

From the optic tectum to the primary visual cortex: migration through evolution of the saliency map for exogenous attentional guidance

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Abstract:

Recent data have supported the hypothesis that, in primates, the primary visual cortex (V1) creates a saliency map from visual input. The exogenous guidance of attention is then realized by means of monosynaptic projections to the superior colliculus, which can select the most salient location as the target of a gaze shift. V1 is less prominent, or is even absent in lower vertebrates such as fish; whereas the superior colliculus, called optic tectum in lower vertebrates, also receives retinal input. I review the literature and propose that the saliency map has migrated from the tectum to V1 over evolution. In addition, attentional benefits manifested as cueing effects in humans should also be present in lower vertebrates.

Highlights

- A saliency map in the primary visual cortex for primates.
- A saliency map in the optic tectum for archer fish.
- Through evolution, the saliency map migrated from the optic tectum to the primary visual cortex.

Introduction

The saliency of a visual location, at least as we define it here, is the degree to which this location attracts attention or gaze exogenously. Exogenous guidance is reflexive or bottom-up, driven by external rather than internal factors (such as the goal of an on-going task), which are endogenous or top-down. For example, the location of an orientation singleton, such as a vertical bar in a background of horizontal bars, is salient or has a high saliency value; so is the location of a color singleton, such as a red dot among many green ones. Such feature singletons, examples of which are shown in Fig. 1a, are so salient that they are said to pop-out perceptually. Saliency at a location in an image can be measured by the brevity of the reaction time (RT) taken to saccade towards, or find a target at, this location. In humans and monkeys, guiding attention exogenously to a spatial location, such as by flashing a brief cue at this location, increases the speed and accuracy of detecting, recognizing, or discriminating visual inputs appearing subsequently at the cued location[1, 2]. This attentional benefit is called the cueing effect and can also be used to measure the saliency of the cue.

Traditional views[3] presume that it is higher brain areas, such as the frontal eye field (FEF) in humans, that contain a saliency map of the visual world to guide attention exogenously. This was partly inspired by the observations that saliency is a general property that could arise from visual inputs with any feature values (e.g., vertical or red) in any feature dimension (e.g., color, orientation, and motion) whereas neurons in lower visual areas such as the primary visual cortex

