

# Reshaping neuronal representations of visual scenes through attention

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## Abstract

The sensory systems supply the information that is used to build a representation of our external world. However, the amount of information provided by highly evolved sensors such as the eyes of higher animals, exceeds the nervous system's capacity. Attention serves as one of the main selection mechanisms that allows these animals and humans to concentrate processing resources on the most relevant information. Here we review selected findings and present some of our own data in macaques about how this selection process effectively and often without the individual's awareness prevents irrelevant information from reaching later stages of processing.

**Key words:** Attention, contrast, illusions, electrophysiology, monkey, visual cortex, motion.

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Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seems several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others.

(William James, 1890,  
*The Principles of Psychology*)

Our senses are the design of eons of evolution. They have evolved not primarily to give us *accurate or complete* information about the world but to supply us with *useful* information. This distinction might seem subtle since information is normally only useful if it is accurate. But the difference between accurate and useful information becomes particularly obvious if we consider the role of attention. Attention is an important part of everyday life. We use it to concentrate on aspects of our sensory input that we deem worthy of further processing. Without such a selection process our sensory systems would be inundated with information. Instead, only a small fraction of the information received by our sensory organs reaches awareness. This small fraction does not represent an accurate representation of the world but rather is the result of the application of two processes, namely, the attentional selection and the attentional weighing of sensory input.

The purpose of this chapter is to present a few examples of how attention shapes the internal representation of the external world generated from the information supplied by our sensory organs. Obviously this cannot be an exhaustive treatment of this issue but rather it is a collection of examples from psychophysics and physiology, that concentrates on the role of attention in the *visual* system.

The chapter should give the reader a sense of how attentional modulation enhances the representation of attended elements of our world and suppresses information from unattended stimuli. The studies presented here will also show that some of these attentional processes are hidden from conscious experience, leaving us to underestimate attention's influence on everyday perception.



## "THE WORLD AS OUTSIDE MEMORY"

We normally are aware of the effort of attending, i.e., of concentrating our attention on a particular sensory detail and experiencing the *increase* in detailed information obtained from attended features. The latter is introspectively the main reason for directing attention in the first place. What we are much less aware of is the *loss* of information from unattended aspects of a visual scene. This loss should degrade our internal representation of our environment. But while we generally concentrate on just a few details of any given scene we still feel that our internal representation has information about many details to which we never paid attention.

In a series of experiments O'Regan, Rensink, and their colleagues investigated the richness of internal representations of the visual environment and the role of attention in creating and maintaining those representations. For this purpose they developed a 'flicker' paradigm (Rensink, O'Regan, & Clark, 1997, 1999). Subjects were asked to detect the difference between two still images of a scene. The images alternated continuously until the observer responded and was then asked to verbally describe the change.

Figure 1 shows the basic paradigm and examples of the image pairs used. The difference between the images could be in an aspect of central interest (Fig. 1b) or of marginal interest (Fig. 1c) to the viewer, and the changed object or feature could either be missing from one image, change colors between images, or change locations. In all cases, subjects had great difficulty detecting changes of marginal interest, requiring on average about 11 seconds (17 image alternations) before identifying the change. Changes of central interest were identified quicker (even though they were on average 20% smaller in area) but still required about 5 seconds (7 image alternations). These difficulties did not exist because the changes were too small to be noticeable: when the measurements were repeated with the blanks between images removed, the identification of both central and marginal interest changes occurred in less than 2 image alternations, requiring only about one second.

One might argue that the flicker paradigm, i.e., the rapid alternation of still images, is an artificial situation that is a poor representation of real-world experiences of the visual scene and tells us little about the richness of our internal representation of the real environment. This ar-



gument has been addressed in experiments where the changes occurred during eye blinks while viewing a picture (O'Regan, Deubel, Clark, & Rensink, 1999a) and using motion picture sequences (Levin & Simons, 1997) where changes were introduced at the moment of a camera cut. Again, subjects had a great deal of trouble noticing even large changes in salient objects. Similar results have been obtained with groups of isolated objects rather than whole scenes (Zelinsky, 1997) and with still image changes in the absence of blank intervals but accompanied by the brief appearance of several small patches covering parts of the image ("mudsplash" experiment, O'Regan, Rensink, & Clark, 1999b).

All these experiments combine the changes subjects are asked to detect, with transients in the visual input, either through whole image changes (such as in the blank intervals of the flicker paradigm, the occlusion of the images by an eye blink, or the movie cuts) or through other large changes in the image (as in the "mudsplash" experiment). If these transients are removed, as when presenting the flicker paradigm without the blank intervals, the changes become immediately apparent.

