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Selective visual attention and perceptual coherence

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Conscious perception of the visual world depends on neural activity at all levels of the visual system from the retina to regions of parietal and frontal cortex. Neurons in early visual areas have small spatial receptive fields (RFs) and code basic image features; neurons in later areas have large RFs and code abstract features such as behavioral relevance. This hierarchical organization presents challenges to perception: objects compete when they are presented in a single RF, and component object features are coded by anatomically distributed neuronal activity. Recent research has shown that selective attention coordinates the activity of neurons to resolve competition and link distributed object representations. We refer to this ensemble activity as a 'coherence field', and propose that voluntary shifts of attention are initiated by a transient control signal that 'nudges' the visual system from one coherent state to another.

Conscious visual experience starts with the image thrown by the scene upon the retina, where local computations immediately begin to transform the representation of stimuli according to their salience (so that, for example, objects with high local contrast are more robustly represented than those with low contrast). This is only part of the story, however. Activity in almost every level of the visual system is also shaped by top-down (voluntary) attentional modulations, which can enhance or attenuate the strength of incoming sensory signals depending on the goals of the perceiver. Visual experience thus depends on the convolution of bottom-up salience and top-down modulations specified by behavioral goals.

Bottom-up and top-down influences on visual information processing are essential aspects of the hierarchically organized visual system's normal operation. Early visual areas such as LGN and V1 respond primarily to simple visual features such as oriented edges within very small receptive fields (RFs) (less than 1.5° of visual angle), whereas anatomically later regions, including inferotemporal cortex (IT), posterior parietal cortex (PPC), and frontal eye fields (FEF), respond to more complex and abstract stimulus properties within RFs that can encompass large expanses of the visual field (Figure 1). This organizational scheme introduces two challenges to perceptual efficiency that are addressed by attentional modulation.

First, the attributes of an object – including both simple, local features such as edge orientation, as well as abstract properties such as identity and behavioral relevance – must be bound together into a unified representation [1]. This requires coordinating the activity of neurons in early regions that code for specific visual features and locations with the activity of neurons at later stages that code for object identity, behavioral relevance and value. For example, the fine spatial and featural details provided by early areas such as V1 complement the view- and position-invariant object representations maintained in IT to jointly specify both what an object is and how it appears in the current scene. Second, because multiple objects often fall within the RF of a single neuron in later stages of the visual system, stimuli must compete to win neural representation. Coherent perceptual experience requires that some sensory elements are selected and others ignored.

In this article we review evidence that bottom-up and top-down attentional influences throughout the visual system address these challenges by promoting coherent neural activity across levels of the visual system, and by selecting salient and/or relevant stimuli for cortical representation. Neural activity evoked by an attended object evolves to take precedence over the activity of unattended objects at each stage of the visual system. After Rensink [2], we refer to the joint activity across stages of the hierarchy as a 'coherence field'. Each participating region of visual cortex contributes domain-specific information as part of a distributed perceptual representation. Once a given coherence field is established, we propose that voluntary attention shifts are initiated by transient switch signals that 'reset' or 'nudge' the brain out of the current attractor state, allowing a new coherence field to be formed based on input from the sensory environment and from working memory, where current task goals are maintained.

Attention biases competition for representation in visual cortex

As stated earlier, the hierarchical structure of the visual system is characterized by two properties: increasing RF size and increasing RF complexity (Figure 1a, [3–5]). When an otherwise effective sensory stimulus appears along with an otherwise ineffective sensory stimulus within a large RF, should the neuron's response be strong (reflecting the influence of the effective stimulus) or weak (reflecting the influence of the ineffective stimulus)? In

