



The neural basis of biased competition in human visual cortex

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Abstract

A typical scene contains many different objects that compete for neural representation due to the limited processing capacity of the visual system. At the neural level, competition among multiple stimuli is evidenced by the mutual suppression of their visually evoked responses and occurs most strongly at the level of the receptive field. The competition among multiple objects can be biased by both bottom–up sensory-driven mechanisms and top–down influences, such as selective attention. Functional brain imaging studies reveal that biasing signals due to selective attention can modulate neural activity in visual cortex not only in the presence, but also in the absence of visual stimulation. Although the competition among stimuli for representation is ultimately resolved within visual cortex, the source of top–down biasing signals likely derives from a distributed network of areas in frontal and parietal cortex. Attention-related activity in frontal and parietal areas does not reflect attentional modulation of visually evoked responses, but rather the attentional operations themselves. Published by Elsevier Science Ltd.

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1. Limited processing capacity and biased competition

In everyday life, the scenes we view are typically cluttered with many different objects. However, the capacity of the visual system to process information about multiple objects at any given moment in time is limited [7,77,98,111]. This limited processing capacity can be exemplified in a simple experiment. If subjects are presented with two different objects and asked to identify two different attributes at the same time (e.g., color of one and orientation of the other), the subjects' performance is worse than if the task had been performed with only a single object [28,29,106]. Hence, multiple objects present at the same time in the visual field compete for neural representation due to limited processing resources.

How can the competition among multiple objects be resolved? One way is by bottom–up, stimulus-driven processes. For example, in Fig. 1(A), the red Square among the multiple blue shapes is effortlessly and quickly detected, because of its salience in the display, which biases the competition in favor of the red stimulus. Stimulus salience depends on various factors, including simple feature properties, such as the color of the stimulus as in this example [107,108], perceptual grouping of stimulus features by Gestalt principles [27,29,64,85], and the dissimilarity between the stimulus and nearby distracter stimuli [32,33,80].

In the display depicted in Fig. 1(B), the competition among the multiple objects is not resolved by salience, and one must actively search through the display to identify the square [107,123,124]. In such cases, where target salience is relatively low, it is possible to bias the competition among the multiple shapes by top–down processes, such as spatially directed attention. For example, if one is spatially cued to attend to the target location, as depicted by the dashed circle in Fig. 1(C), the identification of the square in that location will be

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facilitated [2,83]. This result suggests that spatially directed attention enhances information processing at the attended location at the expense of processing irrelevant information from nearby distracters.

In this review, we will discuss mechanisms of selective attention in the human visual cortex in the context of a biased competition account of attention [9,24,25,30,31,43]. We will focus on our recent functional brain imaging studies, in particular as they relate to results from monkey neurophysiology. In the following sections, we will first describe the evidence for competition among multiple visual stimuli for neural representation. Second, we will describe mechanisms of spatially directed attention operating in visual cortical areas and biasing neural activity through top-down feedback. And third, we will describe a distributed network of higher-order areas, which may serve as sources for generating and controlling attentional top-down bias.

2. The neural basis of competition for neural representation

What are the neural correlates for competitive interactions among multiple objects in the visual field? Single-cell recording studies in the monkey have shed light on this question by comparing responses to a single visual stimulus presented alone in a neuron's receptive field (RF) with the responses to the same stimulus, when a second one is presented simultaneously within the same RF [75,91]. The responses to the paired stimuli were shown to be a weighed average of the responses to the individual stimuli, when presented alone. For example, if a single effective stimulus elicited a high firing rate and a single ineffective stimulus elicited a low firing rate, the response to the paired stimuli was reduced compared to that elicited by the single good stimulus. This result indicates that two stimuli present at the same time within a neuron's RF are not processed independently, for, if they were, the responses to the two stimuli, when presented together would have summed. Rather, the reduced response to the paired stimuli suggests that the two stimuli within the RF interacted with each other in a mutually suppressive way. This sensory suppressive interaction among multiple stimuli has been interpreted as an expression of competition for neural representation. Sensory suppression among multiple stimuli present at the same time in the visual field has been found in several areas of the visual cortex, including areas V2, V4, the middle temporal (MT) and medial superior temporal (MST) areas, and inferior temporal (IT) cortex [74,75,87,91,95,97].

Based on hypotheses derived from these monkey physiology studies, we examined sensory suppression among multiple stimuli in the human cortex using

functional magnetic resonance imaging (fMRI) [52,57]. In these studies, hemodynamic changes as measured by fMRI were used as indirect measures of neural activity [1,63,82]. Complex, colorful visual stimuli, known to evoke robust responses in ventral visual areas of the monkey brain, were presented in four nearby locations of the upper right quadrant of the visual field, while subjects maintained fixation (Fig. 2). Fixation was ensured by having subjects count the occurrences of Ts or Ls at fixation, an attentionally demanding task. The stimuli were presented under two different presentation conditions, simultaneous and sequential. In the sequential presentation condition (Fig. 2(A)), a single stimulus appeared in one of the four locations, then another appeared in a different location, and so on, until each of the four stimuli had been presented in the different locations. In the simultaneous presentation condition (Fig. 2(B)), the same four stimuli appeared in the same four locations, but they were presented together. Thus, integrated over time, the physical stimulation parameters were identical in each of the four locations in the two presentation conditions. However, sensory suppression among stimuli within RFs could take place only in the simultaneous, not in the sequential presentation condition². Based on the results from monkey physiology, we predicted that the fMRI signals would be smaller during the simultaneous than during the sequential presentation condition due to the presumed mutual suppression induced by the competitively interacting stimuli.

The visual areas that were consistently activated in striate and extrastriate cortex during visual stimulation as compared to blank periods were in the calcarine sulcus (Brodmann area (BA) 17), the lingual gyrus (BA 18), the fusiform gyrus (BA 19 and 37), the superior

² It may be argued that, even though the presentation conditions were identical in each of the four locations, there were differences in presentation rate across the whole visual field in the two conditions. To rule out the possibility that the response differences evoked by the two presentation conditions reflected differences in overall stimulation rate, we demonstrated suppressive interactions in an experiment, in which the presentation rate during the sequential and simultaneous presentation conditions was held constant [52]. In this experiment, one stimulus was presented just above the horizontal meridian (HM) to the upper visual field (UVF) and three stimuli were presented in nearby locations just below the HM to the lower visual field (LVF). In area V4, where responses to stimuli presented in nearby locations of the upper and LVF can be spatially resolved, it was found that the responses evoked in V4's UVF by the single stimulus were significantly greater than the responses evoked by the same stimulus presented together with the three stimuli in the LVF. This finding supports the idea of sensory suppressive interactions among multiple competing stimuli and rules out the possible confound of stimulus presentation rate.

