The dark side of visual attention

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The limited capacity of neural processing restricts the number of objects and locations that can be attended to. Selected events are readily enhanced: the bright side of attention. However, such focal processing comes at a cost, namely, functional blindness for unattended events: the dark side of visual attention. Recent work has advanced our understanding of the neural mechanisms that facilitate visual processing, as well as the neural correlates of unattended, unconscious visual events. Also, new results have revealed how attentional deployment is optimized by non-visual factors such as behavioral set, past experience, and emotional salience.

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Abbreviations
FEF   frontal eye field
V4   visual area 4

Introduction

In 1999 alone, 41,611 people were killed and over 3,200,000 people were injured in motor vehicle accidents across the US [1]. The majority of these accidents were due to human error, with inattention and fatigue cited as causal factors in a substantial proportion of these incidents [2]. These tragic statistics illustrate the real-world consequences of what we call the 'dark side' of attention. In the lab, one of the most striking demonstrations of such functional blindness is the failure of 58% of observers to see a gorilla in clear view thumping its chest, while subjects concurrently performed a challenging visual tracking task (Figures 1,3) [3]. In clinical settings, such functional blindness is commonly observed in neglect patients with damage to the frontal and parietal cortices. In many respects, functional blindness in normal observers appears to mirror the inability of neglect patients to attend to, and consciously perceive, events in their contralesional field. This suggests a link between specific brain areas and conscious, attentive vision [4•,5•].

Understanding the costs of inattention is complementary to the study of how attention facilitates perception. Here, we survey both aspects: the bright and dark side of attention. In addition, because visual selection is limited to such a thin sliver of incoming perceptual information, it is important to understand how attention can be optimally and quickly deployed to task-relevant objects. The final

A striking example of inattentional blindness. When attending to the players passing a ball amongst themselves, over half of the viewers failed to notice the man in the gorilla suit appearing in the middle of their game. Reproduced with permission from [3].

section of this review examines some factors that determine what people attend to.

The bright side of visual attention

Attending to a location or object modulates neural processing in an entire network of cortical areas [6•], facilitating perceptual processing [7,8], permitting tracking of an object's dynamic features and positions over time [9–11], and enabling perceptual awareness of attended events [4•,12]. Many recent findings have helped characterize the neural mechanisms for such attentional facilitation.

Consider how attention may enhance the detectability of relatively isolated target stimuli. This is particularly important when the sensory signal is weak. The ability to register a sensory input is determined by the strength of the neuronal response and the variability of this response. It turns out that the main effect of attention is to increase neural responses to attended stimuli [13–16]; the variability of neuronal responses (relative to response rate) does not change with attention [17]. In other words, attention serves to increase the signal, not to reduce the noise of neural responses. Attentional facilitation of neural signals appears to mimic the effects of increasing the sensory signal itself, for example by increasing contrast. Attention does not appear to change the tuning of cells, however. For example, the selectivity of visual area 4 (V4) neurons for orientation remained unchanged across increasing levels of attention [18]. Also note that attention only affects neural responses within a range of signal strengths. Attention has little effect to further improve the response to an oriented stimulus presented at maximum contrast [19].

Figure 2

Increased distractor interference on a target engaged the intraparietal sulcus and the lateral frontal cortex. During letter target identification, distractors that appear close in time, as backward masks, or close in space, as flanking masks, cause perceptual interference [28•]. Such distractor interference (relative to a low interference condition) is associated with increased activity in the intraparietal sulcus and the lateral frontal cortex, as shown by the red areas of fMRI activation. Reproduced with permission from [28•].