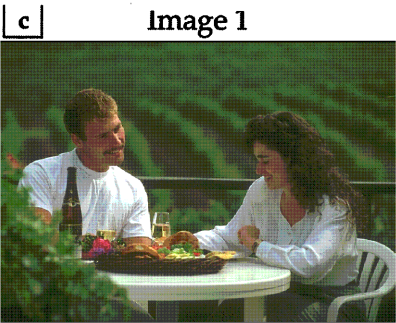
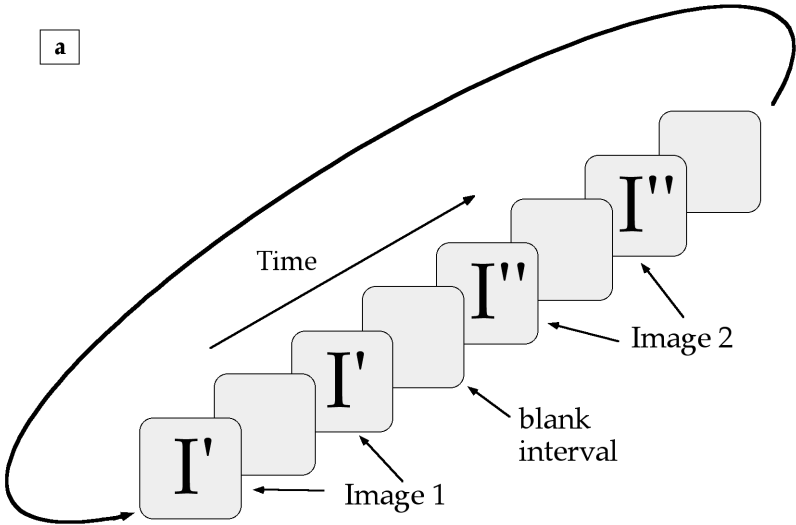
O'Regan and others have interpreted these results as evidence against a detailed internal representation of the visual environment. Rather, given that the physical environment is generally fairly stable, evolution seems to have opted for using "the world as an outside memory" (O'Regan, 1992). A memory or detailed representation is only built up for attended aspects of or objects in the visual scene. To detect changes in this environment, a system that pre-attentively notices changes in the visual scene and attracts attention, i.e., detailed analysis to the corresponding locations has been developed. But note that even at attended locations changes can go unnoticed, as observed by O'Regan and his

*Figure 1. Flicker paradigm.*

Panel A shows the prototypical sequence of images in a flicker paradigm. A pair of images (I' and I'') is each shown twice in rapid alternation with blank frames. The duration of individual image presentations is 240 ms and 80 ms for the blank intervals. The sequence is repeated until the subject reports the difference between image I' and I''.

Panel B shows an example of an image pair with a difference in an aspect of central interest (the helicopter seen through the window), while panel C shows an image pair with a difference in an aspect of marginal interest (the railing in the background). In both of these examples, the position of the object was changed but other changes were also used in the experiments.







colleagues (O'Regan et al., 1999). They monitored the subjects' gaze positions, i.e., which part of the image they were foveating, during experiments where scene changes were applied during blinks. In almost 50% of the cases, subjects were looking (and therefore most likely attending) within  $1^\circ$  of the change at the moment the change occurred. This suggests that even at the attended location, attention is directed at only a subset of the features (form, color, motion, etc.) at that location.

In summary, these experiments suggest that a large proportion of the visual information received by the eyes is not processed, and that the visual system combines an automatic system for detection of transients with the illusion of a rich and detailed internal representation of our environment.

### ATTENTION AS A NON-UNITARY PROCESS

The experiments described above might support the notion of a single "spotlight of attention" that is directed towards the current area of interest in the visual field. While many studies support such a notion (Eriksen & St. James, 1986), and demonstrate that this locus of attention can be moved rapidly and independently of any eye movements (Saarinen & Julesz, 1991), information from outside this region of focal attention can be processed beyond the simple detection of transients. Pylyshyn and his colleagues demonstrated the ability to track several items moving among identically-shaped distractors (Pylyshyn & Storm, 1985). In their experiments, subjects fixated a central fixation point and were presented with ten identical moving white X's one to five of which were designated as targets. After several seconds of Brownian-like, pseudo-random movement, a marker was flashed at the location of one X and the subjects had to respond if the X was a target. The accuracy of responding to target flashes (and of withholding responses to flashes at distractor locations) decreased as the number of targets increased, but was above 80% even for 5 targets. Additional experiments demonstrated that an increased size of the focus of attention encompassing all tracked objects could not be the basis of this phenomenon, since subjects were not more sensitive to changes in items lying within the polygon formed by the targets compared to changes in items outside the polygon. While Pylyshyn and his colleagues argued that the indexing and tracking of objects is a *pre-attentive* process, they were also able to show that



attention can be allocated to multiple locations. They designed an experiment using the line-motion illusion reported by Hikosaka, Miyauchi, and Shimojo (1991). The illusory line motion phenomenon occurs when attending to a location induces the perception of motion of a line that is presented with that location as one endpoint. In a typical experiment, a spatial cue is presented first, in order to draw the subjects' attention to its location. Then, after a brief inter-stimulus interval the line is presented all at once, but instead of perceiving that the complete line appeared instantaneously, subjects reported that the line was "drawn" starting at that end of the line closest to the cued location. Pylyshyn and Storm (1985) presented a ring of cues around a fixation point and after the cues were taken away, a line was presented connecting the fixation point to either a cue location or to a location halfway between two neighboring cue locations. The line illusion was observed significantly less frequently in the latter case, suggesting that attention was only allocated to cued locations. The strength of the effect diminished as the number of cues increased, supporting Pylyshyn's notion that there is a limited number of loci that can be indexed.