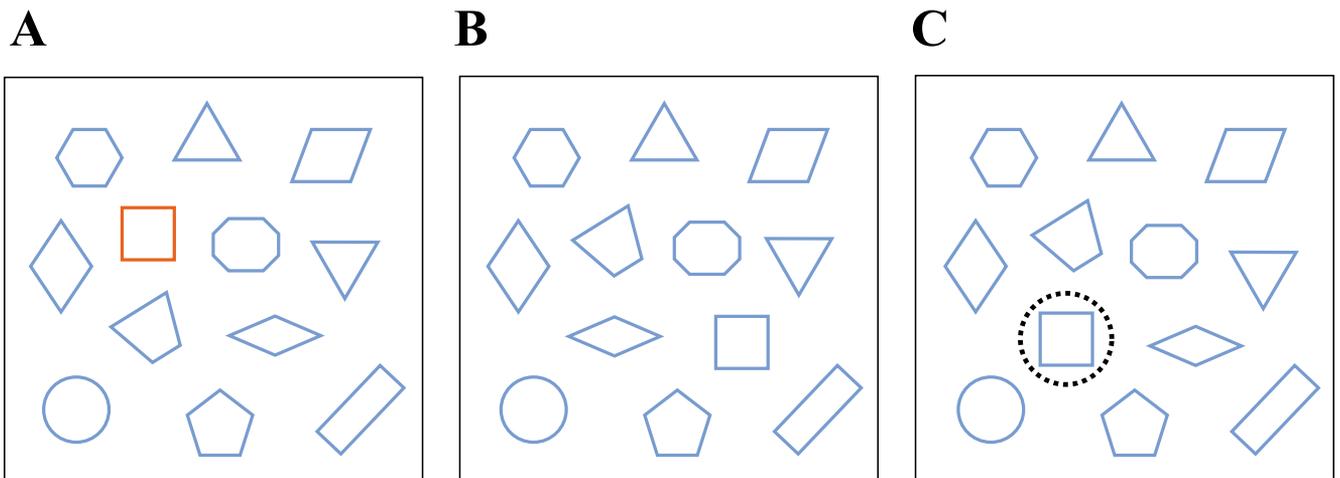


Fig. 1. Cluttered visual scenes. Multiple stimuli present simultaneously in the visual field compete for neural representation due to the limited processing capacity of the visual system. This competition can be biased in several ways. One way is by bottom-up stimulus-driven factors, such as the saliency of a stimulus (A). In a condition, in which the competition is not biased by stimulus saliency (B), it can be biased by top-down processes, such as directing attention to a particular stimulus location (depicted by the dashed circle in (C)). Processing of stimuli occurring at the attended location will be enhanced.

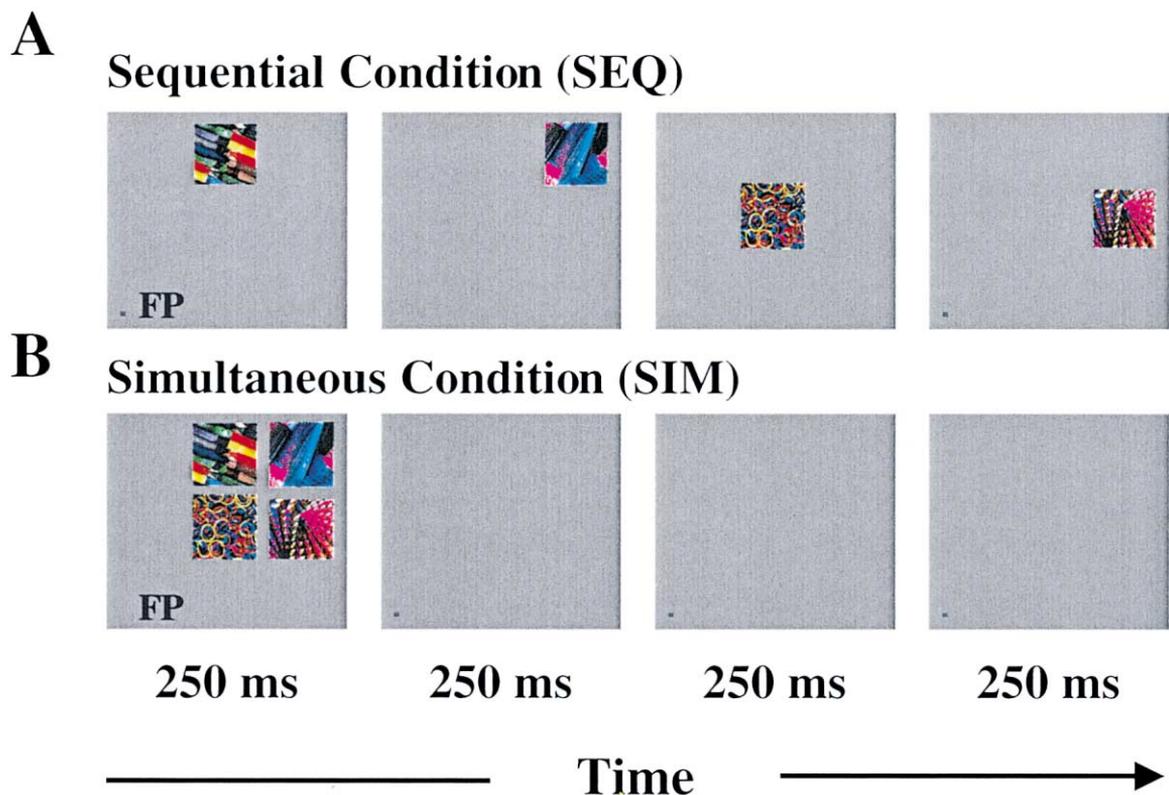


Fig. 2. Experimental design. Four complex images ($2 \times 2^\circ$) were presented in nearby locations at an eccentricity of $6\text{--}10^\circ$ from a fixation point (FP) to the upper right quadrant in two presentation conditions: sequential (A) and simultaneous (B). Presentation time was 250 ms followed by a blank period of 750 ms in each location. A stimulation period of 1 s is shown, which was repeated in blocks of 18 s. Integrated over time, the physical stimulation parameters in the two presentation conditions were identical within each location. But suppressive sensory interactions among stimuli could only take place in the simultaneous, not in the sequential, condition (from Ref. [52]).

occipital gyrus (BA 19), and the lateral occipital sulcus (BA 19) of the left hemisphere. Activated voxels were assigned to retinotopically organized areas V1, V2, V4,

TEO, V3A and the MT complex (hereafter called area MT) by means of meridian mapping or upper and lower visual field topography, respectively, in a blocked design

