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# The brain circuitry of attention

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**From an operational perspective, attention is a matter of organizing multiple brain centres to act in concert on the task at hand. Taking focal visual attention as an example, recent anatomical findings suggest that the pulvinar might act as a remote hub for coordinating spatial activity within multiple cortical visual maps. The pulvinar can, in turn, be influenced by signals originating in the frontal and parietal eye fields, using common visuomotor neural circuitry, with the superior colliculus acting as an important link. By identifying a complex, real neural architecture ('RNA') model for attention, it is possible to integrate several different modes of operation – such as parallel or serial, bottom-up or top-down, preattentive or attentive – that characterize conflicting cognitive models of attention in visual search paradigms.**

In spatial mode, visual attention is often likened to a 'spotlight' – a restricted window within which reaction times are faster, features bound together, and items more finely discriminated [1–3]. What, in neural terms, generates a spotlight and controls its location? Naively, one would think that multiple spotlights should play upon several brain areas at once, because there are multiple visual representations. A generative role for the thalamus was originally proposed by Crick [4] (specifying interaction with the thalamic reticular nucleus in orchestrating high intensity, or 'burst', firing); this article tackles a complementary question, updating the anatomical basis of a multi-spotlight control system [5].

In cognitive terms, spatial attention is controlled by a mixture of bottom-up (BU) and top-down (TD) mechanisms. Much of the psychophysics of visual search has been concerned with isolating these two factors [6]. More recently, functional imaging (MEG and fMRI) studies have provided the impetus for the notion of attentional 'sources' and 'sinks' within the brain [7–10] – finding that fronto–parietal cortex acts as a source of TD attentional signals, whose effects are exerted over occipito–inferotemporal cortex (often known as the ventral visual pathway for object recognition). There is also found to be substantial overlap between the areas of cortex involved in shifting gaze – an overt relocation of attention – and those activated by 'covert' attentional tasks, where the spotlight of attention is able to rove independently of gaze position [11,12]. The aim is therefore to understand the operation of neural circuitry linking visuomotor and visual recognition functions. An effective strategy is to compare the real neural architecture with the architecture of cognitive models of attention, identifying comparable elements and functions.

### Subcortical circuits

In the primate brain, the chief cortical centres for gaze control are the frontal and parietal eye fields (FEF and PEF). In macaques, PEF can be identified with area LIP (Lateral Intra-Parietal); a single homologous area LIP might exist in humans [13] but, for generality, the term PEF is preferred here. Because the study of human areas, and circuitry, is still in its infancy it is obligatory to substitute macaque neuroanatomy (while bearing in mind that, ultimately, 100% homology is unlikely). Both PEF and FEF have direct output to oculomotor layers of the superior colliculus (see Box 1), and FEF has additional output to the brainstem oculomotor centres [14,15].

In so far as they act as the clearing house for transmission of gaze-control signals, areas FEF and PEF are prime suspects for organizing spatial attentional effects in the cortex itself [12]. They are massively interconnected, and each garners visual input from many sources, although not directly from area V1. Because these connections are all reciprocal, cortical feedback from PEF and FEF can certainly influence visual processing. However, cortical feedback operates as a cascade – a network with multiple sources and relatively diffuse local organization [16,60]. The subcortical circuit, by contrast, can be pictured as an integrated hub, or remote control centre for exerting synchronous influence over the cortical network [5,59].

The likely subcortical circuit for mediating attentional influences involves two centres, the superior colliculus (SC) in the midbrain, and the pulvinar nucleus of the thalamus. Both structures are known to be operative in spatial attention (Box 2). The pulvinar is an 'associative' thalamic nucleus, meaning that, in contrast to the lateral geniculate, it receives its major drive not from the retina but from the visual cortex. And, as its total output returns to the cortex, the pulvinar offers a good route for indirect transcortical communication [17]. There is little sign of a cortico–pulvino–cortical circuit specifically engineered to mediate frontoparietal–inferotemporal interactions, however, as these regions of cortex mainly connect with separate subunits of the pulvinar [5].