## ATTENTIONAL BLINKS

While the studies discussed above support the role of attention in selecting stimuli that compete for processing resources, there is also a body of evidence that attention operates over time too. Most notable in this context is the attentional blink or dwell time, so called because it involves the loss of information processing abilities for a brief period of time after the appearance of an attentionally demanding stimulus (Weichselgartner & Sperling, 1987; Raymond, Shapiro, & Arnell, 1992; Duncan, Ward, & Shapiro, 1994; Shapiro, Arnell, & Raymond, 1997). Similar to what happens in eye blinks, the "blindness" created by the attentional blink is not readily noticed introspectively. Figure 2 shows a classical paradigm and exemplary results. Subjects are asked to perform either two (dual-task) or just the second of two tasks (single-task) during the rapid serial visual presentation (RSVP) of individual stimuli. Figure 2b shows the results from an experiment where the RSVP consisted of a stream of random individual black letters. Target 1 was the only white letter in the stream and target 2 (if present) was an X (not used as a distractor or as target 1). Subjects were asked to report,



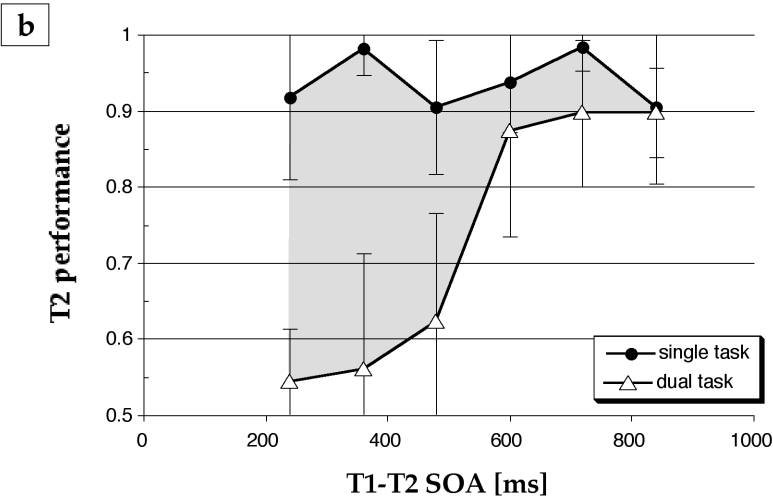
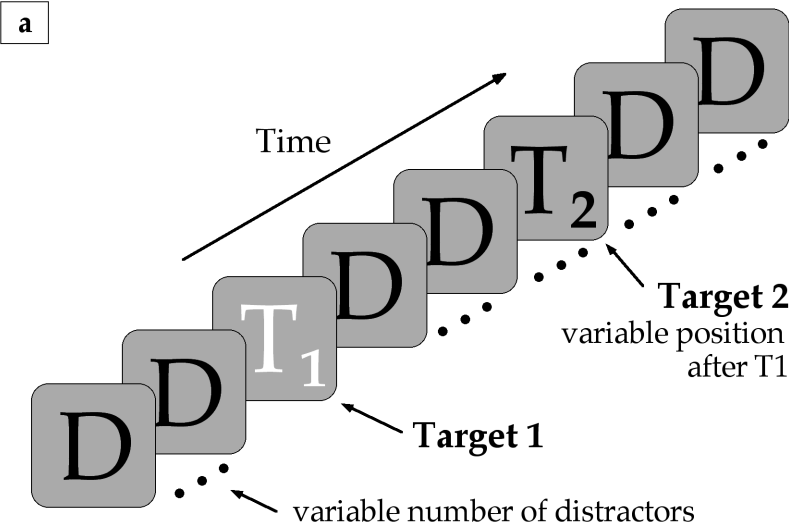
after a trial, if an X had been included in the RSVP, and in the dual task, subjects had to additionally report which white letter had been presented. Figure 2b plots the proportion of correct decisions in target 2 detection in the single task (upper curve, filled circles) and dual-task (lower curve, empty triangles) paradigms. The detection of the X was highly reduced when it appeared within about 500 ms after the white letter (target 1). The single task data showed that the RSVP per se did not cause this drop in performance since the single task curve showed no corresponding drop for short target 1-target 2 separations. These results were interpreted as evidence that attention-demanding tasks (such as identifying the white letter) interfere with the allocation of attention to a task occurring up to several hundred ms after the first task.