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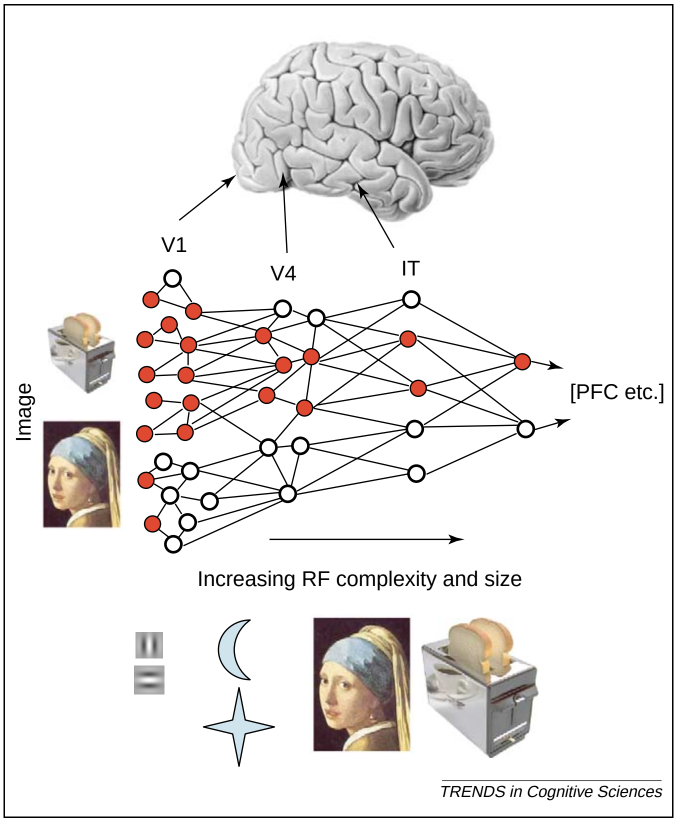

Figure 1. A schematic cartoon of the visual system with two objects, presented in different spatial locations, competing for representation. Receptive fields increase in size and complexity across the cortical hierarchy (e.g. from V1-V4-IT-PPC/PFC). Early regions provide the fine spatial and featural detail that is required to supplement the position-invariant object representations maintained in later regions (e.g. IT) to specify both the location and the identity of objects in the visual scene. Coordinated activity across all levels of the visual system is therefore essential to support efficient perceptual experience.

other words, which of these stimuli will drive the neuron's response?

Desimone and Duncan first articulated the principle of 'biased competition', which posits that attention coordinates selective information processing in the visual system [6]. On this account, subpopulations of cortical neurons that represent different aspects of the scene compete in a mutually inhibitory network. When multiple stimuli are presented within the RF of a single neuron, attentional signals can bias the competition so that the response of the neuron is largely driven by the attended stimulus [1,7,8]. Attention can also enhance the firing rate or gain of neurons when only a single stimulus is present within the receptive field, which results in a population response that is biased in favor of the attended location, object or feature [9–11].

Attentional influences on competition can be implemented by either a top-down feedback signal that depends on goals and expectations (voluntary attentional control) or by a bottom-up signal that depends on the physical salience of a stimulus (stimulus-driven attentional control). A voluntary deployment of attention to a location (or feature) simultaneously increases sensory gain to that feature and attenuates the neural response to distractor stimuli, giving a competitive advantage to the attended stimulus [7,12,13]. Similarly, a highly conspicuous stimulus will evoke a strong afferent volley of neural activity that will propagate through the visual system, biasing cortical activity in favor of the salient stimulus [8,14,15]. Stimulus-driven and voluntary attentional deployments thus serve as the mechanisms that coordinate activity across levels of the visual hierarchy to resolve competition between multiple stimuli for representation, perhaps by synchronizing the firing of neurons that jointly support a selected percept [16–20].

The coordinated process of biased competition acting simultaneously across multiple visual areas results in the formation of a perceptual coherence field, an ensemble of neurons that jointly represent a single selected object or group of objects [6,21]. Depending on current selection demands and on the specific attributes of the stimulus, this distributed representation might include detailed image-specific information about visual features such as edge orientation, color, motion, and so forth (encoded in striate and extrastriate cortex), as well as categorical information about object identity or subjective value (e.g. encoded in IT, PPC or PFC; [22–24]). All of these are part of the same coherence field, and jointly participate in the observer's experience of the object.

Cortical computation of attentional priority

Although the biased competition account provides a useful theoretical framework in which to understand attentional modulations, it leaves open the neural mechanisms by which attentional control is implemented. Many psychological and computational models of attention posit an 'attentional priority map' that reflects the distribution of attention across the visual scene [25–27] (see Box 1). On some accounts, the stimulus array is initially filtered to form a bottom-up (or 'stimulus-driven') map in which the degree of salience is represented (without regard for the meaning or task relevance of the stimuli). Next, top-down (or voluntary) influences, which are based on goals that might involve prior knowledge about target-defining features or locations, combine with stimulus-driven factors to form a 'master' attention map. Thus, attentional priority is a convolution of physical salience (stimulus-driven contributions), and the degree to which either salient or non-salient features match the current goal-state of the observer (voluntary contributions).