Another means by which frontoparietal influences might infiltrate the ventral visual pathway is a re-entrant circuit via the SC, which has diverse ascending projections to many thalamic nuclei, including the pulvinar [18]. Box 1 overviews the relevant signal input–output relationships

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**Box 1. Input–output relationships in the superior colliculus**

Neurons projecting from superior colliculus to the LGN are located in a superficial zone coincident with retinal terminals, and have relatively small cell bodies (Figure I). The output to ventral pulvinar arises from larger output cells in a zone straddling layers II and III. This zone receives direct input from some sources (e.g. retina, prestriate visual cortex and FEF) but can also receive translaminar influences (e.g. from V1, or LIP) via intrinsic collicular connections [63]. There is clearly local processing of visual inputs within the superior colliculus, for its visual responses do not directly resemble those of retina or cortex. Figure I shows an example of one property – selectivity for relative motion – being more frequently found within mid-layer II [39], coincident with the pulvinar output zone. The idea that visual signals from the superficial layers (I, II and III) can descend to layer IV, which houses presaccadic oculomotor cells, is relatively well supported; for example, in the generation of express saccades [64]. The reverse, that is, ascending influences, can be deduced from the absence of visual responses in the superficial layers to stimulus motion caused by saccadic eye movements: this, it is reasoned, demonstrates suppression by a 'corollary discharge' signal (a correlate of the eye movement signal) arising from layer IV [65].
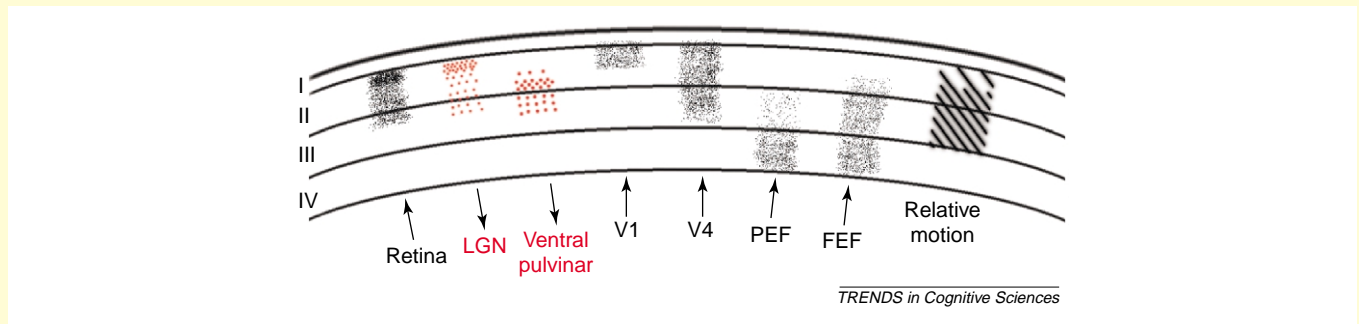


Figure I. The laminar distribution of terminals from the retina and specified cortical areas, in comparison with the laminar source of output to lateral geniculate nucleus (LGN) and pulvinar (shown in red).

in SC. Circuitry for the entire cortico–colliculo–pulvino–cortical loop is summarized schematically in Figure 1. The essence is that cortical connections with the pulvinar can be represented by two parallel gradients, parieto–superotemporal and occipito–inferotemporal – a relationship that we can refer to as 'cortical topography' [5,19]. The former gradient, occupying dorsal pulvinar, includes PEF, and the latter, occupying ventral pulvinar, is a close approximation to the ventral visual pathway. Ascending SC projections not only relay through dorsal pulvinar and other thalamic nuclei (e.g. mediodorsal) to areas PEF and FEF, but also form a visually topographic map in the ventral pulvinar [18,20].

As a vehicle for mediating spatial attention, the preservation of visual topography is clearly essential, and this can be observed in the existence of visual (or visuomotor) maps, and visually ordered connections, throughout the circuit [20,21]. Interestingly the ventral pulvinar has two well-ordered visual maps [19,22], which is why the occipito–inferotemporal gradient of connections is represented in duplicate (see Figure 1); one of these, known as the primary map, has more SC input than the other [5,20]. Figure 1b documents the superposition of visual and cortical topography in ventral pulvinar, that immediately suggests an operating mode for TD spatial attention. The key point is that the connection zones made by the areas along the ventral visual pathway all have registered visual topographies, which overlap and fuse to form the global primary and secondary visual maps in the pulvinar. Frontoparietal signals for covert attention to a particular location (a corollary of saccade-planning signals) can then be relayed into this map via the SC. This is labelled figuratively as a 'beam of attention', extending along the line corresponding to a specific visual locus within the ventral pulvinar. Activity in the beam then sets off conjugate cortical activity in the corresponding loci of all the visual maps along the ventral visual pathway – like a set of subsidiary spotlights emanating from the master one within the thalamus.

### Cognitive models of attention

How does the circuitry operate during standard visual search paradigms? One approach is to compare the neural

**Box 2. Evidence for subcortical attentional mechanisms**

The 'premotor' theory of attention was founded on psychophysical evidence that shifts in spatial attention concurrently activate oculomotor circuits, with predictable consequences on saccade metrics [66]. If saccade planning and spatial attention are inseparable [12,67,68], an obvious consequence is that the (covert) focus of spatial attention, like the (planned) direction of gaze, can only be in one place at one time. Hence, it would seem that covert attention and saccade planning share neural circuitry for resolving conflict between potential targets. The overlap in circuitry might be entirely at cortical level, involving FEF, PEF and other areas, as revealed by functional imaging studies [11,69], but there is direct evidence for endogenous spatial attention affecting SC neurons' activity [31,62]. In the most recent study [62], visuomotor neurons of collicular layer IV showed sustained activity during covert attention to a pre-cued target location located within their movement field, although this target was never a saccadic goal.