*Figure 2. Attentional blink paradigm.*

Panel A shows the prototypical sequence of images in an RSVP experiment designed to demonstrate the "attentional-blink". Here, letters were presented foveally in rapid succession on a computer monitor. Each letter was shown for 53 ms with 67 ms of blank screen between individual letter presentations. The dots are intended to indicate that a variable number of distractors could be presented before Target 1, between Target 1 and Target 2, and after Target 2. The distractor and Target 1 could be any letter other than an "X". Target 1 was the only white letter. Target 2 was an "X" and was present in half of the trials. In the single-task condition, subjects had to state after each series of letters whether an "X" had been present ("target 2 task"). In the dual-task condition, they also had to report which white letter was presented.

Panel B plots the mean correct response rate for 7 subjects in the target 2 task, i.e., judging whether a letter "X" was among the letters presented. Half of the trials contained this letter (always after the target 1 letter), and the other half included another letter in its place. Performance was plotted for trials containing the "X" as a function of its onset asynchrony (SOA) relative to target 1. The upper curve (solid circles) is the performance for the single-task experiments, i.e., when subjects did not have to identify target 1. The lower curve (empty triangles) plots the performance in the dual-task experiments. Error bars denote 95% confidence intervals around the means. The difference between the two curves (shaded area) is the loss in detectability of target 2 caused by performing the target 1 task, i.e., the "attentional blink".







The attentional blink is not restricted to letter tasks or the exact RSVP paradigm shown in Figure 2. Recent experiments have shown that presenting just two motion stimuli or a motion stimulus and a letter in rapid succession (each followed by a mask) also results in an attentional blink (Krope, Treue, & Husain, 1998). Thus, in time, just as in space, attention seems to be needed for visual information to be processed, and conversely, in the absence of allocation of attention to a stimulus, that stimulus appears not to reach higher levels of processing.

### **PHYSIOLOGICAL CORRELATES OF ATTENTIONAL MODULATION**

All of the effects of attention described above share the loss of processing of unattended features. What are its possible physiological correlates? Rensink and O'Regan's work suggests that the impression of a rich and detailed internal representation of our environment is an illusion, and that detailed information is only processed from the few attended features in our environment. This ever-changing weighing and selection mechanism does not seem to occur at the front end of the visual system. Our retinas offer a fairly homogenous and detail-rich matrix of information that, while being influenced by the eccentricity of the stimulation, does not seem to reflect an attentional selection process.

Traditionally, studies on the neuronal encoding of signals in the visual system have concentrated on sensory aspects, i.e., on how stimulus properties are encoded in the firing rates of neurons. This has led to the recognition that visual information processing to a large extent reflects a hierarchical system of cortical areas that extract increasingly complex information from the sensory signals arising in the retinas via a bottom-up process. More recently an increasing number of studies have addressed non-sensory, top-down influences on visual information processing. They have shown that, in addition to purely sensory processing, representations in the visual cortex can be profoundly influenced by the organism's behavioral state, of which attention is an important component (e.g., Moran & Desimone, 1985; Treue & Maunsell, 1996). The interplay between bottom-up sensory information and top-down effects of attention is likely to be an important aspect of cortical processing.



Here we will present one example of such attentional modulation, based on our work on attentional influences on visual motion processing in the macaque monkey cortex. We shall show that there are neuronal phenomena that could be the basis of the selective processing of visual information demonstrated in the psychophysical studies outlined above. Specifically we shall attempt to demonstrate the neuronal correlate of the invisibility of unattended aspects of the visual environment. We shall first review experiments demonstrating a neuronal correlate of attentional modulation, and then we shall suggest a way of transposing those attentional modulations into the sensory domain.

Attentional modulation of neuronal responses is a change in a neuron's firing rate as a function of the attentional state of the animal. To show such changes one has to make sure that they are not generated accidentally by changes in the sensory properties of the stimulation. Our experiments therefore always compare experimental conditions in which the sensory stimulation is identical but the attentional state of the animals is changed. Because the location of a stimulus on the retina is an important sensory parameter, all our experiments require the animal to maintain fixation on a stationary fixation point throughout the trials. This is monitored at a high resolution using the scleral search coil technique, and will insure that the receptive field of a given neuron remains at the same location in visual space.

We recorded responses from neurons in the middle temporal (MT) and medial superior temporal (MST) visual areas in the superior temporal sulcus of two behaving macaque monkeys using standard extracellular recording techniques (for additional details and methods, see Treue & Maunsell, 1996; Treue & Martinez Trujillo, 1999). Both areas contain a high proportion of direction-selective cells, and their sensory responses to moving stimuli have been studied extensively (for a review, see Logothetis, 1994). These cells show a tuned response to the direction of motion inside their receptive field, i.e., the response is strongest when the motion is in the cell's preferred direction and falls monotonically as the direction diverges from the preferred one, reaching a minimum for motion  $180^\circ$  from the preferred direction. These direction-tuned responses are thought to be the substrate of the visual system's encoding of motion information. They are generally bell-shaped and well fitted by a Gauss function (Snowden, Treue, & Andersen, 1992). Combining two moving stimuli inside the receptive field generally evokes a response approximated by the average of the



responses evoked by the individual motions (Snowden et al., 1991; Recanzone, Wurtz, & Schwarz, 1997). Here we review experiments that have demonstrated that attention enables the visual system to overcome this equipotent influence of various stimuli on neuronal responses.