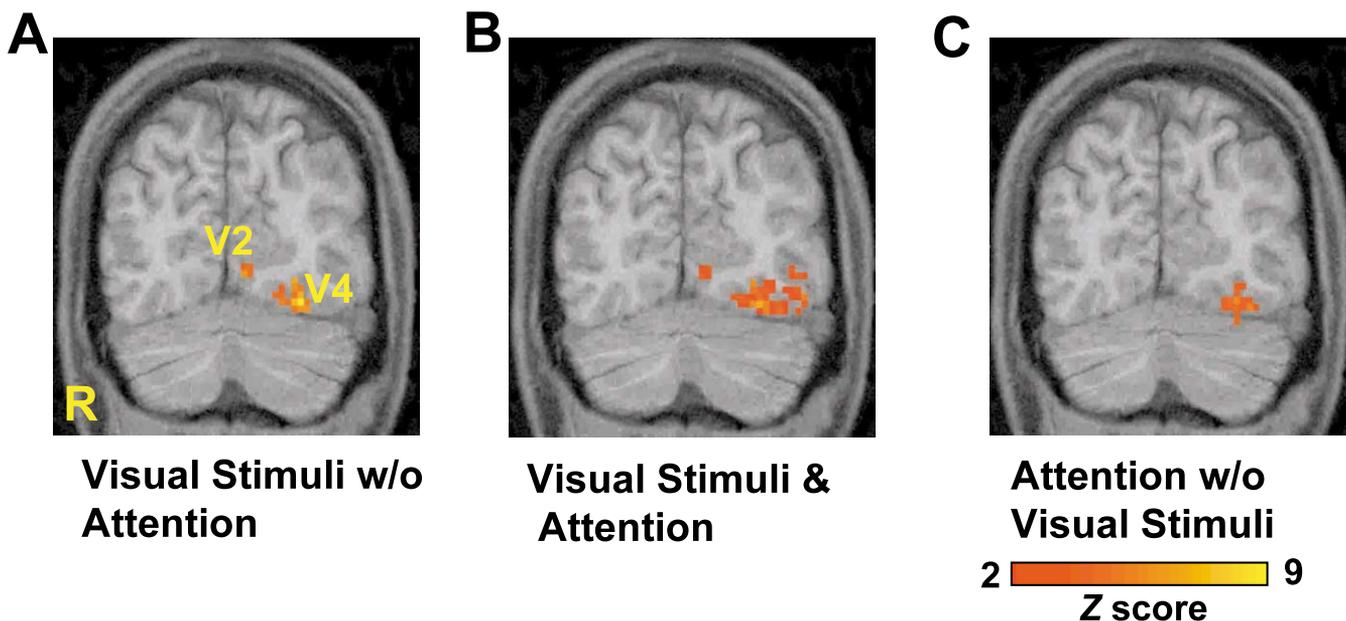


Fig. 3. Activation in visual cortex during unattended, attended, or expected visual stimuli. Coronal brain slice of a single subject at a distance of 25 mm from the posterior pole with overlaid functional activity. The subject was tested under three different conditions in the same scanning session. (A) Visual stimuli were presented to the periphery of the visual field, while the subject performed a letter counting task at fixation (unattended peripheral visual presentations). (B) Activations evoked by the same visual stimuli used in the unattended condition, but when the subject attended to one of the peripheral stimuli performing a pattern discrimination task (attended peripheral visual presentations). A significantly larger brain volume was activated within area V4. (C) Activation evoked by directing attention to a peripheral target location in the expectation of stimulus onset. Area V4 is activated even in the absence of visual stimulation. R indicates right hemisphere.

[58]³. Activations for a single subject are illustrated in coronal sections at different distances from the occipital pole in Fig. 3(A), and on a flattened surface reconstruction in Fig. 4(A).

As predicted by our hypothesis that stimuli presented together interact in a mutually suppressive way, simultaneous presentations evoked weaker responses than sequential presentations for the single subject presented in Fig. 4(B) in areas V4 and TEO and for all subjects, as revealed in the group analysis, in all activated visual areas, as shown by the averaged time series of fMRI

³ Areas V1, V2 and VP were identified by determining the alternating representations of the vertical meridian (VM) and HM, which form the borders of these areas [99]. Because, the representations of the HM, forming the anterior border of V2, and the VM, forming the anterior border of VP, were overlapping in some of the subjects, it was difficult to separate V2 and VP in these subjects. Therefore, the activity was averaged across the two areas in all subjects; the combined region will be referred to as V2. Areas V4 and TEO were identified by their characteristic UVF and LVF topography. The UVF and the LVF are separated in V4 and located medially and laterally, respectively, on the fusiform gyrus. This separation is not seen in the region just anterior to V4, which we term TEO [52]. Area V4 in this study likely corresponds to area V4 of McKeefry and Zeki [71] and appears to overlap with V4 and V8 described by Hadjikhani et al. [41]. Activations in area V3A were identified on the basis of their location in dorsal extrastriate cortex, where the UVF is represented amongst LVF representations of other visual areas [105]. Activations in area MT were identified based on the characteristic anatomical location of this area at the junction of the ascending limb of the inferior temporal sulcus and the lateral occipital sulcus [121].

signals (Fig. 5(A)). The difference in activations between sequential and simultaneous presentations was smallest in V1 and increased in magnitude towards ventral extrastriate areas V4 (Fig. 5(A)) and TEO, and dorsal extrastriate areas V3A and MT. This increase in magnitude of the sensory suppression effects across visual areas suggests that the sensory interactions were scaled to the increase in RF size of neurons within these areas. That is, the small RFs of neurons in V1 and V2 would encompass only a small portion of the visual display, whereas the larger RFs of neurons in V4, TEO, V3A and MT would encompass all four stimuli. Therefore, suppressive interactions among the stimuli within RFs could take place most effectively in these more anterior extrastriate visual areas. In V1 and V2, it is likely that surround inhibition from regions outside the classical RF contributed to the small sensory suppression effects observed [60]. Another possibility is that the complex, colorful stimuli we chose were more effective for activating areas V4 and TEO than areas V1 and V2, and therefore, these stimuli were more likely to induce sensory suppression in these former areas.