Consistent with psychological models, neurophysiological data confirm that both voluntary and stimulus-driven factors play a role in biasing neural activity. However, both of these influences are evident in every

Box 1. The language of attentional control

The literature on attentional control suffers from some terminological ambiguity concerning the term *salience*. It is sometimes used to refer to purely stimulus-related properties (e.g. 'a salient high-contrast stimulus'), sometimes goal-related factors (e.g. a stimulus is salient because it expresses a high-value feature, where value depends on the observer's goals), and sometimes it is used to refer to both at the same time. In this article, we use the term salience to refer only to an intrinsic property of the stimulus (e.g. local feature contrast), independent of its task relevance. We use the term *priority* to refer to the combined influence of stimulus-driven and goal-related factors. Thus, a given stimulus might have high priority by virtue of its salience, because it is task relevant or high value, or both.

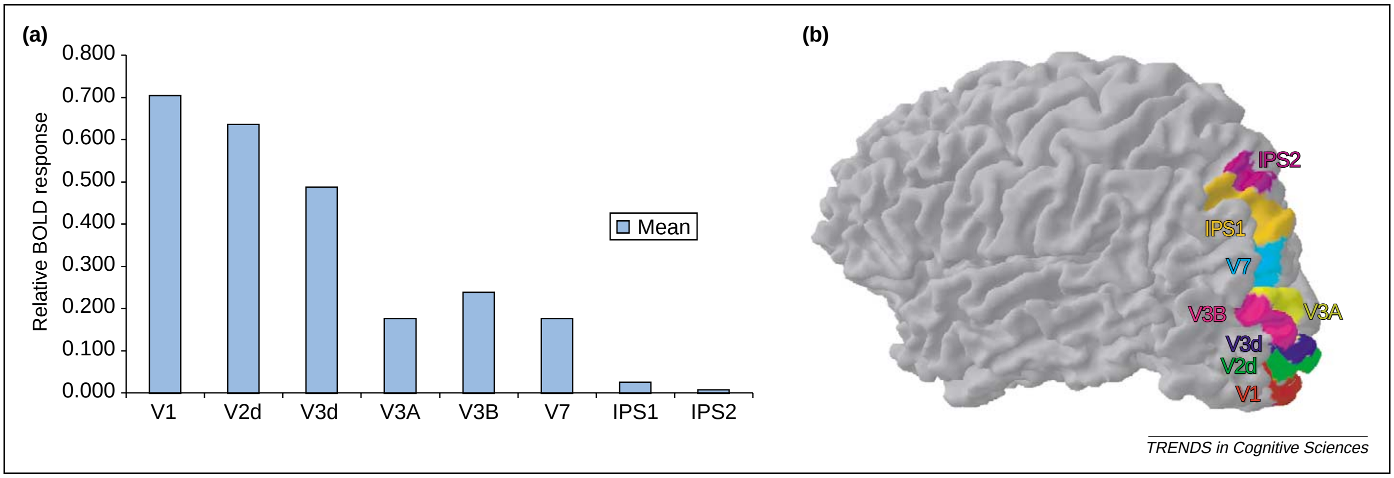

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Figure 2. **(a)** Relative BOLD response amplitude during passive visual stimulation compared with during top-down attentional deployments. The decreasing ratio across visual areas indicates that the relative influence of sensory stimulation is large in early visual areas (e.g. V1), whereas in later areas (e.g. IPS1, IPS2), sensory stimulation and deployments of attention have a comparable modulatory effect. **(b)** 3-D cortical surface reconstruction of the left hemisphere of a single subject showing the locations of dorsal visual areas V1, V2d, V3d, V3A/B, V7, IPS1, and IPS2. (Figures adapted and reprinted with permission from [43].)

cortical visual area, and their relative impact varies more or less continuously as incoming information ascends the cortical hierarchy [28]. Information represented in the retina reflects only the intrinsic properties of the stimulus array (e.g. local feature contrast) with no top-down influences (except, of course, where the eyes are pointing). At successive stages of visual processing (e.g. LGN, V1, V4, etc.), top-down attentional influences increasingly modulate and refine neural representations (Figure 2). Contrary to many psychological models of attention, there does not appear to be a single master map of priority.