Although highly suggestive, this does not yet prove that covert attention signals 'rebound' from SC to re-enter the forebrain. Sifting the evidence for the engagement of the pulvinar in attention (e.g. neurophysiology [32,70] imaging [71] behavioural [72,73] and neuropsychological [74,75] studies), two strands in particular support the re-entrant hypothesis: (a) that SC lesions can closely mimic pulvinar lesions in disrupting endogenous attention; for example, in a task requiring target colour discrimination in the presence of a nearby distractor [73]; and (b) that the suppression of responses to retinal motion during saccades, attributable to a corollary discharge mechanism, is more frequent in both SC *and* ventral pulvinar, than in occipital visual areas [76]. Both imply that the origin of at least some endogenous signals in the pulvinar is collicular rather than cortical.
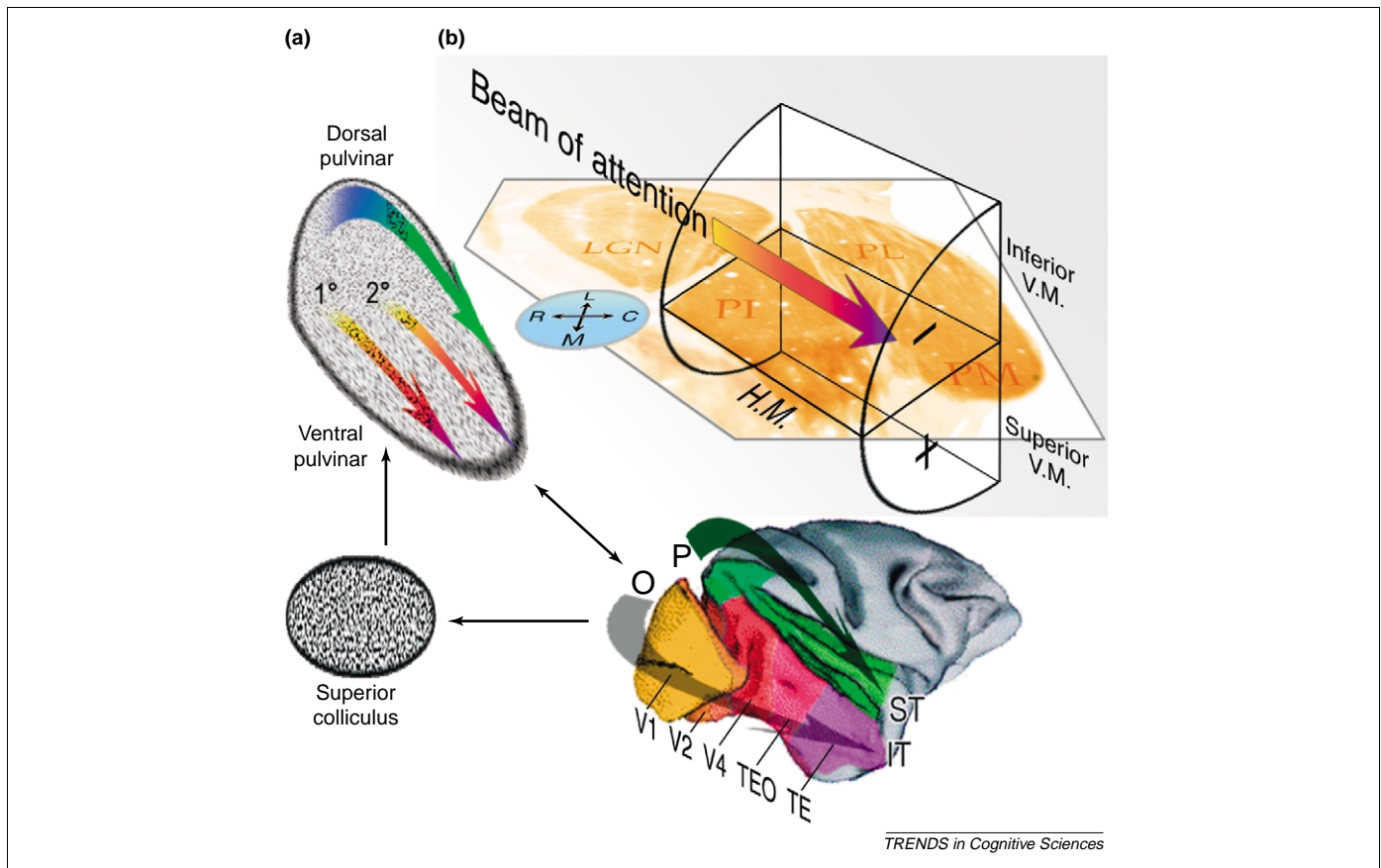
**Figure 1**. Topography of connections between cortex, superior colliculus and pulvinar: an anatomical basis for a spotlight of attention. **(a)** The triangle of black arrows shows the basic circuit – unidirectional from cortex (right) to superior colliculus to pulvinar, and bi-directional (reciprocal) between pulvinar and cortex. The topography of pulvino–cortical connectivity is summarized by two gradients (curved, coloured arrows within pulvinar): one from occipital to inferotemporal cortex (O–IT, yellow-to-purple) in ventral pulvinar, the other from parietal to superotemporal cortex (P–ST, blue-to-green) in dorsal pulvinar. The O–IT gradient is found in duplicate (primary, 1°, and secondary, 2°), each copy corresponding to one of a pair of mirror-image visual maps. Projections from the SC (stippled sectors in the pulvinar arrows) terminate over much of the territory of the primary O–IT gradient, but only over a short, initial segment of the secondary gradient. There is also a separate focus of SC projections to the dorsal, P–ST gradient, coinciding with the position of the parietal eye field (PEF) connection zone in dorsal pulvinar. **(b)** shows, in 3D, how the primary O–IT gradient is coordinated with the primary visual map, based upon a horizontal slice through the thalamus. The primary visual map is schematically depicted as a half-cylinder, formed by projecting a standard 2D visual hemifield (with superior and inferior quadrants defined by the vertical and horizontal meridians, V.M. and H.M.) along the third dimension. The illustrated plane through the thalamus intersects the volume of the map at roughly the same level as the plane of the H.M. In reality, the cylinder should conform to the actual 3D shape of the pulvinar. However, pulvinar sites representing single points in space in fact trace linear, parallel courses along the axis of the cylinder – and this visual mapping axis coincides with the axis of the cortical O–IT connectivity gradient. In other words, the gradient of cortical connection zones produces a series of registered visual maps, occupying serial, overlapping slabs within the half cylinder. The 'beam of attention' arrow represents heightened axial activity representing a point in space, which will thus activate connections to corresponding visual foci in the cortical areas of the ventral visual pathway. LGN: lateral geniculate nucleus; PI, PL and PM: the inferior, lateral and medial pulvinar subnuclei, respectively; the blue dial indicates rostro–caudal and medio–lateral axes in the thalamic section.

