VISION RESEARCH

An International Journal for Functional Aspects of Vision

SPECIAL ISSUE
Visual Attention: Psychophysics, electrophysiology and neuroimaging

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Biochemistry & Cell Biology • Molecular Biology & Genetics
Anatomy, Physiology, Pathology & Pharmacology • Optics, Accommodation & Refractive Error
Circuitry & Pathways • Psychophysics • Perception • Attention & Cognition
Computational Vision • Eye Movements & Visuomotor Control

ISSN 0042-6989 | Volume 49 | Number 10 | 2 June 2009

Vision Research 49 (2009) 1033–1036

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Editorial

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1. Introduction

The appeal of visual attention and the attraction towards its study might be related to the unsettling observation, for a traditional vision scientist, that changing an observer's internal attentional state while keeping the retinal image unchanged can have such dramatic effects on 'sensory' neurons throughout visual cortex and on perceptual performance. Adding to the appeal is the tantalizing possibility that attention may provide a link with the constructs of awareness and consciousness. The study of visual attention retains an allure which has historically attracted some of the greatest thinkers in psychology, neurophysiology and perceptual sciences, including William James, Wilhelm Wundt and Hermann von Helmholtz, and which today still helps fill, wall to wall, the poster rooms of our annual vision meetings.

In the last five decades, Donald Broadbent, Anne Treisman and Michael Posner, among others, changed the field fundamentally by providing distinct theories and experimental tasks with which to explore what attention does and what perceptual processes it affects. In the last decade, there has been a growing interest in the mechanisms of visual attention and the field has expanded with an ever more increasing number of scientists bringing novel tools to the lab: new experimental paradigms, more complex stimuli, better psychophysical tasks, neurophysiology, neuroimaging, and computational modeling. Still, we are far from a consensus on how visual attention works. For this reason, the International Workshops on Visual Attention bring together scientists with different approaches – psychophysics, electrophysiology, neuroimaging and modeling – and competing views and theories with the aim of jump-starting dialogs that can bring about progress in our understanding of visual attention. The first workshop, in 2003, took us to a quaint Franciscan monastery in the Tuscan Town of San Miniato near Vinci, home of the great Leonardo (the resultant special issue was published in Vision Research 2004). This time around, in 2007, we gathered in one of the oldest historical buildings in Buenos Aires, located in the neighborhood of San Telmo, birthplace and still the epicenter of *Tango* (Buenos Aires Workshop on Visual Attention, March 11–15, 2007; http://www.psych.ucsb.edu/research/viu/workshop07).

This special issue on visual attention presents the work of most of the 40 participating scientists (Fig. 1) and addresses fundamental and timely questions in the study of visual attention, encompassing the mechanisms and brain areas involved in the allocation of covert attention, computational models that bridge across behavior and neuroscience methods, spatial vs. feature-based attention, the relation between eye movements and covert attention, the mechanisms and computations guiding saccadic eye movements during visual search, and the relation between visual attention and high-level cognitive functions such as object recognition and visual short-term memory.

2. Mechanisms, spatial extent and neural loci of spatial covert visual attention

Three papers investigate the spatial extent of attention, two focusing on selection and the other on attentional integration. *Datta and DeYoe* used functional magnetic resonance imaging (fMRI) to describe the topography of attention-related cortical activation throughout the central 28° of the visual field and compare it with previous models. They found that attentional activation was highest at the attended target but spread to other segments in a manner depending on eccentricity and/or target size. They proposed an "attentional landscape" model that is more complex than a "spotlight" or simple "gradient" model but includes aspects of both. Moreover, they showed that it is possible to determine accurately the target of attentional scrutiny from the pattern of brain activation alone. *Palmer and Moore* measured the sensitivity to distractors that are identical to the target and spatially close to a cued target location. They found large effects of target/distracter separation on performance. By varying the contrast and separation between target and distracters they are able to determine the size and profile of the spatial extent of attention and reject a contrast gain model based on their results. *Burr*, *Baldassi*, *Morrone and Verghese* investigated the effect of attention on the spatial extent of motion integration. They showed that humans can combine motion signals from cued regions in an optimal manner, even when the regions are distant from each other. They conclude that the spatial extent of motion integration is not compulsory, but is under the control of voluntary attention.