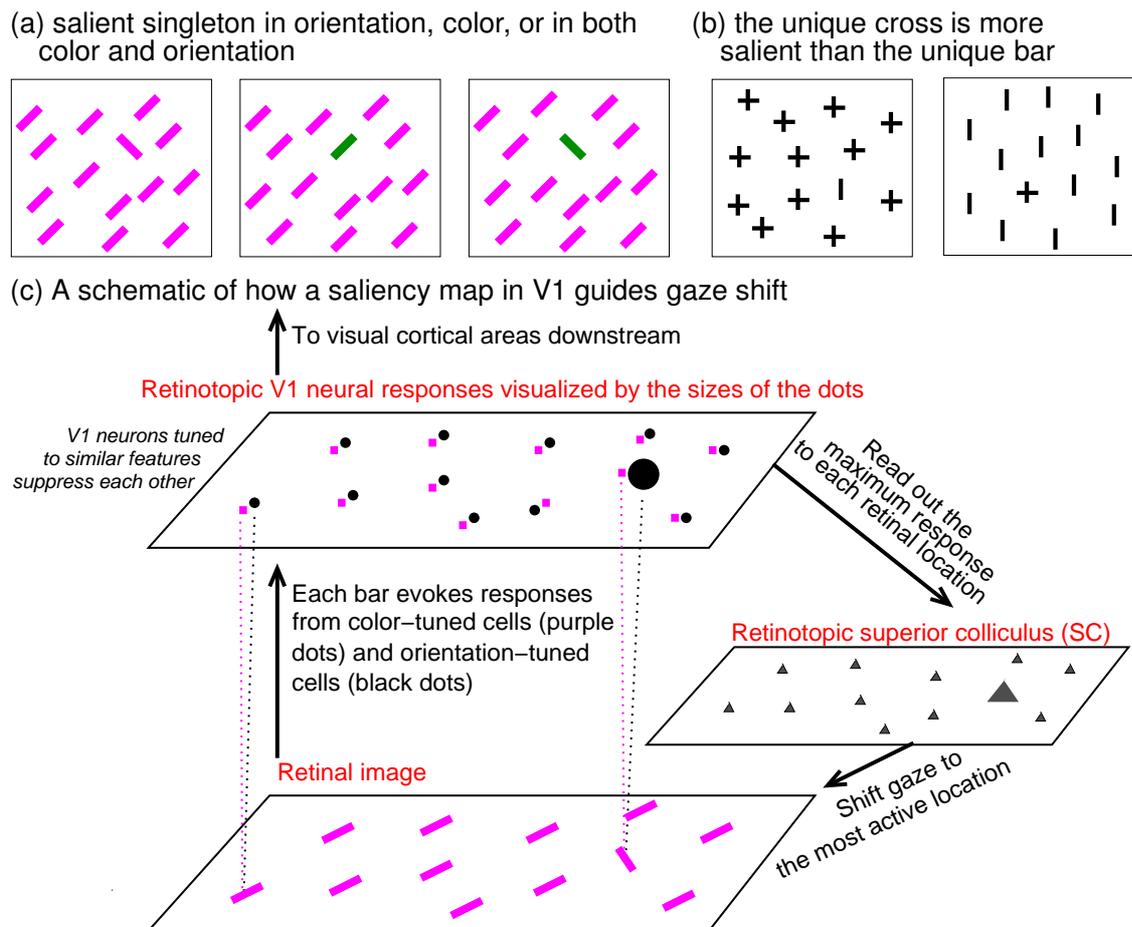


Figure 1: Visual saliency and its neural mechanisms in primates. (c) is from Figure 1 of [9].

(V1) are tuned to specific feature values (e.g., the vertical orientation) rather than being feature untuned. However, recent behavioral data in humans, combined with physiological knowledge, support the hypothesis that V1 creates the saliency map[4, 5**]. Meanwhile, FEF is often considered to be responsible for the different function of endogenous attentional guidance.

Although the idea of computing saliency without frontal/parietal brain areas contradicts traditional wisdom, it is perhaps more appealing when considering lower mammals such as rats or non-mammalian vertebrates such as fish. All vertebrates should have visual attentional mechanisms, as attention helps to focus brain's limited processing power to a fraction of visual inputs; however, prefrontal cortical areas (which include FEF) comprise a smaller fraction of the whole cortex[6, 7] in lower mammals, and fish lack neocortex. For such lower vertebrates, it appears that the superior colliculus (SC) (called optic tectum (OT) in non-mammals) is involved in visual (attentional) orienting[8].

Note that saliency at a location of the same visual item is context dependent, for example, a vertical bar is salient among many horizontal bars but not among other identical vertical bars. Hence building a saliency map requires analyzing visual features (such as color, orientation, and motion direction) and comparing features at different visual locations. Fig. 2a outlines the essential building blocks for generating and utilizing the saliency map in vision. To generate the map,

some degree of visual analysis is necessary to, first, build feature tuning in neurons and to, second, compute saliency by additional processing of the responses from feature tuned neurons, effectively comparing features at different visual locations. For the saliency map to impact behavior, there should be (1) a winner-take-all (WTA) computation over the saliency map to identify the most salient location (when the saliency map is combined with endogenous factors and other sensory input, the net outcome is what is called a priority map[10, 11], and WTA will then identify the location of the highest priority); and (2) either overt or covert orienting towards the winning location (for simplicity, we omit avoidance behavior). In overt orienting, the attended location is shifted to the center of the visual field or is acted upon/towards (e.g., in predatory behavior). Both covert and overt orienting impact visual analysis by, for example, gain controls to enhance neural responses or sensitivities[2, 11, 12], to lead to the cueing effects.

The location of the WTA computation appears to be conserved over evolution. Across vertebrates[13••, 7], SC/OT is retinotopic. Its upper layers receive visual inputs (from the retina and forebrain/V1); its intermediate and deep layers receive inputs from the upper layers and receive context inputs, which include (spatially aligned) sensory inputs of non-visual modalities and other inputs from the forebrain (such as endogenous inputs from FEF in primates)[13••, 7]. WTA appears to occur in the intermediate and deep layers of SC/OT, activities at different visual locations suppress each other so that the response to the winner location is higher than the responses to the other locations[13••, 14••, 15•, 7, 16•, 17••, 18]. Along with orienting to the attended location (e.g., by directing a saccade), the outcome of WTA can impact visual analysis in at least two further ways via efferent projections from SC/OT. One of these innervates dorsal thalamic regions (such as pulvinar and lateral geniculate nucleus (LGN)), which in turn project to cortex or to forebrain areas in non-mammals. The second efferent projection is direct to the retina in lower vertebrates[7].