architecture (Figure 2a) with a variety cognitive models (Figure 2b–f) that reflect particular hypotheses of attentional function. Even if the models' components are not explicitly identified in neural terms, they can generate useful hypotheses regarding the functional interactions between neural structures, synthesized here as a real neural architecture ('RNA') model of attention (Figure 2g).

*Bottom-up function: the computation of salience*
The most salient object in a scene is the most conspicuous one. At root, this is a raw visual quality – the lemon amongst oranges, the teaspoon amidst forks etc. Such items 'pop-out' of a display, in that they draw attention to themselves [23]. Psychophysically, the search time for a 'pop-out' item is independent of the number of non-target, or distractor, items in a display, as if the underlying visual processing of each element in a display were performed in parallel. This processing is considered automatic, or 'preattentive' in nature [2,3,6,24].

A 'saliency map' was first proposed by Koch and Ullman [25], as the key part of a model for implementing parallel search, or 'pop-out', in biological systems (Figure 2b). The essential feature of a saliency map is that it pools the outputs of different feature maps across space, while retaining visual topography. The final level of salience at any point is thus indiscriminate with regard to its origins in colour/brightness, form, motion properties, and so forth, and should even be additive across features [26]. The contents of the saliency map compete, in 'winner-take-all' fashion to establish, at any moment, the most salient location that directs the focus of attention [27,28].