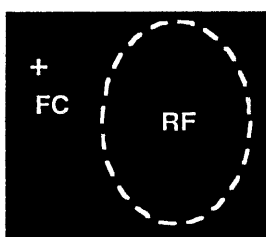
The stimuli were two random dot patterns (RDP) made up of small bright dots moving within a stationary virtual aperture on an otherwise dark computer monitor in front of the animal. Each trial began with the appearance of a small fixation cross on the screen (see Figure 3). After the monkey had foveated this cross, in two thirds of the trials (the "attend-in" trials) a single moving RDP (the "cue") appeared somewhere on the screen. The animal responded by touching a lever which caused the cue pattern to disappear. Within a few hundred milliseconds, two moving RDPs appeared, one (the "target") at the cued location and the other (the "distractor") right next to it. Both the target and the distractor started to move continuously at the same speed. One RDP (the "null pattern") always moved in the direction opposite to the cell's preferred direction, the 'anti-preferred' or 'null' direction, while the other RDP (the "tuning pattern") moved in one of 12 possible directions chosen to cover the range of possible directions evenly (0, 30, 60, ..., 300, 330°, with 0° denoting the preferred direction). Both the target and distractor positions were chosen such that the two stimuli were inside the receptive field of the cell under study. The animal's task was to attentionally track the target and to release the lever quickly when it transiently increased its speed or changed its direction. Since the change occurred after a random amount of time, the animal had to maintain attention on the target for the whole time. Sometimes the distractor changed first, but a response of the animal to that change ended the trial without a reward, providing a strong incentive for the animal to respond to changes in the target only. In the remaining third of the trials (the "attend-out" trials) the cue stimulus was a small square appearing on top of the fixation cross.

*Figure 3. Time course and stimulus layout of the experimental conditions used in the physiology experiments.*

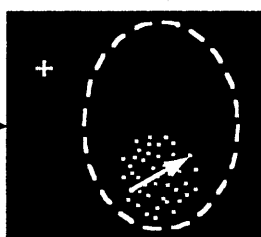
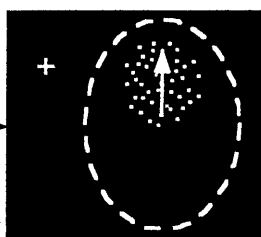
A trial started with the fixation acquisition phase. By foveating the fixation cross (FC) the monkey initiated the trial. This caused the appearance of one of three possible cues (a moving random dot pattern and one of two possible locations, or a colored square on top of the fixation cross) for 250 ms, indicating to the monkey the task for the selective attention phase. After a blank interval



Fixation  
acquisition  
phase



Cue phase



Selective  
attention  
phase



of 400 ms (during which only the fixation cross was on the screen) the selective attention phase, in which two moving random dot patterns were presented inside the receptive field, started. After a random interval of 500 to 3000 ms the luminance of the fixation point ("attend-out" trials) or the direction or speed of the target pattern changed (in the "attend-in" trials). Responding to this change (but not to changes in the other pattern) within a few hundred milliseconds triggered a reward for the animal. Throughout the trial, the animal had to maintain its gaze on the fixation cross.

The white arrows symbolize the direction of motion of the random dot pattern. Neither they nor the dashed ellipse denoting the receptive field (RF) were actually shown on the monitor. The tuning pattern could move in one of twelve directions, whereas the null pattern always moved in the cell's null-direction (upward in this example, but chosen individually for every cell). Random dot patterns were matched to the cell's preferred speed and positioned at about equipotent locations in the receptive field.



This served as an instruction to the animal to respond to a subtle luminance change on this square. The attend-out trials also included the presentation of the two moving RDPs inside the receptive field. They included the attention-demanding task of detecting the luminance change to control the animal's attention. Without such a task the animal would be free to attend to whatever stimulus it pleased without the experimenter's knowledge.<sup>1</sup>

Throughout every trial, the animal had to maintain its gaze on the fixation cross. Only those portions of correctly completed trials before any RDP had changed were analyzed. This ensured that all trial periods analyzed represented identical sensory stimulations. By using tuning patterns moving in different directions, we were able to modulate the response of a given neuron. Since this sensory modulation was recorded for three attentional conditions, we were able to determine both the effect of moving the "spotlight of attention" into the receptive field as well as shifting it from the null pattern to the tuning pattern on the sensory responses.