To directly test the idea that sensory suppressive interactions are scaled to RF size, we undertook a second study, in which the spatial separation between the four stimuli was increased [57]. According to the RF hypothesis, the magnitude of sensory suppression should be inversely related to the degree of spatial separation among the stimuli. In agreement with this idea, separat-

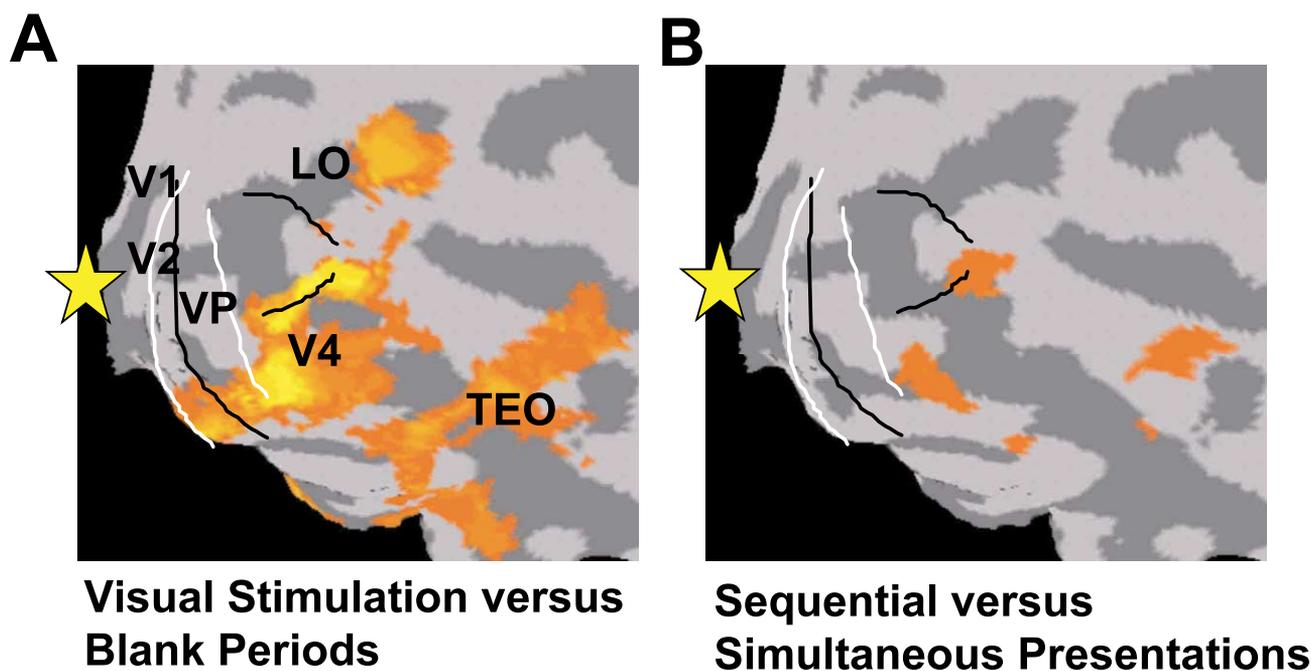


Fig. 4. Activated brain regions on flattened surface reconstructions. The flattened surface reconstruction shows areas in ventral visual cortex from V1 to TEO. White lines indicate representations of the vertical meridians, which form the areal boundaries of V1/V2 and VP/V4, respectively. Black lines indicate representations of the horizontal meridians (HM), which form the areal boundary of V2/VP and separate the UVF and LVF within V4, respectively. Another HM representation separates V4 from the lateral-occipital complex, LO. (A) Colored regions indicate activations evoked by sequential and simultaneous visual presentations to the periphery of the visual field compared to blank periods. Ventral visual areas from V1 to TEO were activated. In this subject, there is also activity in the LO. (B) Colored regions indicate activations evoked by the sequential compared to the simultaneous presentations. The sequential presentations evoked stronger responses than the simultaneous presentations in V4 and TEO. The star indicates the region of foveal representations of the visual field (from Ref. [57]).

ing the stimuli by 4° abolished sensory suppressive interactions in V2, reduced them in V4, but did not affect them in TEO. Separating the stimuli by 6° led to a further reduction of sensory suppression in V4, but again had no effect in TEO. By systematically varying the spatial separation among the stimuli and measuring the magnitude of suppressive interactions, it was possible to get an estimate of average RF sizes across several areas in the human visual cortex. From these experiments, we estimated that, at an eccentricity of about 5° , RF sizes were $< 2^\circ$ in V1, in the range of $2\text{--}4^\circ$ in V2, and about 6° in V4. In TEO, the RFs were larger than in V4, but still confined to a single quadrant of the contralateral hemifield [57]. It should be noted that these numbers may underestimate RF sizes due to additional suppressive influences from beyond the RF, which cannot be distinguished from interactions within RFs in our experimental paradigm. In monkeys, RF sizes have been defined at the level of single cells, whereas we have measured hemodynamic responses, i.e., BOLD contrast, to determine RF sizes in the human visual cortex. Even though there are several important differences between these two methods, it was striking that these estimates of RF sizes in human visual cortex are similar to those measured in the homologous visual areas of monkeys (Table 1; [5,37,38,116]). The results in humans need to be ex-

tended in future studies that will investigate RF sizes at different eccentricities.

In summary, these fMRI studies have begun to establish in the human visual cortex a neural basis for competition among multiple stimuli present at the same time in the visual field. Importantly, the degree to which this competition occurs appears to critically depend on the RF sizes of neurons across visual cortical areas. The role of additional factors in the competition, such as stimulus-driven bottom-up influences (e.g., stimulus contrast; [92]) or the selectivity of neuronal populations to process certain stimulus features (e.g., color, motion), remains to be investigated.

3. Attentional response modulation in visual cortex: evidence for top-down bias

Convergent evidence from single-cell recording studies in monkeys and functional brain imaging and event-related potential studies in humans indicates that endogenous spatially directed attention can modulate neural processing in visual cortex. The first evidence of attentional modulation of visually evoked activity was provided by electrophysiological studies on selective attention in humans [34,117]. In single-cell recording studies in monkeys, neural responses to visual stimuli

