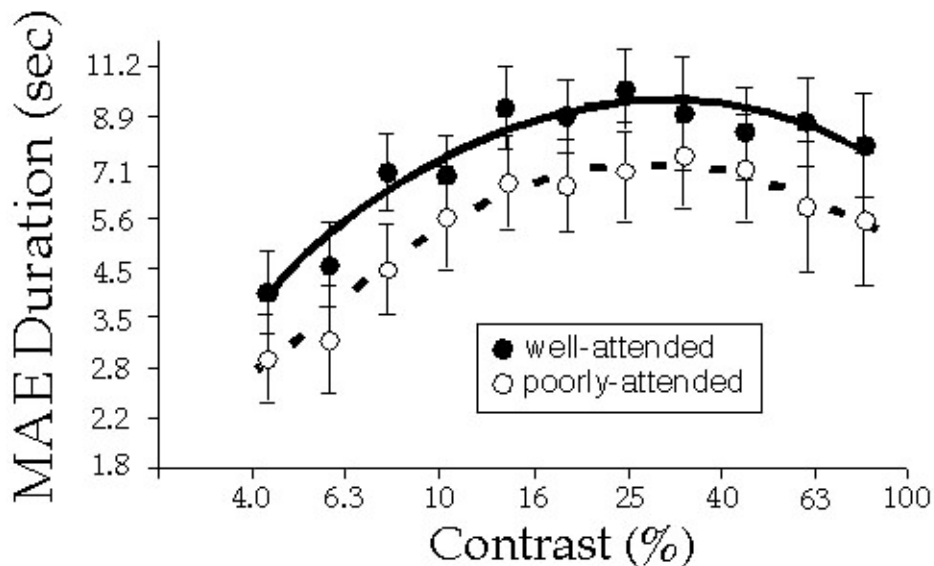


Figure 2: Effects of Attention as a Function of Luminance Contrast: Psychophysical Data.

Mean MAE durations (second) are plotted for well-attended (*filled circles*) and poorly-attended (*open circles*) moving grating stimuli as a function of stimulus contrast (Rezec, Krekelberg, and Dobkins, 2003). Error bars denote standard errors of the means across subjects ($n = 6$). The effect of attention obtained by dividing MAE duration for well-attended stimuli by that for poorly-attended stimuli was 1.4-fold and did not vary significantly as a function of contrast ($p = 0.23$). A model incorporating the effects of *adaptation* to motion, in addition to the effects of attention to motion, suggests that the data are consistent with the “contrast gain model” of attention (see text for details).

Conclusions

The psychophysical and neural studies described above provide the first glimpses into how and which areas of the brain may mediate the effects of visual attention revealed perceptually. However, since attentional effects are observed within several different cortical areas along the motion pathway (e.g., MT, MST and VIP), it is perhaps naïve to believe that a single brain area underlies the perceptual effects. Rather, perceptual effects may be mediated by joint activation in several brain areas and/or the contribution of different areas may be weighted depending on the particular task at hand. Future experiments will continue to elucidate the relationship between neural and psychophysical effects of attention on motion, and other aspects of visual, processing.

References

- Alais, D. and R. Blake (1999). Neural strength of visual attention gauged by motion adaptation. *Nat Neurosci*, 2, 1015-8.
- Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature*, 344, 60-2.
- Cook, E.P. and J.H. Maunsell (2002). Attentional modulation of behavioral performance and neuronal responses in middle temporal and ventral intraparietal areas of macaque monkey. *J Neurosci*, 22, 1994-2004.
- Dobkins, K.R. and R.G. Bosworth (2001). Effects of set-size and selective spatial attention on motion processing. *Vision Res*, 41, 1501-17.
- Lankheet, M.J. and F.A. Verstraten (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Res*, 35, 1401-12.
- Lu, Z.L., C.Q. Liu, B.A. Doshier (2000). Attention mechanisms for multi-location first- and second-order motion perception. *Vision Res*, 40, 173-86.
- Kohn A. and J.A. Movshon (2003). Neuronal adaptation to visual motion in area MT of macaque. *Neuron*, 39, 681-91..
- Martinez-Trujillo, J. and S. Treue (2002). Attentional modulation strength in cortical area MT depends on stimulus contrast. *Neuron*, 35, 365-70.
- O'Craven, K.M., B.R. Rosen, K.K. Kwong, A. Treisman, R.L. Savoy (1997). Voluntary attention modulates fMRI activity in human MT-MST. *Neuron*, 18, 591-8.
- Palmer, J. (1994). Set-size effects in visual search: the effect of attention is independent of the stimulus for simple tasks. *Vision Res*, 34, 1703-21.
- Rees, G., C.D. Frith, N. Lavie (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science*, 278, 1616-9.
- Rezec, A., B. Krekelberg, K.R. Dobkins (2003). Effects of attention and contrast on motion processing. *Journal of Vision*, Vol. 3 (*Vision Sciences Society Meeting, Sarasota, FLA*).
- Rezec, A & Dobkins, K. R. (2004). Attentional weighting: A possible account of visual field asymmetries in visual search? *Spatial Vision* (in press).
- Saenz, M., G.T. Buracas, G.M. Boynton (2002). Global effects of feature-based attention in human visual cortex. *Nat Neurosci*, 5, 631-2.

Saenz, M., G.T. Buracas, G.M. Boynton (2003). Global feature-based attention for motion and color. *Vision Res*, 43, 629-37.

Seidemann, E. and W.T. Newsome (1999). Effect of spatial attention on the responses of area MT neurons. *J Neurophysiol*, 81, 1783-94.

Thiele, A., A. Rezec, K.R. Dobkins (2002). Chromatic input to motion processing in the absence of attention. *Vision Res*, 42, 1395-401.

Treue, S. and J. C. Martinez-Trujillo (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, 399, 575-9.

Treue, S. and J.H. Maunsell (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature*, 382, 539-41.

Treue, S. and J.H. Maunsell (1999). Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *J Neurosci*, 19, 7591-602.