Although many studies demonstrate that non-spatial deployments of selective attention can be directed to features and objects, the domain of location-based selection has received the most empirical investigation and is therefore used here as a model to discuss the representation of attentional priority in visual cortex. In the following sections, we review evidence that multiple subcortical and cortical visual areas represent attentional priority. We organize the discussion based on a feedforward conception of the visual system (LGN to occipital cortex to parietal to prefrontal cortex to superior colliculus), while noting that reciprocal connections form feedback loops throughout the visual system and that neural onset latencies vary across regions (e.g. many SC and FEF neurons respond with short latencies to visual stimulation; see [3,29–31]).

Lateral geniculate nucleus, V1, and extrastriate cortex

The LGN and early regions of occipital visual cortex (e.g. V1–V4) are retinotopically organized, and neurons here generally code for low-level features such as edge orientations, or basic combinations of features such as 'convexity' [32]. Kastner and colleagues used fMRI in human subjects to demonstrate both retinotopic organization and voluntary attentional modulations within the LGN [33,34]. Neurons in V1 are sensitive both to voluntary shifts of spatial attention following an instructional cue, and to stimulus-driven factors, such as feature contrast [35–39]. Similar observations have been made in macaque V4, where stimulus salience and voluntary deployments of attention have both been found to bias the competitive relationship between two stimuli presented within the RF of a single neuron [14,15] (Figure 3).

Neural activity within area V4 also indexes the degree to which a stimulus within the neuron's RF expresses a target-defining feature, reflecting attentional modulations influenced by prior knowledge of target identity [20]. This sensitivity to both stimulus-driven and voluntary factors is crucially important because these modulations might be

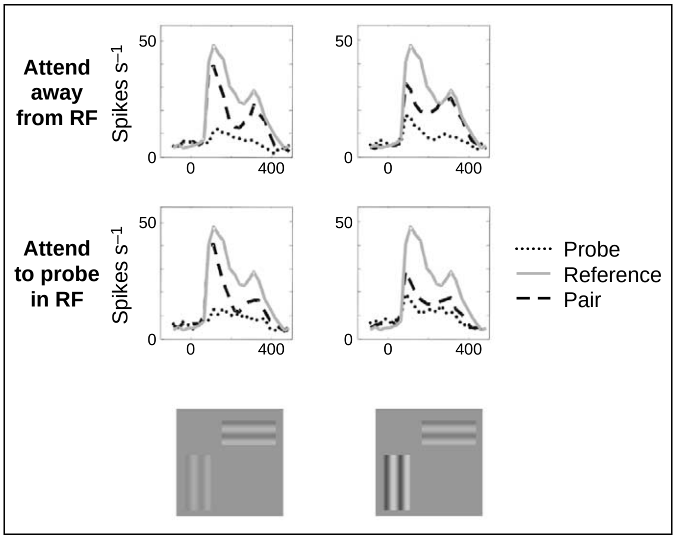

Figure 3. Mean response across 19 feature selective macaque neurons preferring a horizontal grating (the reference stimulus). Panels are arranged according to the contrast of the probe stimulus (the vertical grating), increasing from left to right. The upper two panels shows responses when the monkey attended away from the RF. The lower two panels shows the responses of the same neurons, under identical stimulus conditions, but when attention was directed to the probe stimulus in the RF. Each panel shows the average response to the probe alone (dotted line), reference stimulus alone (solid line), and pair (dashed line), with time zero corresponding to the onset of the stimulus. The top row reveals a diminished response evoked by the pair of stimuli for a high-salience probe (compare dashed line, upper left and upper right panels). The attenuation is further magnified following a voluntary deployment of attention to the non-preferred probe (compare relative position of the dashed line in lower panels with the relative position of the dashed line in the upper panels). (Figures adapted and reprinted with permission from [14].)

magnified as information is passed to later stages of processing. For example, one biologically plausible computational model suggests that a scalar estimation of bottom-up salience in V1 – independent of the feature dimension – can account for behavioral performance under a variety of psychophysical conditions [40].