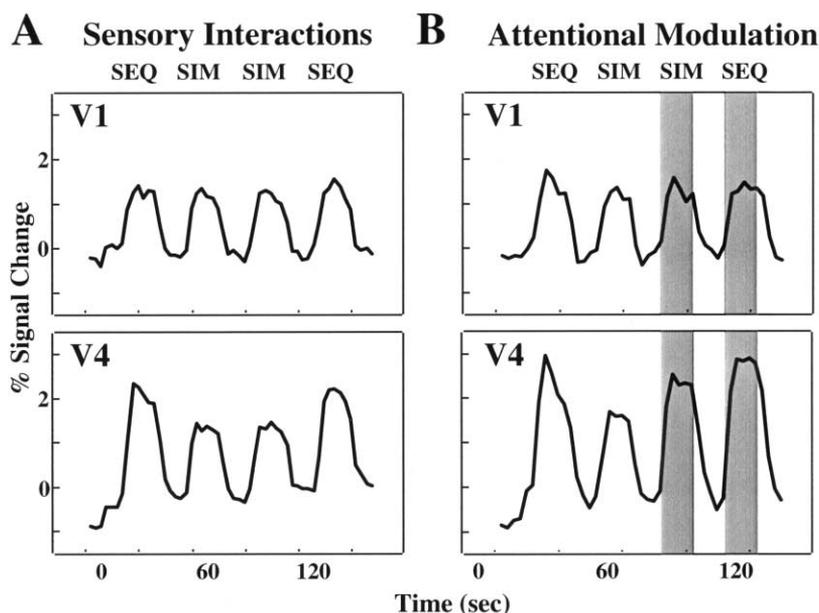


Fig. 5. Sensory suppression and attentional modulation in human visual cortex. (A) Sensory suppression in V1 and V4. As shown by the time series of fMRI signals, simultaneously presented stimuli evoked less activity than sequentially presented stimuli in V4, but not in V1. This finding suggests that sensory suppressive interactions were scaled to the RF size of neurons in visual cortex. Presentation blocks were 18 s. (B) Attentional modulation of sensory suppression. The sensory suppression effect in V4 was replicated in the unattended condition of this experiment, when the subjects' attention was directed away from the stimulus display (unshaded time series). Spatially directed attention (blue shaded time series) increased responses to simultaneously presented stimuli to a larger degree than to sequentially presented ones in V4. Presentation blocks were 15 s (from Ref. [52]).

presented within a neuron's RF have been studied under conditions, in which the animal covertly (i.e., without executing eye movements) directs its attention to a stimulus within the RF, or when the animal directs its attention away from the RF to another location in the visual field. Several studies have shown that neural responses to a single stimulus presented within the RF are enhanced, when the animal directs its attention within the RF compared to when the animal attends outside the RF. This effect, which increases with task difficulty [102,103], has been demonstrated in V1 [76], in V2 [65,76], in ventral extrastriate area V4 [18,19,42,65,70,76,102] and in dorsal extrastriate areas MT/MST [109,110] and LIP [10,16]. This finding suggests that mechanisms of spatial attention operate by enhancing neural responses to stimuli at attended locations, thereby biasing information processing in favor of stimuli appearing at that location.

Similar results have been found in functional brain imaging and event-related potential studies in the human visual cortex. In these experiments, identical visual stimuli were presented simultaneously to corresponding peripheral field locations to the right and left of fixation, while subjects were instructed to direct attention covertly to the right or the left. Directing attention to the left hemifield led to increased stimulus evoked activity in extrastriate visual areas of the right hemisphere, whereas directing attention to the right hemifield led to increased activity in extrastriate visual

areas of the left hemisphere [35,46,115]. Thus, responses to the stimuli were enhanced on the side of extrastriate cortex containing the representations of the attended hemifield. Response enhancement due to spatially directed attention that was found with ERP recordings from electrodes placed over extrastriate cortex occurred as early as 80–130 ms after stimulus onset [46,47,66,67].

Thus far, we have considered that spatial attention enhances neural responses to a stimulus at an attended location. However, a typical visual scene contains multiple stimuli that are often cluttered together in nearby locations, each competing for processing resources. As we have described above, competition among multiple stimuli in nearby locations for representation is evidenced by mutually suppressive sensory interactions that take place most effectively at the level of the RF;

Table 1

RF sizes in monkey visual cortex and estimated RF sizes in human visual cortex at 5.5° eccentricity

Area	Human	Monkey ^a
V1	<2	1.5
V2/VP	2–4	2.5
V4	4–6	4
TEO	>7 ^b	8
V3A	>6 ^b	?

^a From Refs. [5,37,38,116].

^b Confined to a quadrant.

such interactions were demonstrated in both single-cell recording [91] and fMRI studies [52,57]. What is the role of spatially directed attention in this competition?

3.1. Filtering of unwanted information

Single-cell recording studies have demonstrated that spatially directed attention can bias the competition among multiple stimuli in favor of one of the stimuli by modulating sensory suppressive interactions. In particular, in extrastriate areas V2 and V4, it was shown that spatially directed attention to an effective stimulus within a neuron's RF eliminated the suppressive influence of a second ineffective stimulus presented within the same RF. When a monkey directed attention to one of two competing stimuli within a RF, the responses were as large as those to that stimulus presented alone [91]. The attentional effects were less pronounced, when the second stimulus was presented outside the RF, suggesting that competition for processing resources within visual cortical areas takes place most strongly at the level of the RF. These findings imply that attention may resolve the competition among multiple stimuli by counteracting the suppressive influences of nearby stimuli, thereby enhancing information processing at the attended location. This may be an important mechanism by which attention filters out unwanted information from cluttered visual scenes [24,25].

Our recent fMRI studies suggest that a similar mechanism operates in the human visual cortex [52]. We studied the effects of spatially directed attention on multiple competing visual stimuli in a variation of the paradigm we used to examine sensory suppressive interactions among simultaneously presented stimuli, described above and illustrated in Fig. 2. In addition to the two different visual presentation conditions, sequential and simultaneous, two different attentional conditions were tested, where the peripheral stimuli were unattended or attended. During the unattended condition, attention was directed away from the peripheral visual display by having subjects count Ts or Ls at fixation, exactly as in our original study. In the attended condition, subjects were instructed to attend covertly to the peripheral stimulus location closest to fixation in the display and to count the occurrences of one of the four stimuli, which was indicated before the scan started. Based on the results from monkey physiology, we predicted that attention should reduce sensory suppression among stimuli. Thus, responses evoked by the competing, simultaneously presented stimuli should be enhanced more strongly than responses evoked by the non-competing sequentially presented stimuli [13,14,65,75,91,110].

The same areas in striate and extrastriate cortex were activated during both the unattended and attended condition, including V1, V2, V4, TEO, V3A, and MT.

However, in the attended condition, activated volumes increased significantly in V4, TEO, V3A, and MT. The volume increase in V4 is illustrated for a single subject in Fig. 3(B). As illustrated in Fig. 5(B) for area V4, directing attention to the location closest to fixation in the display enhanced responses to both the sequentially and the simultaneously presented stimuli. This finding confirmed the effects of attentional response enhancement shown in numerous previous studies in monkeys and humans, as cited above. More importantly, and in accordance with our prediction from monkey physiology, directed attention led to greater increases of fMRI signals to simultaneously presented stimuli than to sequentially presented stimuli. Additionally, the magnitude of the attentional effect scaled with the magnitude of the suppressive interactions among stimuli, with the strongest reduction of suppression occurring in ventral extrastriate areas V4 (Fig. 5(B)) and TEO, suggesting that the effects scaled with RF size. These findings support the idea that directed attention enhances information processing of stimuli at the attended location by counteracting suppression induced by nearby stimuli, which compete for limited processing resources. In essence, unwanted distracting information is effectively filtered out.

In contrast to ventral extrastriate areas, in dorsal extrastriate areas V3A and MT, spatially directed attention led to comparable increases of activity to sequentially and simultaneously presented stimuli, indicating that the spatial filter mechanism did not operate within these areas. Because, we used visual stimuli that activated ventral areas more effectively than dorsal areas, this finding suggests that the spatial filtering of unwanted information depends not only on RF size, but also on the selectivity of neural populations to process preferred stimulus features.