Figure 4 presents the three tuning curves recorded from a typical MT neuron under these three attentional conditions. Like most cells we encountered, this neuron showed an intermediate level of response during the attend-out trials. When attention was switched into the receptive field, responses increased if the tuning pattern was the target and decreased if the null pattern (moving downward for this cell) was the target. These changes are a neuronal correlate of spatial attention. Attention seems to be able to reduce the influence of the unattended stimulus, thus increasing responses if the inhibitory null pattern is suppressed and decreasing responses when the tuning pattern is suppressed. On average we found a 31% increase over the attend-out responses when the target was the tuning pattern, and a 27% reduction in responses (i.e., of the sensory modulation) when the target was the null pattern. While this is a substantial change in neuronal responses that

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1. The exact task an animal is performing outside the receptive field can influence the response of the neuron to a stimulus inside the receptive field, demonstrating that attention does not only operate within the receptive field (for details, see Treue & Martinez Trujillo, 1999). Attending to a color change at the fixation point is the most neutral condition and was therefore chosen for the experiments presented here.



clearly demonstrates that the neural representations in MT and MST are influenced by the behavioral significance of the stimuli in the receptive field and not only by their sensory properties, the suppression of the unattended patterns seems far from complete.

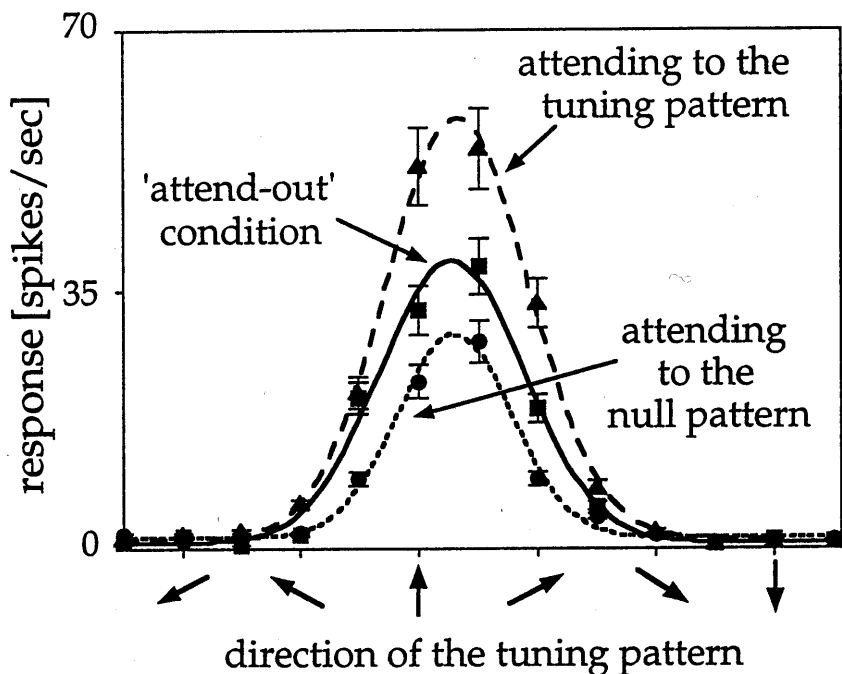


Figure 4. Example of the attentional modulation of an MT cell between the three attentional conditions used.

The solid line is a Gauss function fit over the responses of a neuron to various directions of motion of the tuning pattern when the animal was cued to respond to a luminance change at the fixation point. Similarly the other lines represent fits over the responses using the identical stimuli inside the receptive field but with the animal directing its attention into the receptive field, either to the tuning pattern (dashed line, direction of tuning pattern is shown along the x-axis) or to the null pattern (dotted line, for this cell the null pattern moved downward). Clearly, directing attention to the tuning pattern increased responses (by about 50% for this neuron), whereas directing attention to the null pattern decreased responses (by about 30%).