Two papers manipulated sensory inputs to examine the substrates and mechanisms of attention. *Mishra and Hillyard* used Event Related Potential (ERP) recordings for dichoptic vs. monocular viewing of dot surfaces to determine the stage in processing at which endogenous attentional selection occurs. Their results indicate that processing of the attended surface is biased at an earlier level in extrastriate visual cortex under conditions of inter-ocular vs. intra-ocular competition. *Lu*, *Tse*, *Dosher*, *Lesmes*, *Posner and Chu* used auditory and visual peripheral cues in conjunction with external noise to identify the mechanisms of attention. They found that cross-modal cueing of visual spatial attention with simulta-

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doi:10.1016/j.visres.2009.04.022

Fig. 1.

neous auditory cues is more effective than other cue types. In addition, they report that visual central pre-cuing (endogenous attention) excludes external noise while both visual and auditory peripheral pre-cuing (exogenous attention) additionally enhance the stimulus.

3. Computational models of covert attention

Three studies draw on computational theory to bridge neuroscience studies and relate neural measures of covert attention to behavior. *Eckstein*, *Peterson*, *Pham and Droll* used the framework of statistical decision theory and Bayesian ideal observer to develop biologically plausible versions of two classic theories of covert visual attention – limited resources/sensitivity change vs. differential weighting – and suggest that measured effects of visual attention (cues) on common neural variables (mean firing rate, Fano factor, tuning curve) fail to distinguish across the two classic theories of covert attention. They show that this can be achieved by appropriately measuring the area under the receiver-operating-characteristics (ROC) curve. *Boynton* reviewed seven studies of spatial and feature-based attention including monkey electrophysiology (areas V4 and MT) and function magnetic resonance imaging (fMRI) studies in human visual cortex to try to reconcile three different mechanisms for attention: contrast gain, response gain and a baseline shift in firing rate with attention. His reanalysis shows that a similar combination of attentional mechanisms can account for most of the previous results.

Pestilli, *Ling and Carrasco* implemented a population-coding model that estimates spatial attentional effects on population contrast response given psychophysical data. Consistent with their psychophysical data showing a different signature for the effects of attention on contrast sensitivity for endogenous (sustained, voluntary) and exogenous (transient, involuntary) attention, the results of their modeling show that endogenous attention changes population contrast response via contrast gain while exogenous attention changes population contrast response via response gain.

4. Visual attention and competition

Three studies focus on the idea of attention as a limited resources phenomenon and on the mechanisms underlying competition for resources. *Beck and Kastner* reviewed evidence and neural predictions for three fundamental principles of the biased competition theory of selective attention: the representation in the visual system is competitive, that top-down and bottom-up biasing mechanisms influence the ongoing competition, and that competition is integrated across brain systems. *Pastukhov*, *Fischer and Braun* investigated the conflict between the concept of separate forms of attention for different visual attributes and Duncan's integrated competition theory of visual attention. Using attention-operating-characteristics for four pairs of visual discrimination tasks they show that results conform to the predictions of visual attention as a single integrated resource. *Blaser and Shepard* measured the effect of attention on the motion aftereffect (MAE) to isolate the processing resources that accompany the allocation of visual attention from those underlying cognitive supervision – working memory, decision processes and awareness. They find that diverting attention from the adaptor does not affect the magnitude of the MAE and suggest that attention is allocated automatically to the adaptor, without requiring executive control or awareness.

5. The interaction of spatial- and feature-based attention

Three studies deal with the relation between the spatial- and feature-based attention systems. Two electrophysiological studies evaluate how spatial and feature-based attention affect neural responses. *Hayden and Gallant* showed that the responses of V4 neurons are consistent with independent processes and neural control systems mediating spatial and feature-based attention, respectively. They suggest that these two attention systems are controlled by distinct neural substrates whose effects combine synergistically to influence the responses of visual neurons. *Patzwahl and Treue* investigated the effects of feature-based attention on responses of direction-selective neurons in the middle temporal area (MT) of macaque visual cortex to attended stimuli inside the receptive field. They show that redirecting attention between the preferred and null direction of transparent random dot motion patterns causes a mean modulation of responses about half of what is observed when the two patterns are spatially separated, letting feature-based and spatial attention work in concert. This is consistent with models of visual attention (such as the feature-similarity gain model) that interpret the attentional modulation of a neuron as the combination of all attentional influences, treating stimulus location simply as another feature.

In the third study, *Ling*, *Liu and Carrasco* used a motion task and the equivalent noise paradigm, which measures performance as a function of external noise, to distinguish two mechanisms that have been proposed for how attention improves signal processing: gain and tuning. They link these psychophysical results to neurophysiology by implementing a simple, biologically-plausible model to show that spatial attention operates by boosting the gain of the cell population response while feature-based attention operates by additionally sharpening the tuning of the population response.