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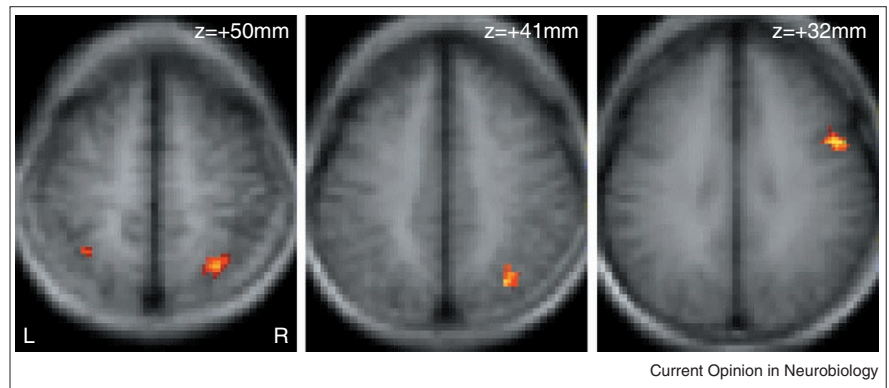
In addition to facilitation, attention serves to filter irrelevant distractors that compete for limited neural resources, especially when these appear close to a target stimulus [20]. Behaviorally, this situation causes lateral interference, reducing the visibility of the 'crowded' target [21,22•]. Neurophysiologically, the presence of both a distractor and a target within a neuron's receptive field introduces interference and ambiguity that is suppressed by attention [23–25]. In addition to these suppressive effects, recent findings also suggest that attention may amplify target signals appearing amongst distractors, by modulating the synchonization of neuronal firing to the target [26•,27].

Although flanker interference typically produces suppression of neural activity in early visual areas such as V4 [23–25], opposite effects are typically observed in frontal and parietal areas. When distractor interference on a target is increased, the right intraparietal sulcus and lateral frontal cortex (at the junction of the inferior frontal, middle frontal, and precentral gyri) show greater activation, as measured by functional magnetic resonance imaging (fMRI), shown in Figure 2 [28•]. This pattern of activity suggests that frontal and parietal regions serve to bias competitive interactions between targets and flanking distractors [29]. If so, tying up frontal control processes with a dual task should lead to larger distractor interference effects. Indeed, a recent study showed that increasing working memory load led to larger frontal activation and larger ventral (fusiform, lingual and inferior occipital cortex) activation in response to distractors that were to be ignored [30•]. Further evidence for this effect comes from the finding that damage to the dorsolateral prefrontal cortex was correlated with reduced neural activity in ipsilesional extrastriate cortex and impaired detection of contralesional visual targets [31]. These findings reinforce the hypothesis that frontal cortex regulates visual processing in posterior visual areas.

Another frontal area that plays an important role in attentional selection is the frontal eye field (FEF). Not only do FEF neurons reveal attentional discrimination of targets versus distractors with high reliability [32,33], but also microstimulation of FEF neurons facilitates target detection even when eye movements are not elicited [34]. Future research should reveal how frontal, parietal, and ventral areas coordinate their activity to enhance perception and reduce distractor interference [35,36].

The dark side of visual attention

The bright side of visual attention, facilitation of task-relevant information, comes at a cost and researchers have developed a lively array of paradigms to study perceptual deficits caused by inattention. Three of the most popular tasks are inattentional blindness, change blindness, and the attentional blink. Although not reviewed here, other new paradigms continually emerge to reveal the dark side of atttention [37•,38].

Inattentional blindness occurs when subjects fail to see a secondary event, such as a dot flashed on the computer screen, while performing another visual task [39]. Observers tend to miss the unexpected event (even when it is a gorilla!), but such errors are limited to the first trial of testing. Once subjects start expecting unusual events, they become readily detectable.

Change blindness, a failure to detect changes in the presence, identity or location of objects in scenes, is also strongest when subjects do not expect changes to occur. For example, over half of real-world observers failed to note a change in the identity of a person that they were conversing with, when the change was made during a brief occlusion (such as workers carrying a door between the conversing people) [40]. Unlike inattentional blindness paradigms, however, visually salient changes can be difficult to detect even when the observer expects and actively searches for such changes. For example in lab tasks, subjects may take several seconds to note a jet engine appearing and disappearing from the wing of a Boeing 747 jetliner [41].

Finally, the attentional blink paradigm reliably blinds observers by taxing their attention to the limit [42,43].