It has been shown that attentional response enhancement in visual cortex occurs in the representations of the attended locations, i.e., the attentional effects are retinotopically organized and spatially specific [6,104]. In accordance with these findings, the attentional response modulation found with our paradigm was topographically organized, inasmuch as it was seen only in visual areas with a representation of the attended location (i.e., the upper right quadrant; see Fig. 3(B)).

Importantly, the attentional response enhancement to both simultaneously and sequentially presented stimuli appeared to increase from early to later stages of visual processing. Attentional effects were absent or small in V1 and V2, respectively, and much stronger in more anterior extrastriate areas V4 and TEO, suggesting that the latter areas were the primary target of the attentional top-down biasing signals. Single-cell recording studies have shown that neural responses can be modulated by attention as early as in V1 [76,94], and functional brain imaging studies have demonstrated

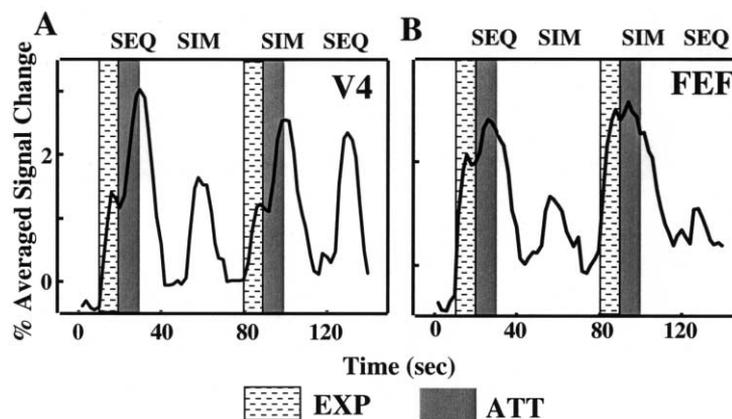


Fig. 6. Increases of baseline activity in the absence of visual stimulation. (A) Time series of fMRI signals in V4. Directing attention to a peripheral target location in the absence of visual stimulation led to an increase of baseline activity (textured blocks), which was followed by a further increase after the onset of the stimuli (gray shaded blocks). Baseline increases were found in both striate and extrastriate visual cortex. (B) Time series of fMRI signals in FEF. Directing attention to the peripheral target location in the absence of visual stimulation led to a stronger increase in baseline activity than in visual cortex; the further increase of activity after the onset of the stimuli was not significant. Sustained activity was seen in a distributed network of areas outside the visual cortex, including SPL, FEF and SEF, suggesting that these areas may provide the source for the attentional top-down signals seen in visual cortex (adapted from Ref. [54]).

attentional response modulation in V1 with moving [39,101,118,119] and stationary stimuli [68]. Yet, in all of these studies, the magnitude of the attentional response modulation in V1 was smaller than that in more anterior extrastriate areas, suggesting that attentional effects in V1 may be caused by reactivation from higher-order extrastriate areas [68]. This idea is supported by single-cell recording studies, which have shown that attentional effects in area TE of IT cortex have a latency of about 150 ms [13], whereas attentional effects in V1 have a longer latency of about 230 ms [94]. An alternative view, however, is that these latency differences are due to local computations within areas. For example, facilitatory or suppressive effects of stimuli from beyond the classical RF on responses to stimuli shown in the RF occur with a delay [60]. This contextual response modulation has been attributed to local circuits within an area.

3.2. Increases of baseline activity

There is evidence that attentional biasing signals can be obtained not only for the modulation of visually driven activity, but also in the absence of any visual stimulation whatsoever. Single-cell recording studies have shown that spontaneous (baseline) firing rates were 30–40% higher for neurons in areas V2 and V4, when the animal was cued to attend covertly to a location within the neuron's RF before the stimulus was presented there, i.e., in the absence of visual stimulation [65]. A similar effect was demonstrated in dorsal stream area LIP [16]. This increased baseline activity, termed the 'baseline shift', has been interpreted as a direct demonstration of a top-down signal that feeds back from higher-order to lower-order areas. In the

latter areas, this feedback signal appears to bias neurons representing the attended location, thereby favoring stimuli that will appear there at the expense of those appearing at unattended locations. Thus, stimuli at attended locations are biased to 'win' the competition for processing resources [9,24,25,30,31,43].

We studied attentional biasing signals in the human visual cortex in the absence of visual stimulation by adding a third experimental condition to the design used to investigate sensory suppressive interactions and their modulation by attention [54]. In addition to the two visual presentation conditions, sequential and simultaneous and the two attentional conditions, unattended and attended, an expectation period preceding the attended presentations was introduced. The expectation period, during which subjects were required to direct attention covertly to the target location and instructed to expect the occurrences of the stimulus presentations, was initiated by a marker presented briefly next to the fixation point (FP) 11 s before the onset of the stimuli. In this way, the effects of attention in the presence (ATT in Fig. 6) and absence (EXP in Fig. 6) of visual stimulation could be studied.

We found that, during the expectation period preceding the attended presentations, regions within visual areas with a representation of the attended location were activated. This activity was related to directing attention to the target location in the absence of visual stimulation (see activation of area V4 for a single subject in Fig. 3(C)). Notably, the increase in activity during expectation was topographically specific, inasmuch as it was only seen in areas with a spatial representation of the attended location. As illustrated for area V4 in Fig. 6(A), the fMRI signals increased during the expectation period (textured epochs in the

figure), before any stimuli were present on the screen. This increase of baseline activity was followed by a further increase of activity evoked by the onset of the stimulus presentations (gray shaded epochs in the figure). The baseline increase was found in all visual areas with a representation of the attended location. It was strongest in V4, but was also seen in early visual areas. It is noteworthy that baseline increases were found in V1, even though no significant attentional modulation of visually evoked activity was seen in this area. This dissociation suggests either that different mechanisms underlie the effects of attention on visually evoked activity and on baseline activity, as suggested by Luck et al. [65]. However, it is also possible that some of the attentional effects previously reported with visual stimulation in V1 actually derive from sustained shifts in baseline activity rather than increases in the stimulus evoked response, per se. Importantly, the increase in baseline activity in V1 has also been found to depend on the expected task difficulty. Ress et al. [88] showed that increases in baseline activity were stronger, when subjects expected a visual pattern that was difficult to discriminate compared to a pattern that was easy to discriminate. In areas that preferentially process a particular stimulus feature (e.g., color or motion), increases in baseline activity were shown to be stronger during the expectation of a preferred compared to a non-preferred stimulus feature [12,56,100]. Increases in activity caused by the expectation of particular stimulus features may be closely related to neural signals associated with visual imagery; the latter signals have been found in visual areas that are preferentially processing the sensory stimulus [50,62,81].