6. The relation between covert attention and eye movements

A number of studies investigate the relation between covert attention and eye movements. In an electrophysiological study, *Zhou and Thompson* used a spatial cueing task that dissociates saccade related neuronal activity in the frontal eye field (FEF) from covert attention. Monkeys' performance in a luminance discrimination task was better at cued locations than at unpredictable locations. They found selective anticipatory activity in many FEF neurons without any visual stimulus appearing in their response field that was not related to saccade choice or latency. Their findings provide evidence that FEF neurons serve an important role in covert (endogenous) spatial attention aside from the well-known role in saccade planning. *Gottlieb*, *Balan*, *Oristaglio and Schneider* reviewed recent evidence showing that LIP encodes a priority map of the external environment that specifies the momentary locus of attention and is activated in a variety of behavioral tasks. The priority map in LIP is shaped by task-specific variables. Gottlieb and colleagues suggest that the multifaceted responses in LIP represent mechanisms for allocating attention, and that the attentional system may flexibly configure itself to meet the cognitive, motor and motivational demands of individual tasks. *Moore and Chang* used receiver-operating-characteristic (ROC) analysis to quantitate how well V4 neurons discriminate stimuli targeted by visually guided saccades or ignored during saccades directed elsewhere. They found that discrimination was transiently enhanced prior to saccades to stimuli within the receptive field of the neuron whereas it was diminished prior to saccades elsewhere. The authors highlight the similarity of mechanisms driving covert spatial attention and the preparation of visually guided saccades in area V4.

Two papers examine the connection between selective attention and the receptive field remapping that is known to occur in conjunction with saccades. *Berman and Colby* focused their review on the representation of attended location in parietal cortex and earlier visual cortical areas and on the circuitry involved in the remapping target locations just prior to a saccade. They present evidence from experiments in monkeys and humans to show that the spatial representations are modulated not only by selective attention but also by the intention to move the eyes. They conclude that selective attention and remapping together contribute to the percept of spatial stability and that remapping is accomplished not by a single area but by the participation of parietal, frontal and extrastriate cortex as well as subcortical structures. *Melcher* investigated the effects of divided covert attention and saccadic eye movements on the magnitude of the tilt aftereffect. He found that divided attention and eye movements independently reduce the magnitude of the tilt aftereffect. He suggests that trans-saccadic perception is not limited to a single object but instead depends on the allocation of selective attention.

Three papers examine the spatial allocation of attention during eye movements. *Gersch*, *Kowler*, *Schnitzer*, *and Dosher* used an orientation discrimination task during sequences of saccades through an array of targets and distracters. They found that attention is distributed along the saccade path when the paths were marked by color cues whereas it was mostly concentrated around the goal of the upcoming saccade when the paths were followed from memory. The findings suggest that there are separate processes of attentional control during saccadic eye movements, one triggered by top-down selection of the saccadic target and the other by activation of visual mechanisms not directly linked to saccadic planning. *Findlay and Blythe* measured saccadic eye movements to a target in the presence of a nearby visually identical distracter. The authors found that the distracter only affected the accuracy of the saccadic targeting when it was placed on the same axis as that of the movement of the saccade. The authors suggest that a perceptual selection process, operating with higher resolution than that often associated with covert visual attention, can be used in the selection of saccadic targets. *Lovejoy*, *Fowler and Krauzlis* used a dual-task paradigm to investigate the spatial allocation of attention during smooth pursuit. Measuring the ability of human observers to correctly discriminate a probed character they found that the primary focus of attention during smooth pursuit is centered on the tracked target with no appreciable lead or lag. Spatial cues were only partly effective in directing attention to other locations in their task, and these cueing effects were biased for locations ahead of the tracked target.

7. Mechanisms and neural computations driving the deployment of saccades

Two computational papers examine the strategies driving eye movements. *Najemnik and Geisler* investigated a biologically-plausible model of eye movement planning during search that approximates the Bayesian ideal searcher, which maximizes the information gained on each saccade. They derive an entropy limit minimization searcher (ELM) that saccades to the maximum of the current posterior probability distribution for the target locations after the distribution is filtered by the retinotopic target detectability map. They show that when constrained by a human-like retinotopic map of target detectability and by human search error rates, the ELM searcher performs as well as the Bayesian ideal searcher, and produces fixation statistics similar to human. *Itti and Baldi* investigated the extent to which humans orient their gaze toward surprising events or items while watching television and propose a formal Bayesian definition of surprise in terms of posterior and prior beliefs of the world. They implement a simple computational model where a low-level, sensory form of surprise is computed by simulated early visual neurons and validate the model's prediction that surprising locations tend to attract human gaze.