The neurobiological identity of the saliency map is not specified in the Koch and Ullman model, and all the structures we have so far considered – FEF, PEF, SC, pulvinar – might be invoked as candidates [29–32]. However, we should start with an addition to the list – area V1, whose role as a salience map has been modelled in most detail: Li has shown how two factors, (i) the response tuning of V1 neurons, and (ii) the specificity of their
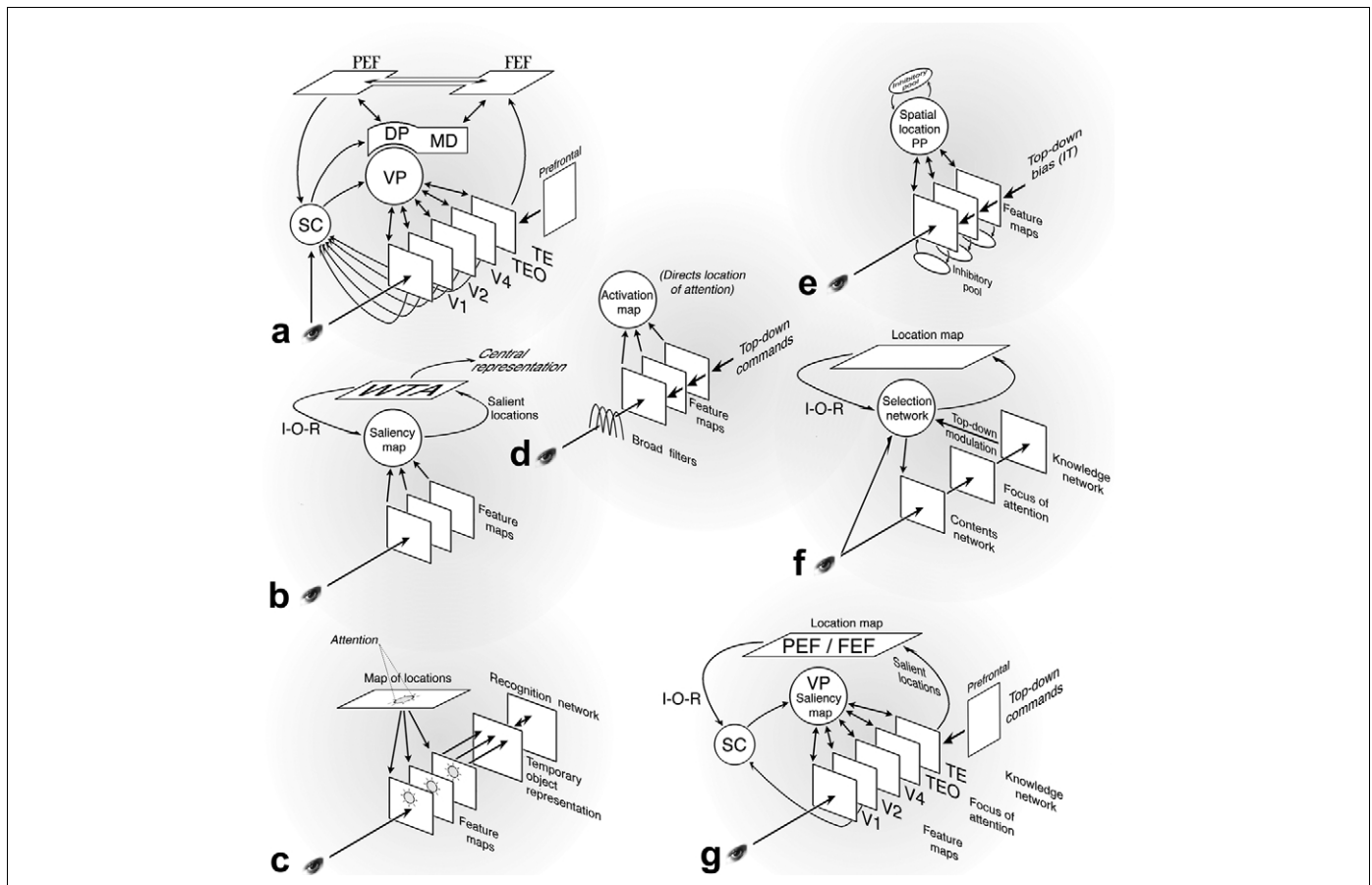
**Figure 2**. Cognitive models of attention. Each model has been redrafted to preserve its unique architecture (conserving labelled components and communications) but using a standard pictography to show equivalent elements across models, and potential correspondence to real neural components. **(a)** Brain circuitry: the core loop is composed of ventral visual pathway (cortical areas V1, V2... TE), superior colliculus (SC) and ventral pulvinar (VP). Top-down influences on this loop originate from prefrontal cortex, and from parietal and frontal eye fields (PEF and FEF), shown as a linked unit. Note that the output from PEF/FEF to superior colliculus (SC) originates from both areas, and that both PEF and FEF receive input from areas such as V2, V4 and TEO. A parallel loop involves PEF/FEF, SC and thalamus [dorsal pulvinar (DP), and mediodorsal nucleus, (MD)]. **(b)** The original proposal for a salience map (since updated computationally without alteration of the basic architecture) [25,27]. Spatial competition is initiated within each feature map, and is continued in their convergence upon a final topographic saliency map. The WTA (winner takes all) mechanism detects the most salient location and directs attention towards it. The IOR (inhibition of return) mechanism transiently suppresses this location, inducing attention to switch to the next most salient location. **(c)** Treisman's model of Feature Integration Theory [44] suggesting how TD input from a master map of locations to feature maps directs spatial search. Only items from the selected zone ('sun' symbol) in each feature map are fed, in parallel outputs (arrow triplet) to the subsequent stages. **(d)** 'Guided Search 2.0' [46]. The feature maps receive 'categorical' input from broadly tuned filters, and their internal spatial competition is influenced by TD commands as well. Their outputs are pooled within the activation map, similar to the salience map in (b). **(e)** The model of Deco *et al.* [49] ('DPZ'). The feature maps integrate bottom-up and top-down inputs, much as in model (d), but using a different spatial competitive mechanism, a common inhibitory pool. The combined salience at each spatial location is computed by 'PP' ('posterior parietal' cortex) and, importantly, fed back to the feature maps themselves. The feature maps and 'PP' iteratively converge on a single winning location, obviating the requirement for serial relocation of an attentional focus. Hence, also, there are no direct descending influences on 'PP' to mediate IOR. **(f)** The 'SAIM' model [54] lacks separate feature maps, but the 'contents network' can be thought of as a topographic feature map for a single type of feature. Spatial competition takes place only in the 'selection network', which receives a parallel visual input. The selected salient location influences transmission from the contents network into the focus of attention, which acts a translatable, magnified window onto the visual map. The 'knowledge network' can recognize certain simple objects, and prime the selection network to select their location. SAIM can mimic serial search using an IOR mechanism mediated by a location map. **(g)** The real neural architecture ('RNA') model of attention, a reduced version of (a) incorporating functional labels borrowed from models (b)–(f).