Posterior parietal cortex

In visually selective regions of PPC – lateral intraparietal area (LIP) in monkeys and intraparietal sulcus (IPS) in humans – there is a coarse representation of spatial topography, and feature selectivity is somewhat diminished [41–43]. LIP has been shown to represent both voluntary and stimulus-driven contributions to attentional priority. A rapid ‘on-response’ is observed when a stimulus is flashed within the RF of an LIP neuron; this response reflects the stimulus-driven capture of attention by a salient onset stimulus and not just the luminance change within the neuron’s RF [44,45]. Moreover, the activity of LIP neurons represents the location of a cued target, reflecting the voluntary allocation of attention to a region of space away from fixation [46,47]. Stimulus-driven and voluntary attention signals can also coexist in neurons with different spatial RFs: on-responses induced by abrupt onsets rise to a peak ~40–60ms post-stimulus, and sustained attention to a target location results in a gradual ramping of activity reaching a peak ~200 ms post-stimulus [46]. These two competing representations overlap for a short period of time, indicating a graded selection dynamic in LIP that closely mirrors the behaviorally observed time course of attentional facilitation induced by stimulus-driven and voluntary orienting, respectively [48,49].

Frontal eye field

The FEF has long been known to play a role in generating contralateral saccades [50], and most neurons show little stimulus-driven feature selectivity [51]. Converging evidence collected over the past decade suggests, however, that some FEF neurons play a role in representing the current locus of attention. Transcranial magnetic stimulation [52–54] and neuroimaging studies [55–59] in humans show that activity in FEF reflects both voluntary and stimulus-driven deployments of attention during spatial cueing and visual search tasks, even when no eye movements are made. Microstimulation in FEF that is below the threshold to evoke an eye movement can induce a topographically targeted modulation of activity in V4 neurons, as well as a corresponding shift in the locus of spatial attention [60,61]. FEF neurons respond more strongly to salient singleton (or ‘oddball’) targets under conditions that have been shown psychophysically to induce stimulus-driven attention shifts [62], and a heightened response is evoked by stimuli that partially express target-defining features during conjunction search [63]. Finally, Juan *et al.* used microstimulation to show that some FEF neurons covertly select singleton targets, even when an eye movement is being simultaneously planned in the opposite direction [64]. Thus, many FEF neurons selectively represent the attentional priority of a stimulus, independent of motor plans or overt movements.

Superior colliculus

Like the FEF, the SC mediates both overt eye movements and covert shifts of visual attention. At least three distinct types of neurons are found in the SC: some code the location of a visual stimulus, others code the destination of an impending eye movement, and a third type is driven by a combination of visual and motor influences. Fecteau and colleagues demonstrated that activity in visuomotor SC neurons is modulated by voluntary attention shifts, stimulus-driven attention shifts, and ‘inhibition of return’ following the presentation of a peripheral cue [65]. Ignashchenkova *et al.* observed heightened activity in visual and visuomotor neurons when attention was shifted in anticipation of a target stimulus; the magnitude of this attentional modulation was strongly associated with the degree of sensory enhancement measured psychophysically, even though no eye movements were directed to the target location [66]. In line with these results, subthreshold microstimulation of visuomotor neurons in SC has been shown to induce a covert shift of attention and behavioral facilitation in the corresponding spatial location [67]. Finally, signals from the superficial and intermediate layers of the SC are relayed to regions of occipital cortex, PPC, and FEF and signals from the SC’s superficial layers are relayed to topographically organized maps in the pulvinar, a thalamic region thought to participate in coordinating cortico–cortico activity by virtue of overlapping terminal inputs from multiple visual areas (reviewed in [68]).

Distributed attentional priority maps and perceptual coherence

The neurophysiological evidence reviewed in the previous section supports a view of attentional priority in which perceptual coherence fields are formed when the distributed representation of an attended stimulus comes to dominate activity within multiple topographically organized visual areas. Early regions like V1 provide high-acuity information about simple visual features and closely track the contents of the retinal image, intermediate levels like V4 and IT represent more complex feature configurations increasingly influenced by attention, and activity in later areas like LIP, FEF and SC represents the behavioral relevance of a stimulus, regardless of its constituent features. These selective perceptual representations might be coordinated by thalamic structures such as the pulvinar and supported by synchronized oscillation in spiking activity. For example, recent studies show that synchronized neural activity in regions of extrastriate cortex is enhanced under conditions of focused attention, which could facilitate the formation of coherence fields by increasing the efficacy of spike transmission to downstream visual areas [16–18,69].