Two papers examine the automatic and voluntary inhibition of saccades. *Theeuwes and Van der Stigchel* investigated the automatic inhibition of return (IOR) using a classic exogenous cueing task. They manipulate the delay between cue and target appearance and found that when observers responded manually, they were slower and less accurate when the target was presented at a cued rather than an uncued location (IOR). However, when observers had to move their eyes to a location in space, the authors found no saccade trajectory deviation away from the location due to IOR unless participants had to process the target presented at the inhibited location. Based on these findings, the authors suggest that inhibition resulting in IOR does not occur at the saccade map level but IOR seems to reduce the magnitude of signals going into the saccade map. *Montagnini and Chelazzi* investigated human oculomotor behavior in a Go–NoGo saccadic task in which the saccadic response to a peripheral visual target was to be inhibited in a minority of trials (NoGo trials). By analyzing the latency and the metrics of saccades erroneously executed after a NoGo instruction they found that introducing a probability bias in the random sequence of target locations improved the capacity to inhibit the impending saccade for the most likely target location. The authors conclude that the results challenge the notion of a central inhibitory mechanism independent from movement preparation and indicate that the mechanisms of action preparation and action inhibition interact dynamically.

8. Covert attention, objects, memory and load

Two psychophysical studies investigate object-based attention. *Yeshurun*, *Kimchi*, *Sha'shoua and Carmel* investigated whether the organization of visual elements into an object will automatically attract attention. In support of their hypothesis they find that indeed there is a performance benefit when targets appeared at the center of the object rather than outside, and that this automatic deployment of attention to the object is robust and involves a spatial component. *Liu*, *Dosher and Lu* examined the effects of judgment frames and judgment prediction on dual-object report deficit as an index of object attention. They find a modest deficit when the report requires a congruency judgment within one feature and a more substantial deficit when the report requires precision judgments. They interpret the dual-object deficit as a combined effect of multiplicative noise and external noise exclusion in dual-object conditions, both related to the effects of attention on the tuning of perceptual templates.

Two studies deal with the relation between covert attention and visual short-term memory. *Offen*, *Schluppeck and Heeger* probed the involvement of early visual cortex in visual attention and visual short-term memory using function magnetic resonance (fMRI). They placed different demands on attention and short-term memory while human observers viewed two visual stimuli separated by a variable delayed period. Early visual cortex exhibited sustained responses throughout the delay when observers performed attention-demanding tasks, but exhibited no significant activity when they performed a task that required short-term memory. These findings suggest that different computational mechanisms underlying the two processes. *Smith*, *Lee*, *Wolfgang and Ratcliff* investigated the behavioral effect of a simultaneous and delayed mask on the detection of a radial frequency stimulus. They find large cueing effects in the delayed mask condition and small cueing effects for simultaneous condition, replicating previous findings with sinusoidal gratings. The data are well described by a model in which masks affect the informational persistence of stimuli and cues affect the rate at which stimulus information is transferred into visual short-term memory.

Giesbrecht, *Sy and Lewis* tested the common assumption in attentional blink phenomena (AB) that the unattended information is processed to the post-perceptual level prior to selection for access to consciousness. They test the assumption by manipulating the perceptual load of the first target task (T1). They found that the T1-load increased the severity of the attentional blink suggesting that selection during the AB is not fixed at the post-perceptual stage, but rather that the stage at which selection occurs during the AB is flexible.

9. Concluding remarks

Finally, but most importantly, the papers in this issue reflect the fruit of the exchanges in those five late summer days and nights in Buenos Aires: thinking that only comes about through face to face interactions, thirty minutes of back and forth uninterrupted discussion, urgent requests for clarification of terminology and concepts, questions followed by arguments and counter-arguments, questions followed by moments of silence, empty looks at the ceiling and head scratching, and animated dinners, where the scientists specializing in different approaches agree, at least, to identify the right questions. We believe that bringing together scientists from many complementary disciplines – psychophysics, primate neurophysiology, oculomotor research, functional imaging and computational neuroscience – will continue to advance our knowledge and understanding of the mechanisms of attention and to foster multidisciplinary collaborations. We thank those who attended the workshop, whose presentations and discussions made it such a success, and particularly those who have also contributed to this special issue. We hope that the papers in the special issue will motivate many discussions and future endeavors in the study of attention.

Acknowledgments

We are grateful to the International Brain Research Organization (IBRO) and Argentina's Centro Nacional de Investigaciones Cientificas (CONICET) for providing financial support for the meeting, the Zanjon de Granados for providing the splendid venue for the workshop, and the local organizing committee, Elisa Colombo and Jose Barraza from the Luminotecnia, Luz y Vision Institute at the National University of Tucuman.

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