horizontal connections, combine to predict much psychophysical salience data [33]. The contribution of (ii) is vital, because the saliency of any stimulus is crucially dependent on its context. The 'just noticeable difference' for pop-out is determined not by the tuning of the neuron *per se*, but by the 'tuning' of its horizontal connections – in other words, its context sensitivity [33].

So far, so good – but can V1 be the sole source of salience? There are some pop-out phenomena that defy explanation by V1 alone. These include pop-out over a large range of spatial scales, far exceeding V1 receptive field sizes [3], and pop-out of high level features, such as cars, faces and 3D shapes [34]. By including all the areas from V1 to IT as sources for the final salience map, the RNA model (Figure 2g) can account for such observations.

Another issue concerns dimensional additivity of salience. Psychophysically, the highest additivity is found between combinations of dimensions that are least common in cortical cells, for example, colour and motion in areas V1 or V2 [26,35]. A second stage, explicitly pooling salience across dimensions, appears to be necessary – identified here as the subcortical loop through SC and pulvinar. By cortical standards, the SC and pulvinar are relatively unselective for any feature, but can show evidence of pooling [36–38]. Cells in SC, for instance, are not selective for direction of motion, but do exhibit a pan-directional sensitivity to motion contrast, that is, responding best when the motion in their receptive-field centre and surround is in different directions [39]. This behaviour, unknown in any cortical area, is ideal for a generalized

'motion pop-out' detector. The case for a role in registering salience can also be made, less directly, from several aspects of pulvinar physiology [32].

### Salience and the focus of attention

The RNA model implies a distributed salience system, in which the ventral pulvinar figures as the ultimate stage of pooling. But the salience output is exported back to the cortex – to the very same areas that are the source of the raw salience data (Figure 2g). This is a key modification to Figure 2b – that the feature maps, and the site of the focus of attention, might be overlapping sets of structures. The immediate implication is that the focus of stimulus-driven (or BU, or exogenous) attention might be determined by colliculo–thalamic interactions along the ventral visual pathway, without reference to the frontoparietal system; or, essentially, that the circuitry achieves a consensus between areas as to what is the most important (salient) location, so that they all concentrate on the same thing.

### Frontoparietal descending influences

The above formulation immediately requires some modification, to include a more significant role for frontoparietal input. One specific contribution might be the generation of 'inhibition of return' (IOR), the final essential component of the model in Figure 2b. IOR is a bias against re-orienting attention to a previously cued location, an important component of a successful search strategy, for example, in checking through an array of potential targets without repetition [40]. The SC is known to be involved in mediating IOR [41], but the mechanism need not involve neural inhibition. Rather, it appears to depend on SC activation from FEF/PEF in the hemisphere ipsilateral to the site of IOR, outcompeting the 'inhibited' location [40,42,43]. A cortical contribution would appear to be essential, given, for instance, that IOR can track with a moving object, and not merely lock on to a static location in space [40].