Figure 3
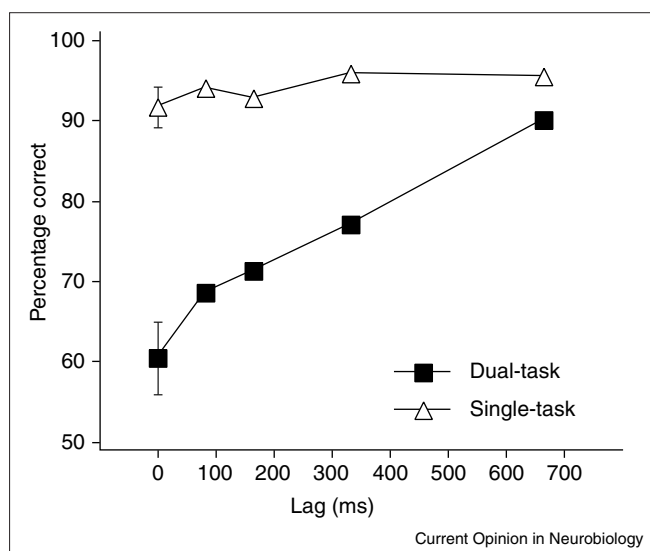
Orientation pop-out is impaired in the attentional blink paradigm [44]. On each trial, a colored letter appeared amidst a rapid serial visual presentation sequence of other black letters. After a variable lag, a search array appeared in which a uniquely oriented target was embedded with 50% probability. When subjects ignored the letter task and tried to detect the orientation pop-out target only, performance was very high across all lags. However, in the dual-task condition, using the same display sequences, attention to the letter task severely impaired detection of the orientation pop-out targets. Note how performance systematically improved as the temporal lag between the letter task and pop-out detection task increased. This lag manipulation allows one to parametrically control the magnitude of functional blindness to visual events. Reproduced with permission from Nature [44], © 1997, Macmillan Publishers Ltd.

When subjects try to detect two visual targets presented in rapid succession, they typically fail to 'see' the second target appearing within 500 ms of the first. Attention to the first target prevents awareness of the second. This deficit is so powerful that subjects cannot even report a very salient target stimulus, such as a uniquely oriented item, that would otherwise support a rapid and efficient 'feature pop-out' search (Figure 3) [44,45].

These paradigms offer insights into basic questions about the role of attention in conscious perception. What is the fate of unreported visual events? This issue addresses the classic debate of early versus late selection [46]. In other words, is the unreported visual event identified at some level beneath awareness (late selection) or is it filtered out during an early stage of processing (early selection)? Clever experiments affirm the late selection view. In change blindness, changes that went undetected still activated some category-sensitive areas in ventral cortex, although the effects were not very consistent [47]. In attentional blink experiments, unreported target words produced semantic priming for subsequent targets [48], and they also triggered event-related potential components sensitive to semantic mismatch, thus providing evidence that brain areas related to word meaning were activated for these unconscious percepts [49].

Another issue concerns the patterns of neural activity associated with visual awareness. Across studies and tasks, a frontal–parietal network appears to be activated during conscious visual states, as compared to unconscious visual states [4•]. This frontal–parietal network is commonly observed in tasks that require attention [50], consistent with the central role that attention plays in conscious perception. For example, Marois *et al.* [28•] manipulated the difficulty of target processing and showed that this modulated the severity of the attentional blink. Importantly, activity in the intraparietal sulcus correlated tightly with this manipulation, suggesting that this structure plays a role in bringing visual information into awareness and in doing so, creates an attentional bottleneck that causes functional blindness for other 'unattended' stimuli.

Together, the findings discussed above support a two-stage model of visual processing, originally proposed to explain the attentional blink [43]. The basic idea is that most unattended visual stimuli are initially processed to the level of identification [51], but limited-capacity attentional processes are needed to bring these visual representations into a state that can be consciously reported. In neurobiological terms, this model suggests that most visual events may activate category-specific and even item-specific representations in ventral cortex, but dorsal and frontal mechanisms are required for the explicit perception of these events. This does not imply that conscious perception takes place in this frontal–parietal network *per se* [28•]. Rather, the parietal and frontal cortices form a limited-capacity processing stage that visual information must pass through in order to be consciously reported [28•]. Accordingly, neurological damage to the areas involved in the network may lead to deficits in conscious perception [4•,5•].

Deploying visual attention

Because of the clear benefits for selected events and the drastic costs resulting from inattention, it is critically important to deploy attention as efficiently as possible, when confronted with a multitude of potential objects that compete for selection. There are a number of mechanisms and strategies that guide attentional deployment. For example, salient visual events, such as abrupt onsets or moving stimuli, tend to attract attention [52]. However, attentional deployment cannot be understood in terms of bottom-up features alone. One of the most interesting aspects of attentional control and deployment is that these processes rely not only on visual cues, but also on close interactions with 'other' neural systems in the brain, such as those involved in working memory, long-term memory, and emotional processing.