This model can account for the subjective observation that unattended portions of the scene do not simply disappear from awareness: stimuli outside of the current coherence field are still registered by early visual regions that represent the contents of the scene with little attentional modulation (see also [70]). In addition, because attentional modulations occur to some degree or another at every level of the visual system past the retina, no single brain region can be said to be a ‘master’ attention map, concerned solely with specifying attentional priority. Rather, attentional priority is reflected in the relative strength and coherence of neural activity coding the properties of the attended stimulus across functionally complementary regions of the visual system [6,21].

Many details of this model are currently underspecified. For instance, recent studies show that attention can be split between multiple objects or locations [71,72], suggesting that more than one coherence field can exist at a given moment in time. Additional research is needed to specify the constraints on the formation of coherence fields and how they interact when multiple objects are selected.

Switching attention by reconfiguring perceptual coherence fields

The neural representation of an attended stimulus is more robust than that of other competing objects at every level of the visual system. However, the studies reviewed above do not specify how the selected coherence field is reconfigured when a new target stimulus is specified by either stimulus-driven or voluntary attentional control factors. In the case of stimulus-driven control, the physical salience of a stimulus might override the current coherence field by strongly activating visually responsive neurons that are hard-wired to respond more robustly to stimuli with high luminance or feature contrast [14,15,39,40]. Voluntary deployments of attention have been shown to enhance signal gain and reduce distractor interference, thereby influencing the formation of new coherence fields [10,13,14,73]. However, this begs a deeper question: how does the brain implement a voluntary act of selective attention?

Recent studies carried out in our laboratory have identified a transient signal that is time-locked to voluntary attention shifts evoked by interpreted cues. In these studies, observers attend to one of two or more rapid serial visual presentation (RSVP) stimulus streams; the streams contain stimuli that change over time, and observers must covertly monitor the attended stream for the presentation of a target that instructs them to either shift attention to the currently ignored stream, or to maintain attention on the currently attended stream.

In the first of these studies, observers shifted attention between two peripheral spatial locations in response to numerical cues embedded within RSVP streams consisting of letter distractors (Figure 4a). Regions of topographically organized occipital visual cortex were dynamically modulated as attention was shifted between the two locations: activity was relatively high when attention was directed to the (preferred) contralateral visual field, and relatively low when attention was directed to the (non-preferred) ipsilateral visual field [74]. These spatially-specific modulations reflect the changing attentional priority assigned to each peripheral location as attention was deployed in response to the numerical cues.

By contrast, regions of the superior parietal lobule (SPL) were transiently active whenever attention was shifted between locations, regardless of the direction of the shift (Figure 4b). Therefore, the SPL activity did not appear to convey information concerning the direction of the attention shift, but rather reflected a more abstract signal to reconfigure or reinitialize the current state of selection – the current coherence field – in response to explicit task instructions (for a similar result, see [75]). Note that this transient SPL activity did not arise from the topographically organized regions of IPS, which reflect the spatial locus of attention, but from an anatomically distinct region of medial superior PPC. These results were mirrored in experiments that required non-spatial shifts of attention between visual features (e.g. motion and