The next three models (Figure 2c–e) specifically incorporate top-down influences, to facilitate visual search. Figure 2c relates to Treisman's Feature Integration Theory, the original account of a qualitative distinction between parallel and serial search strategies [2,44]. Serial search occurs when the target is no more salient than the distractors, and is found as if by serial scanning of the spotlight across display items. Treisman proposed that this required directorial input to topographic feature maps from a single 'master map of locations' (perhaps parietal cortex [44]). By selecting the corresponding location in all feature maps, and suppressing other locations, only one item's set of features would become available for recognition by higher centres. The archetypal serial search paradigm is 'conjunction search', where the target is defined by a unique combination of two features that are both common within the display (e.g. a red circle amongst green circles and red squares). However, the initial generalization that conjunction targets do not pop-out was soon invalidated – for example, conjunctions of colour and depth, or motion and depth can permit parallel search [6,45].

A plethora of visual search studies further eroded the qualitative distinction between parallel and serial search, suggesting that a continuum of search efficiencies is possible, depending on the distinctiveness of the target from the distractor items. Accordingly, Wolfe's Guided Search model (GS 2.0) [6,46] (Figure 2d) used a salience map with the addition that salience is jointly determined by TD as well as BU criteria. The TD influences are not spatially specific, but are tuned to boost any instance of a particular (target) feature within the relevant map (a phenomenon known as 'priming' – for which there is now good evidence; e.g. [47,48]). The feature maps' outputs are pooled, as before, into a salience map (Figure 2d, 'activation map') and attention shifts serially from item to item, in rank order of salience.

In GS 2.0, priming can be multi-dimensional: for example, 'red' and 'circular' can be simultaneously primed, acting to guide search towards a red ring target. This computational strategy is capable of finding a conjunction target instantly – it was found necessary to add noise to the computations to induce serial search behaviour [46]. As with the models of Figures 2b and 2c, the attentional module that actually recognizes features and objects is not part of GS 2.0. The requirement for serial treatment of the display items arises from the assumption that it is by nature a limited-capacity process, analysing one item at a time. However, such serial operation of the attention module is not a foregone conclusion.

### Top-down influence in parallel search

The next example, the 'DPZ' model [49] (Figure 2e) treats visual search as a totally parallel process, implementing a proposal of Duncan and Humphreys [50], later (incorporating neurophysiology) known as the 'biased competition' theory of visual attention [51–53]. Unlike the previous models, DPZ is explicitly cast in a neuroscience framework. It includes two forms of TD influence upon basic feature maps. One is a feature-biasing signal derived externally to the model, from 'IT cortex'. Although the computational strategy differs, the action of this signal can be regarded as analogous to that in GS 2.0: activity within feature maps depends on a combination of visual input and the TD bias signal, and the feature maps' outputs are pooled within a topographic, modality-free element labelled 'posterior parietal' (PP). The latter acts something like a salience map, and it is the second source of TD input to the feature maps. In other words, the feature maps and 'PP' are reciprocally linked, and it is through their iterative interaction that the model gradually converges to a single winning-item location.

The importance of the feedback to the feature maps from 'PP' is that, as mooted for the RNA model, it identifies these maps as the cortical embodiment of the focus of attention. Attention is thus a dynamic, emergent property of the modelled system, not a separate mechanism operating elsewhere. In the converged state, the selected location is active in all feature maps – even if, for a given map, the target item is of low (raw) salience. The model thus offers a computational solution to one of the precepts of the biased-competition theory [51–53]: that the representation of the winning object achieves dominance in all feature dimensions, regardless of which features might have been the target of attention. A second important

consequence is that DPZ blurs the distinction between pre-attentive and attentive cognitive phases, stemming from Neisser [24]. From an operational perspective, one phase gradually mutates into the other, with no sharp division in time course or participating structures.

### Why is processing capacity limited?

The final model to be discussed (Figure 2f), the Selective Attention for Identification Model (SAIM) [54], again models the use of salience by cortical maps to guide the spotlight. Uniquely amongst the cognitive models here, SAIM resembles the RNA model by combining visual BU input to the salience system with TD input from a location map. TD bias from an object-recognition system (rather than individual feature-bias) is fed into the salience system directly. Although the elements of SAIM are not explicitly identified with neural structures, good correspondence in this respect derives from its roots in the 'shifter' model of attention of Olshausen *et al.* [55]. The latter took the form of a computational model of pulvino–cortical interactions, and SAIM utilizes much the same mechanisms. Briefly, the pulvinar (i.e. 'selection network' of SAIM) acts as a salience map, whose role is to control the spatial selection of signals ascending successive cortical maps (i.e. serially along the ventral visual pathway in the RNA model, simplified to a two-stage process in SAIM). The final cortical map embodies the focus of attention, which is a freely translatable and scalable window within the overall visual field. SAIM models only the spatial translation of the focus and, using IOR, follows a serial search strategy. In other words, the selection network (salience system) is the site of spatial competition, and the contents network represents the circuitry that must serially switch its processing capacity from one location to the next.