The baseline increases found in human visual cortex [12,48,49,54,56,100] may be subserved by increases in spontaneous firing rate similar to those found in the single-cell recording studies [16,65], but summed over large populations of neurons. The increases evoked by directing attention to a target location in anticipation of a behaviorally relevant stimulus at that attended location are thus likely to reflect a top–down feedback bias in favor of the attended location in human visual cortex.

In summary, neural activity in visual cortex is modulated by spatially directed attention. Biasing signals due to spatial attention affect neural processing *in several ways*. These include: enhancement of neural responses to an attended stimulus; the filtering of unwanted information by counteracting the suppression induced by nearby distracters; and the biasing of signals in favor of an attended location by increases of baseline activity in the absence of visual stimulation.

4. Source areas generating attentional top–down bias

Thus far, we have argued that there is competition among objects within visual cortical areas for neural

representation. Further, we have proposed that this competition can be biased in favor of a particular object by mechanisms of selective attention; that is, through top–down inputs. Lesion studies in monkeys have provided evidence that the competition may ultimately be resolved within visual cortex. Monkeys with restricted lesions of V4 and TEO show serious deficits in their ability to filter out distracter stimuli presented at higher contrast relative to the target stimulus [26]. However, even though extrastriate areas may be a critical site, where the competition among multiple stimuli is resolved, there is evidence that the top–down biasing signals derive from areas outside visual cortex and are transmitted via feedback projections to visual cortex [8,48,54,68,72,73,84]. What areas might be the source of these top–down signals?

Both studies in patients suffering from attentional deficits due to brain damage and functional brain imaging studies in healthy subjects performing attention tasks have given insights into a distributed network of higher-order areas in frontal and parietal cortex. This network appears to be involved in the generation and control of attentional top–down feedback signals.

4.1. Lesion studies

There is a long history demonstrating that unilateral brain lesions in humans often cause an impairment in spatially directing attention to the contralateral hemifield, a syndrome known as visuospatial neglect. In severe cases, patients suffering from neglect will completely disregard the visual hemifield contralateral to the side of the lesion [3,45,86]. For example, they will read from only one side of a book, apply make-up to only one half of their face, or eat from only one side of a plate. In less severe cases, the deficit is more subtle and becomes apparent only if the patient is confronted with competing stimuli, as in the case of visual extinction. In visual extinction, patients are able to orient attention to a single visual object presented to their impaired visual hemifield; but, if two stimuli are presented simultaneously, one in the impaired and the other in the intact hemifield, the patients will only detect the one presented to the intact side, denying that any other object had been presented. These findings suggest that visual extinction reflects an attentional bias towards the intact hemifield in the presence of competing objects [15,31,59,69,90].

Visuospatial neglect may follow unilateral lesions at very different sites, including the parietal lobe, especially its inferior part and the temporo-parietal junction [114] and more often with right-sided parietal lesions than with left-sided parietal lesions [113], regions of the frontal lobe [23,44], the anterior cingulate cortex [51], the basal ganglia [23] and the thalamus, in particular the pulvinar [120]. The finding that lesions of many different areas may cause visuospatial neglect has led to the notion that

these areas form a distributed network for directed attention [72,84].

4.2. Functional brain imaging studies

Results from our and other functional brain imaging studies support the idea that top-down signals related to spatially directed attention may be generated by a distributed network of areas in frontal and parietal cortex. In addition to activations within visual cortex, we were able to examine activations of parietal and frontal cortex with the experimental design used to study competitive interactions and their modulation by spatial attention, as described above [53,54]. Results for a single subject are shown in Fig. 7(B). In this subject, the frontal eye fields (FEF) were activated bilaterally, together with the supplementary eye field (SEF) and the superior parietal lobule (SPL). Remarkably, none of these areas were activated to a significant degree, when subjects were processing visual information in an unattended condition (Fig. 7(A)). A network consisting of areas in the SPL, FEF, and SEF was consistently activated across subjects. A similar network has been found to be activated in a variety of visuospatial tasks [20–22,36,79,96,115]. In addition, but less consistently, activations in the inferior parietal lobule (IPL), the

lateral prefrontal cortex in the region of the middle frontal gyrus (MFG), and the anterior cingulate cortex have been reported. A common feature among these visuospatial tasks is that subjects were asked to maintain fixation at a central FP and to direct attention covertly to peripheral target locations in order to detect a stimulus [20,21,79,96], to discriminate it [36,53,54,115] or to track its movement [22]. Thus, there appears to be a general attention network that operates independent of the specific requirements of the visuospatial task (for a meta-analysis, see Ref. [55]).

Evidence from fMRI studies suggests that the attention-related activity in parietal and frontal areas may not reflect attentional modulation of visual responses; instead, the activity is largely due to the attentional operations themselves. In a study conducted by Rees et al. [89], attentional modulation of visually evoked activity was found to be rate-dependent in the IT cortex, but rate-independent in prefrontal cortex. This result thus suggests two distinct effects of attention: one, in the frontal lobe, which may generate modulatory influences, and another, in the temporal lobe, in which the visually evoked responses themselves are modulated. In a more recent study, we investigated activations in frontal and parietal cortex during directed attention in the presence and in the absence of visual stimulation in