Top-down attentional set and attentional shifting

Observers spend a lot of time scanning the environment. This involves shifting one's attention from one location to

another and from one time point to the next. Early studies of the neurophysiology of attentional shifting revealed the involvement of a network of parietal and frontal areas [53]. Exogenous attention can be deployed to visual locations on the basis of external cues, such as a bright light, sound, or even touch [54]. Endogenous attention can be wilfully commanded from one object to the next on the basis of instruction or volition. Interestingly, these two modes of attentional shifting differ greatly in their efficiency and time course [55–57]. Enforcing a scan path through a visual array with deliberate, volitional shifts of attention is much slower than letting attention run freely in an anarchic, uncontrolled manner [58•].

Naturally, it helps if the goal of an attentional search is explicit. Neural processing may be restricted to objects that match templates in mind, such as searching for a blue-colored journal amongst a pile of other books and papers [59]. Representations in working memory may serve to bias neural activity towards objects that share features with the target [60,61]. Interestingly, such selective tuning makes attention obligatory for any event that matches the template. When holding a target in mind, subjects have difficulty ignoring task-irrelevant stimuli that match the working memory representation [62,63•]. One possible mechanism for this involves feature-based selection. Neurons in V4 show enhanced activity when attention is directed to a location or to a feature. Interestingly, when attention is directed to a feature such as orientation, oriented neurons throughout the entire visual field exhibited increased activity [64] (see also [65]).

Even when visual stimulation is absent, neural mechanisms prepare for upcoming visual events. When cued to expect a target in a certain location, significant preparatory activity is observed in frontal and parietal cortices [66,67•,68•]. Attention can be cued to points in time as well [69]. Preparatory activity can be distinguished from neural activity associated with target detection.

Effects of experience
In addition to top-down attentional tuning, the past history of the observer also affects how attention is deployed. Both short-term and long-term perceptual experiences influence attention. Across short time durations, attention and eye movements are deployed more efficiently towards features that were viewed within the previous 30 s [70,71]. Within an ongoing context of repeated stimuli, attention becomes biased towards, indeed even captured by, novel events. The inferior parietal cortex/temporoparietal junction appears to play a particularly important role in the detection of novel targets, or in the appearance of targets in previously unattended locations [68•,72,73•].

The effects of long-term experience are not fully characterized yet, but learning appears to influence visual activity and attention in a number of visual areas. In anterior inferior temporal cortex, training increases neural responses to stimuli that are behaviorally relevant [74]. Some intriguing findings, important for saccadic control, have also been observed in FEF. Neurons in FEF are not typically selective for visual features, but they can become selective with extensive training [75]. FEF is also biased towards features that defined targets in previous testing sessions [76]. These findings illustrate the existences of neural correlates of long-term visual priming.

More complex forms of visual experience may be encoded in the form of visual context. The visual context of a scene helps define which objects and locations should be attended to [77,78•]. For instance, vehicle drivers are more likely to detect and fixate a stop sign at a street intersection than a sign appearing along a street mid-block [79]. Contextual information is a form of top-down knowledge that must be acquired through learning [78•]. Hence, memory systems within the brain play an important role in attentional processing. In fact, amnesic patients with medial temporal lobe damage do not exhibit contextual benefits in visual search tasks [80,81]. Such contextual knowledge encoded by medial temporal lobe areas appears to interface rapidly with posterior visual areas to guide perception [82].

Emotional salience
Emotionally salient events attract attention, serving to enhance responses to potentially threatening stimuli [83]. For example, aversive words, such as 'rape', are detected more readily than common neutral words controlled for word frequency. If presented during an attentional blink interval, smaller deficits are observed for the emotional words [84•]. What is the neural mechanism that summons attention to motivationally significant stimuli? The amygdala plays a critical role in the affective modulation of attention and perception [85]. Accordingly, patients with bilateral or left amygdala damage do not show enhanced perception of aversive events, even though they clearly comprehend the meaning of the stimuli presented [84•].

Conclusions
We have divided the study of attention into three domains. The first concerns how neural mechanisms select and enhance processing of attended information. The second examines the behavioral costs and neural representations of unattended information. The third addresses how the brain quickly deploys attention to the information most relevant to behavior. In our view, the most remarkable aspect of attentional processing is that it works in concert with other memory, emotion, and executive mechanisms throughout the brain, to optimize deployment and to minimize the costs of functional blindness to unattended information. This makes attention a rich topic of study in cognitive neuroscience.

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