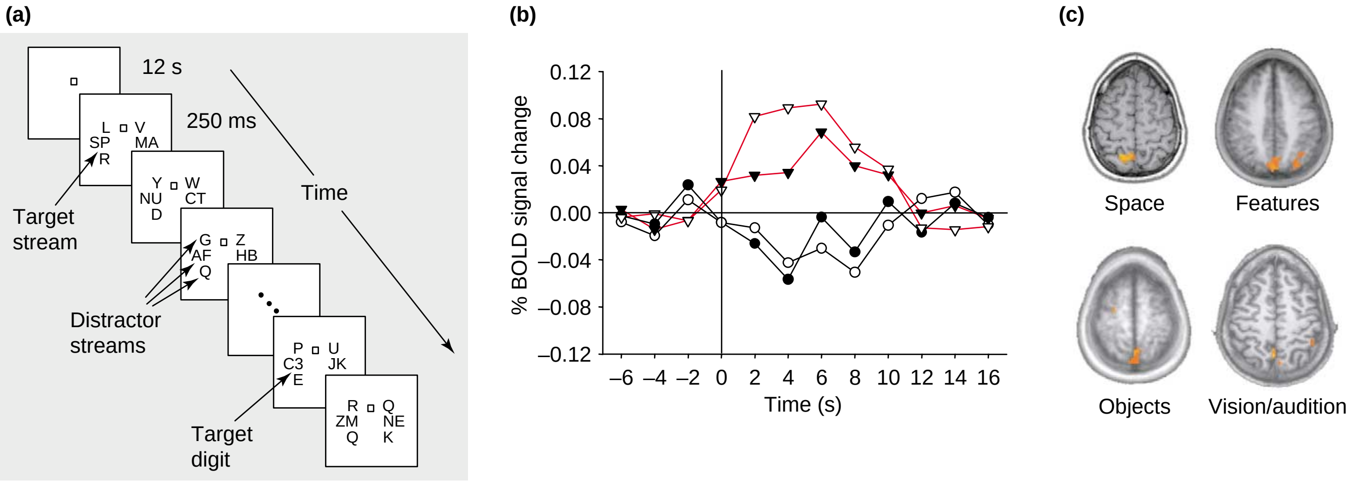

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Figure 4. (a) Behavioral paradigm to examine spatial attentional control [74]. Observers maintained fixation on the central square throughout each run and began by attending to the central stream of letters on one side (left in this example). Letters changed identity simultaneously four times per second. Hold and shift target digits (e.g. 3, 7) instructed the observer to maintain attention on the currently attended side or to shift attention to the other side, respectively. **(b)** BOLD time courses from a region of right SPL that showed an increased BOLD response when attention was shifted between spatial locations (red lines, open and closed triangles) compared with when attention was maintained at the currently attended location (black lines, open and closed circles). **(c)** Statistical maps showing the regions of SPL exhibiting enhanced activity following shifts of attention between spatial locations, features, objects, or sensory modalities (Figures adapted and reprinted with permission from [74,76–78]).

color; [76]), between spatially superimposed objects (faces and houses; [77]), and between sensory modalities (vision and audition; [78]). In each case, attentional modulations in domain-specific regions of cortex reflected the currently dominant coherence field, and transient activity in SPL (and FEF in some studies) was observed whenever attention was shifted, without carrying information about the direction or the type of the attentional deployment (Figure 4c).

The role of switch signals in altering perceptual coherence

How can a transient signal that carries no information about the target of an attention shift effectively establish a new coherence field as behavioral demands change over time? Two possibilities can be considered. First, the visual system might tend towards a chaotic or incoherent state when relatively unconstrained by selection demands; this incoherent state would be 'equidistant' from all possible coherent states, which would minimize reconfiguration time on average. On this account, the transient switch signal would serve as a synchronizing signal to induce coherent activity across regions of the visual system that are required to efficiently support current selection demands (e.g. a signal to coordinate activity across topographically organized regions of cortex when a particular location must be selected, similar to a conductor synchronizing musicians at the beginning of a movement). Second, the visual system might naturally gravitate towards a coherent attractor state because behavioral goals typically exhibit sequential dependencies over time. The most efficient way to prepare for the next coherent state might be to slightly alter the current state, assuming that radical reconfigurations of the system are rare. According to this alternative, the transient switch signal would serve to 'reset' the visual system at the end of one act of selection, so that the current coherence field is disrupted and a new one can be formed.

On both these accounts, the new coherence field is specified by a combination of stimulus salience and top-down goals stored in prefrontal working memory regions. The domain-independent transient switch signal participates in attentional control by enabling a new attentional state (perhaps via one of the two mechanisms described above). However, the transient signal does not seem to carry any information about the parameters of the new state (e.g. the direction of an attention shift). The neural mechanisms that transform abstract behavioral goals into modulatory signals that specify a new coherence field are currently unknown (see also Box 2).