## "TITRATING" THE ATTENTIONAL MODULATION WITH CHANGES IN CONTRAST

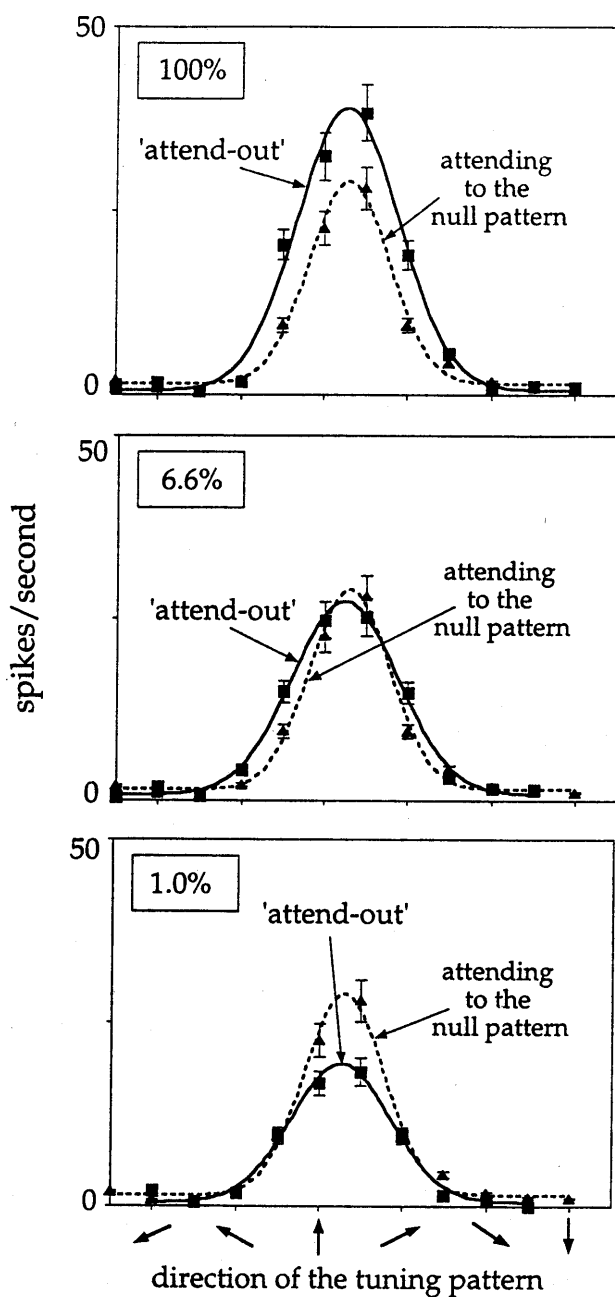
It is difficult to establish the level of neuronal response suppression that would correspond to the psychophysical effects of attention discussed above. The psychophysical experiments suggest that unattended stimuli become largely invisible. By attempting to translate the attentional suppression we observed into a measure of stimulus visibility, we were wondering whether the attentional modulation could be mimicked by a reduction in stimulus visibility in the absence of changes in the attentional state. In our physiological experiments described above, we determined how much a change in attentional state could change a neuron's firing rate. Now we tried to determine if and how much of a change in stimulus visibility would create the same modulation in the absence of a change in attentional state.

As discussed above, attention seems to suppress the influence of unattended stimuli. Therefore the flattened tuning curve observed when the animal was attending to the null pattern (dotted curve in Figure 4) might reflect the reduced influence of the unattended tuning pattern that supplies the sensory modulation. We therefore attempted to mimic this attention effect with a reduction in the luminance of the corresponding stimulus. More specifically, we recorded neuronal responses in a variant of the attend-out condition used before. The only difference was that we reduced the luminance levels of the tuning pattern in an attempt to create response levels that resembled the ones recorded in the corresponding attend-in conditions, i.e., when the null pattern was the target.

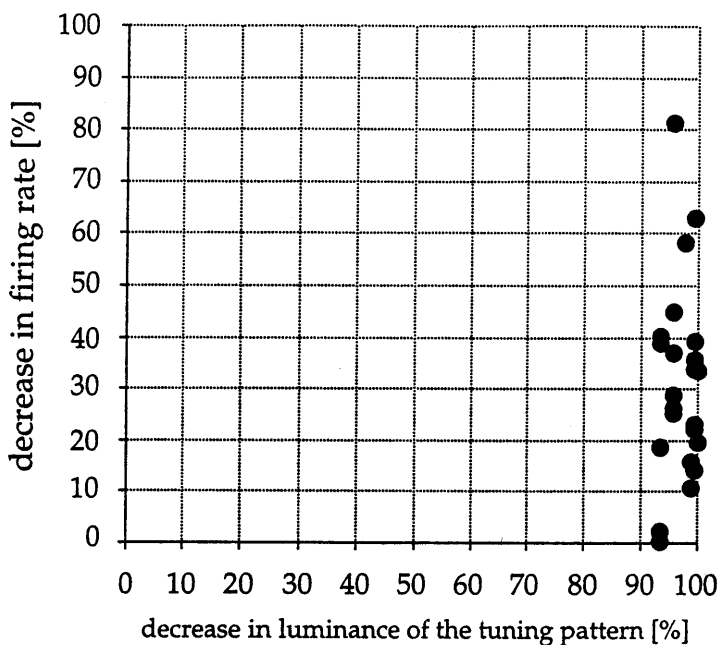
*Figure 5. Attentional titration experiment: Effect of attention and of reducing luminance on the response of one MT cell (the same as shown in Figure 4).*

The top panel replots the attend-out responses and the responses when the animal was attending to the null pattern from the previous figure. The middle and bottom panels replot the attend-in curve from the top panel, i.e., with 100% luminance (the brightest luminance that could be achieved on our monitor) of both stimuli, and also show the responses in attend-out conditions where the luminance of the tuning pattern was reduced (to 6.6% and 1% of the maximal luminance, respectively). The data shows that the reduction of luminance lowered the height of the cell's tuning curve. Around a luminance of 7% the attend-out tuning curve is similar to the attend-in tuning curve derived at full luminance.