Both DPZ and SAIM represent a complete attention system, in contrast to the other models (Figure 2b–d) that deal only with the guidance system. Note that, unlike DPZ (which is intended as a dedicated search machine), SAIM captures a variety of attentive phenomena, including (when 'lesioned') aspects of clinical unilateral neglect syndrome [54]. More fundamentally, perhaps, it clearly specifies the origins of limited processing capacity (the spotlight can only be in one place at one time). In a parallel model, like DPZ, competitive mechanisms mimic the state of focal attention, but not its root cause; there is no specified gain in processing capacity at the attended location.

### The operation of an attentional spotlight

The 'spotlight' is a useful but not universal metaphor (it holds for spatial but not featural modes of attention) [1]. In the RNA model it arises naturally from the circuitry of the thalamic pulvinar nucleus: an anatomical analogue for the spotlight of attention would take the form of a localized 'beam' of activity across the 3D visual and cortical topography of the pulvinar. Intrinsic competitive mechanisms, as envisaged for salience maps [27,28], would act to focus the beam. The BU inputs are visual signals relayed via V1 and other occipital areas. TD inputs, from higher frontal or inferotemporal areas, could modulate the computation of salience, for example, by changing the

weights attached to different features [46]. A separate form of fronto–parietal TD input, principally from FEF and PEF, can impose cognitive control over the locus of attention [44], perhaps via a pathway from SC to pulvinar. Finally, subcortical processing of salience interacts iteratively with the cortex, such that a focal state of attention is an emergent property of the whole system, with no sharp divide between preattentive and attentive phases [49,54].

Areas PEF (i.e. LIP) and FEF have been proposed as salience maps in their own right [29,30], and the inference here would be that they utilize, rather than generate, salience signals. Their general purpose would be to serve as cognitive maps of locations, capable of updating across eye movements, remembering locations of hidden items, and translating behavioural goals into search strategies, incorporating IOR. Regarding overt shifts of attention, LIP might be relatively more important for reflexive saccades towards non-anticipated targets, whereas FEF plays a greater role in predictable or memorized targets [15]. Regarding covert attention, the locus of activity in each area is found to predict the locus of attention – that is, as if driving the spotlight [12,56,57]. The FEF, however, has the more direct re-entrant circuitry, its inputs to SC actually overlapping the source of the output to the ventral pulvinar, whereas those from LIP lie a little deeper in the SC (Box 1).

In the models surveyed above, input to salience maps and/or feature maps from location maps is associated with serial mechanisms of attention, whereas a parallel mechanism (model DPZ; Figure 2e) is associated with iterative interactions between salience and feature maps. As the RNA model uses both architectures, it could be capable of combining serial and parallel modes. Interestingly, one recent theoretical treatment of visual search picks a hybrid model as the best fit to empirical data, in which a serially deployed spotlight analyses local groups of items in parallel [58]. To relate this more specifically to the RNA model, note that the re-entrant input from a location map, via SC, is most prominent at the occipital (or V1) pole of the pulvinar's cortical map, where the visual map will have fixed coordinates. Proceeding by successive cortico–thalamic iterations to the opposite pole, dominated by inferotemporal cortical connections, the visual map in pulvinar and cortex might become more dynamic, such as modelled by the shifter hypothesis [55], and 'zoom' onto the attended item. It is thus possible, at least in outline, to envisage how the serial re-location of local parallel processing might operate. The underlying neural mechanisms are unknown, although neural synchronization is likely to play an important role [5,59,60] (see Box 3 for other future research questions).

### Conclusion: cortical and sub-cortical mechanisms

The key component of the RNA model of attention is the pulvinar, which is suitably connected to coordinate trans-cortical activity, and to combine both BU and TD influences within a single theatre of salience computation. Other important components are the FEF, PEF and SC which, being active in shifts of gaze, account for the close ties between overt and covert shifts of attention. Because the pulvinar, together with the FEF and SC, maintain good

spatial topography but are poorly feature specific, the RNA system described here is more obviously a vehicle for spatial attention than feature attention. This is not to outlaw direct cortico–cortical participation in spatial attention, because cortical feedback can also be modelled as a modulatory attentional influence [61]. Indeed, a very recent study suggests that symbolically cued spatial attention is not mediated via the SC (i.e. not subcortical) and that, behaviourally, the spotlight is correspondingly considerably broader [62].

**Acknowledgements**

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