Sources and targets of attentional deployments

In this article, following standard practice, we have drawn a distinction between the *sources* of attentional control (e.g. the transient switch signal) and the *targets* of those attentional control signals (the visual areas participating in a given perceptual coherence field including subcortical, occipital, parietal, and frontal regions). However, this dichotomy has typically been drawn along rather sweeping anatomical boundaries, with PPC and FEF (and perhaps SC and pulvinar) classified as sources of attentional control, and regions of occipital visual cortex classified as the targets of modulatory input (for reviews that reflect this point of view, see [56,79,80]).

Box 2. Questions for future research

- How is activity in multiple cortical areas coordinated to give rise to coherent perceptual representations? As technology advances, simultaneous recordings from multiple cortical areas will allow a direct assessment of these mechanisms. Combining targeted deactivation methods (e.g. cortical cooling, TMS) with single-cell recording will help constrain the functional roles of different areas.
- Is the same transient switch signal responsible for initiating shifts of attention *within* perceptual domains (e.g. between two locations or between two colors) and shifts of attention *between* domains (e.g. between a color and a location)?
- What is the relationship between the transient switch signal and working memory, which contains representations of current task instructions, prior probabilities and reward history?
- How are behavioral goals and intentions (e.g. acting on an instruction to 'attend to the location 5 deg to the left of fixation') translated into a spatially targeted modulation of the corresponding neural representation?
- How are non-spatial deployments of attention (e.g. 'attend to red items and not other colors, regardless of their locations') translated into modulatory neural signals?

This dichotomy is supported by two sources of evidence. First, damage to regions of parietal and frontal cortex can cause visual neglect, a deficit in which objects appearing in the neglected region of space fail to attract attention and therefore escape awareness (e.g. [81]). Second, multiple factors such as behavioral relevance, subjective value, and motor intention all seem to influence neural activity in PPC, FEF, and SC (reviewed in sections above). By contrast, activity in earlier regions of occipital cortex is influenced more by the sensory properties of the stimulus array.

This differential selectivity across the visual system raises a provocative question: should we classify attention signals in different brain regions according to a strict 'source/target' dichotomy? Or, should we view the visual system as a continuum, where there is a gradual transformation of incoming sensory information from a concrete representation of the retinal image into abstract representations that are more and more closely tied to conscious perceptual experience [28]? Studies reviewed in this article suggest that the relative influence of stimulus properties and behavioral goals upon the activity of neurons in topographically organized regions of occipital cortex, PPC, FEF and SC varies along a continuum, and it is difficult to pinpoint the locus in this network at which a qualitative shift from 'target' to 'source' occurs. Many regions of the visual system are both sources and targets of attentional modulation signals.

This graded and distributed account does not imply that the representations at every stage of the system are equivalent; each level plays a complementary role in the representation of attended objects in the visual scene. Conditions such as visual neglect might arise from damage in (say) PPC because it disrupts processing at a point along the continuum that is strongly influenced by the behavioral relevance or the value of a stimulus, not because ablating PPC destroys the sole source of attentional control.

On the other hand, recent evidence for a reconfiguration signal originating in PPC that does not vary as a function of the sensory properties of the stimulus suggests that there might be some neural signals that are classified as pure sources of attentional control because they operate independently of the current sensory input [79]. Additional evidence suggests that subregions of parietal and frontal cortex exhibit distinct temporal profiles during attention switching [55], and distinct parietal regions might contribute to attentional control by supporting different aspects of cue processing [82]. It is likely that regions subserving attentional control and regions that are targets of these attentional control signals are anatomically intermingled; a good deal more work is needed to flesh out these distinctions. The complexity of this issue highlights the need to carefully consider the possible functional role that observed attention signals might play in shaping visual experience, and not just the regions of cortex in which the signals are recorded.

Conclusion

To understand visual perception, we must understand how the brain resolves competition among objects in the scene, and how the anatomically distributed bits of information belonging to each object are bound together. The studies reviewed here demonstrate that selective attention operates at each level of the visual hierarchy to resolve competition between multiple stimuli. Moreover, the ubiquity of these attention effects highlights a potentially larger role for selective attention in coordinating the activity of neurons across visual areas to form perceptual coherence fields, or stable attractor states, in which different visual regions contribute complementary information to support selective object perception. Understanding the mechanisms that guide the formation of coherent neural activity across multiple regions of cortex, and how state transitions are achieved, will bring new insights into how the visual system supports active visual experience.

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