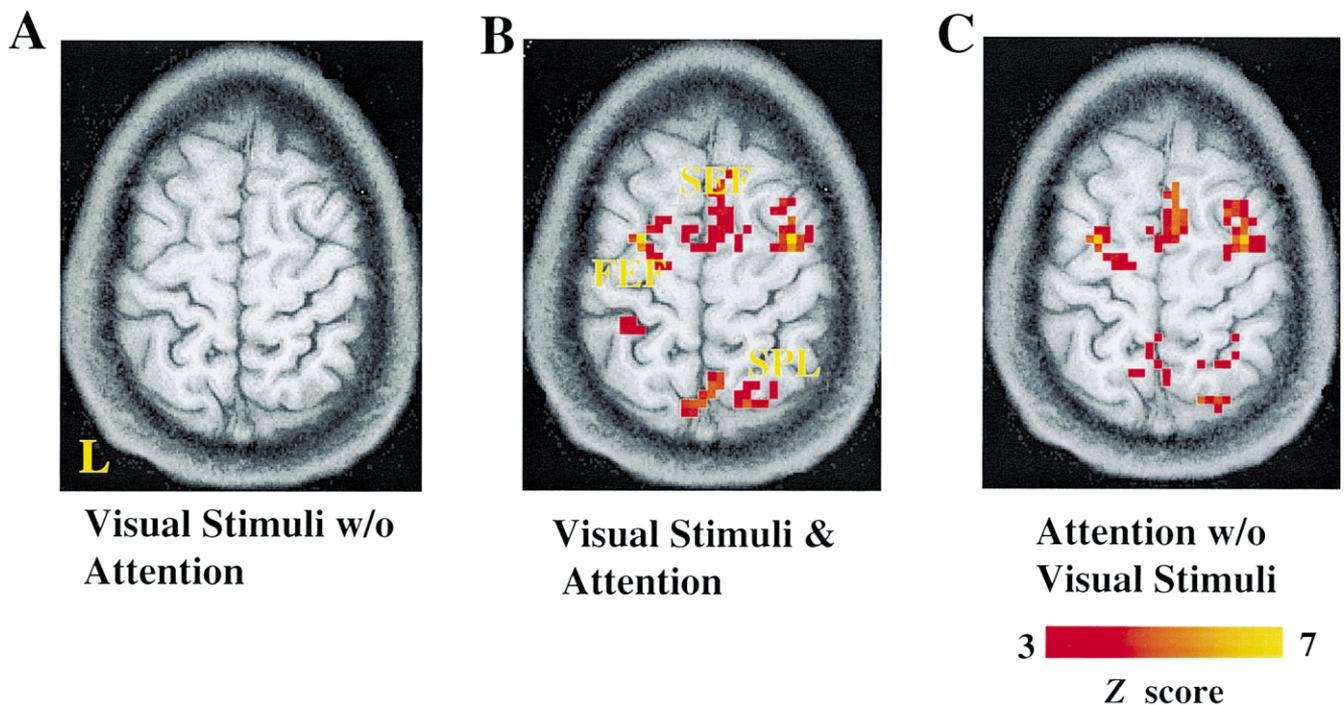


Fig. 7. A fronto-parietal network sub-serving biased competition and spatially directed attention. Axial slice through frontal and parietal cortex; same subject and experimental conditions as in Fig. 3. (A) Visual stimulation did not activate frontal or parietal cortex reliably, when attention was directed elsewhere in the visual field. (B) When the subject directed attention to a peripheral target location and performed an object discrimination task, a distributed fronto-parietal network was activated including the SEF, FEF, and SPL. (C) The same network of frontal and parietal areas was activated, when the subject directed attention to the peripheral target location in the expectation of the stimulus onset, i.e., in the absence of any visual input whatsoever. This activity, therefore, may not reflect attentional modulation of visually evoked responses, but rather attentional control operations themselves. L indicates left hemisphere.

the paradigm described above [54]. During directed attention in the absence of visual stimulation, the same distributed network for spatial attention as during directed attention in the presence of visual stimulation was activated, consisting of the FEF, SEF, and SPL (Fig. 7(C)). A time course analysis of the fMRI signals revealed that, as in visual cortical areas, there was an increase in activity in these frontal and parietal areas due to directed attention in the absence of visual input. However, first, this increase in activity was stronger in SPL, FEF, and SEF than the increase in activity seen in visual cortex (as exemplified for FEF in Fig. 6(B)), and second, there was no further increase in activity evoked by the attended stimulus presentations in these parietal and frontal areas. Rather, there was sustained activity throughout the expectation period and the attended presentations (Fig. 6(B)). Taken together, these findings suggest that the activity reflected the attentional operations of the task and not visual processing. These results, therefore, provide first evidence that these parietal and frontal areas may be the sources of feedback that generated the top-down biasing signals seen in visual cortex.

Because the magnitude of the activity in the parietal and frontal areas was the same during directed attention in the absence and in the presence of visual stimulation, it appears that this activity may be independent of the particular visual task, be it detection or discrimination. This would explain the finding that functional brain imaging studies using different visuospatial attention tasks have described very similar attentional networks.

The anatomical connections of SPL, FEF, and SEF put them in a position to serve as sources of top-down biasing signals within visual cortex. In the monkey, FEF and SEF are reciprocally connected with ventral stream areas [112,122] and posterior parietal cortex [11], and the posterior parietal cortex is connected with ventral stream areas via the lateral intraparietal area (area LIP) [122]. Further, single-cell recording studies in monkeys have shown that neural activity can be modulated by attention in these parietal and frontal areas. In regions of parietal cortex, enhancement of neural responses was demonstrated during covert shifts of attention to peripheral visual stimuli [10,16,93]. The strongest determinant of neural responsiveness in parietal cortex turned out to be the salience of the stimulus [17]. In the FEF and SEF, such response enhancement was originally shown only in the context of activity related to the preparation of saccadic eye movements [40,125]. More recent recording studies suggest, however, that the response enhancement in these frontal areas during covert shifts of attention to peripheral visual stimuli does not depend on the subsequent execution of saccades [4,61]. Thus, results from single-cell recording and functional brain imaging studies con-

verge to support the idea that areas in parietal and frontal cortex are potential sources for generating and controlling attentional top-down bias [49,78,90]. However, because results from functional brain imaging studies demonstrate only correlated activity of distributed brain areas and cannot establish the functional significance of a particular brain area in a given task, future studies using reversible lesion techniques, such as cooling of brain tissue or transcranial magnetic stimulation are needed to test these ideas further.

5. Summary and conclusions

In this review, we have considered the mechanisms of selective attention in human visual cortex in the context of a biased competition account of attention. Evidence from functional brain imaging studies in humans, supported by results from single-cell recording studies in monkeys, indicates that, first there is competition among multiple stimuli for representation in visual cortex. Thus, multiple stimuli presented at the same time are not processed independently, but rather interact with each other in a mutually suppressive way. Such sensory suppressive interactions are scaled to the RF size of neurons within visual cortical areas. Second, competition among multiple stimuli can be biased by top-down feedback mechanisms. Top-down influences on visual cortex, as in the case of selective attention, can affect neural processing in several ways, which include: (1) the enhancement of neural responses to attended stimuli; (2) the filtering of unwanted information by counteracting the suppression induced by nearby distracters; and (3) the biasing of signals in favor of an attended location by increases of baseline activity in expectation of a visual stimulus. Thus, attentional modulation of activity in visual cortex can occur not only in the presence, but also in the absence, of visual stimulation. Third, although competition is ultimately resolved within visual cortex, the source of top-down biasing signals may derive from a network of areas outside visual cortex. For spatially directed visual attention, these areas include the SPL, FEF, SEF, and, less consistently, areas in the IPL, the mid-lateral prefrontal cortex, and the anterior cingulate cortex. Attention-related activity in frontal and parietal areas may not reflect attentional modulation of visually evoked responses, but rather attentional control operations. Future studies will be needed to elucidate the functional nature of these operations and to determine the functional significance of these higher-order areas in spatially directed attention. Finally, the stimulus that wins the competition for representation in visual cortex will gain further access to memory systems for mnemonic encoding and retrieval and to motor systems for guiding action and behavior.

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