*Figure 6. Scatter plot of attentional modulation and contrast modulation at the titration point for all cells.*

The x-axis represents the luminance reduction that is necessary (in the absence of a shift of attention) to achieve the same response modulation as the one caused by attention. A large x-value represents a cell where the tuning pattern's luminance had to be reduced so much that it became almost invisible. The y-axis represents the attentional modulation, i.e., the reduction in response when the animal attended to the null pattern inside the receptive field vs. when attention was directed outside the receptive field (in this comparison all patterns have 100% luminance). A large y-value represents a cell with a strong attentional modulation. For example, a point with an x-value of 95% and a y-value of 25% represents a cell whose firing rate decreased by 25% when the animal directed its attention (but not its gaze) from the fixation point to the null pattern inside the receptive field. To achieve the same 25% reduction in firing rate while the animal kept attending to the fixation point, the luminance of the tuning pattern had to be reduced by 95%, i.e., to 5% of the value used for the previous measurement. All data points fell on the far right of the graph, indicating that luminance reductions of more than 90-95% were needed to equal the effect of directing attention towards the null pattern and away from the tuning pattern. This was true even for cells where the response modulation evoked by directing attention from outside the receptive field (solid curve in Fig. 4) to the null pattern inside the receptive field (dotted curve in Fig. 4) was small.



Thus the luminance of the tuning pattern was reduced so as to decrease the attend-out firing rate to the level observed when the target was the null pattern and both RDPs had full luminance.

Figure 5 shows the results with this approach for one neuron. In the three panels we replotted the tuning curve for the attend-in condition with the null pattern as the target (dashed tuning curve). The first panel also shows the response in the attend-out condition with both RDPs at full luminance (solid tuning curve). This condition is the same as the one shown in Figure 4. As demonstrated there, the attend-out condition led to a larger response, presumably because the processing of the tuning stimulus was not suppressed (as in the attend-in condition) and therefore was able to strongly modulate the response. The other two panels show the tuning curve in the attend-out condition with reduced levels of luminance (reduced to 6.6% and to 1.0% of the full luminance) on the tuning pattern, in an attempt to mimic the suppressing effect of attention on the processing of the tuning pattern when the null pattern was behaviorally relevant. The responses decreased with decreasing luminance until they fell below the levels of the attend-in tuning curve in the bottom panel. This means that for this neuron, the attentional modulation of switching from the attend-out condition to the target being the null pattern caused a reduction in distractor luminance of about 93%. We call the corresponding luminance level the titration point. A reduction in luminance of more than 90% makes the dots in the tuning pattern so dim that it becomes almost invisible. Figure 6 shows the *attentional* modulation (corresponding to panel 1 in Figure 5) and the *luminance* modulations necessary to match it for the 23 cells we recorded.

## SUMMARY AND DISCUSSION

Our physiological data demonstrate that it is possible to create changes in neuronal firing rate by changing the sensory properties of the visual input that are virtually indistinguishable from the changes caused by different attentional conditions. Furthermore these data show that attentional suppression of unattended stimuli, even when it results in only moderate changes in firing rate (average suppression of about 30% in the experiments presented here), can represent large changes (lumi-



nance reduction needed to reach the titration point of more than 90%) in the effective visibility of the unattended stimuli.

These findings are clearly consistent with similar results from experiments in areas along the temporal visual pathway (Reynolds & Desimone, 1997) and with the effects observed psychophysically. The psychophysical and physiological studies discussed here all point to a powerful influence of attention on the processing of sensory information. The same is true for a large number of studies using functional brain imaging techniques, all of which support the claim that without the allocation of attention, stimuli lose much of their ability to activate even sensory neurons, i.e., neurons that are considered sensory because they can be strongly modulated by sensory changes in the stimulus. These attentional effects in the sensory cortex and the similarity of attentional and sensory influences on neuronal firing rate might even suggest that the two aspects share neuronal mechanisms.

The convergence of data recorded in awake macaque monkeys regarding the influence of attention on the processing of visual information, and the data collected from human subjects using functional brain imaging and psychophysical methods, strongly suggest that even though selective attention is a complex cognitive function, it is not only present in humans but can be demonstrated in primates and presumably other animals. This suggests that monkeys and humans share an important and advanced aspect of visual information processing, allowing us to gain important insight into human vision through the study of non-human primates. Inversely, it seems reasonable to expect that scene perception in animals shows the same constraints imposed by attention as demonstrated in the flicker-paradigm and attentional-blink experiments in humans.

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## RÉSUMÉ

Les systèmes sensoriels fournissent les informations utilisées pour construire une représentation du monde externe. Toutefois, la quantité d'informations fournies par les organes sensoriels hautement évolués, tels que les yeux des animaux supérieurs, dépasse les capacités du système nerveux. L'attention est un des mécanismes de sélection qui permet aux animaux et à l'homme de focaliser les ressources de traitement sur les informations les plus pertinentes. Dans cet article, nous présentons quelques données issues de la littérature, ou de nos propres travaux sur le singe, montrant comment, souvent sans que l'individu s'en rende compte, ce processus de sélection empêche efficacement les informations sensorielles non pertinentes d'accéder aux derniers stades de traitement.

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