This paper argues that the brain region that realizes the saliency map is not conserved across species. I will review recent findings which suggest that V1 could realize a saliency map which guides attention exogenously in primates, and propose that, over the course of evolution, the saliency map migrated from the OT/SC to V1, just as much visual analysis migrated from sub-cortical areas to the cortex.

To avoid confusion, we must first clarify what is meant by the claim that a saliency map arises in a particular brain region. This is that the saliency values are first computed and explicitly represented in neural responses in this brain region. Downstream brain regions can inherit the saliency values for further processing or action. For example, when this map is first created in V1, it can be projected directly or indirectly to SC or FEF. In turn, they can read out the saliency values to execute a shift in attention or arrange for exogenous and endogenous influences over attention to compete or be combined. Although the read-out makes a copy of the saliency map in downstream areas, these downstream areas are not deemed responsible for the saliency map, just as a printer attached to a computer is not responsible for any graphics sent from the computer for printing. SC neurons in monkeys are normally untuned to any visual feature[13••], making the monkey SC a relatively pure map of space that is devoid of visual feature analysis. Of course, such a pure space map is appropriate for performing a WTA operation on a saliency map read out from an upstream source.

Saliency maps in vertebrate species

A saliency map in V1 for primates

Noting that the activities of V1 neurons could serve as a universal currency to bid for attention regardless of those neurons' preferred features, Li[4, 5**] proposed that the saliency map is created in V1. According to this, the saliency at any location in a scene is the highest V1 response to input at that location relative to the highest responses to other locations, see Fig 1c. The neural mechanism by which V1 responds more vigorously to salient feature singletons than to the non-salient background items is iso-feature suppression[19•, 4], which makes V1 neurons tuned to the same or similar features suppress each other. For example, nearby V1 neurons tuned to the same orientation, for example, right-tilt, suppress each other. Thus, in an image containing many background right-tilted bars (Fig 1c), the responses to these background bars are lower than the response to the salient singleton, the unique left-tilted bar, because the V1 neuron responding to this orientation singleton escapes iso-orientation suppression. Similarly, iso-color suppression makes salient a color singleton, like that in Fig 1a.

Data supporting this V1 saliency hypothesis have since emerged. In particular, behavioral data confirmed its surprising prediction that an eye-of-origin singleton should be very salient. This singleton is for example an item uniquely shown to the left eye among many items shown to the right eye. Such a singleton, if it is unique only in terms of its eye-of-origin feature, can scarcely be distinguished in its appearance from the surrounding visual items. Nevertheless, it is no less salient in terms of its ability to attract gaze than a salient and highly distinctive orientation singleton[20**, 21]. This finding provides a hallmark that the saliency map is in V1 rather than extrastriate cortical areas, since cortical neurons outside V1 (unlike those in V1) are not tuned to eye-of-origin[22, 23] and hence cannot contribute to a saliency computation based on this feature. Indeed, it is the insensitivity of the extrastriate cortical neurons to the eye-of-origin that makes this feature (unlike orientation, color, or motion direction) invisible to perception.

V1 projects monosynaptically and retinotopically to the upper layers of the superior colliculus (SC)[13**, 24, 25•]. This is likely how the saliency map is copied from V1 to SC, see Fig 1c. Since the saliency value of a location is represented by the highest V1 response to this location regardless of the preferred features of the V1 neurons, some sort of neural circuitry is needed to convey this saliency value from V1 to SC without projecting the feature tuning property. For example, V1 circuit could be such that each SC projecting layer 5 neuron combines local neural responses such that its response is equal to the largest response from the other V1 neurons sharing its receptive field location. Another possibility is that both the circuitry around layer 5 in V1 and the circuit inside the SC onto which the V1 fibers project and converge play a role in copying the saliency map[11]. In either case, in V1, the SC projecting layer 5 neurons, compared to the other layer 5 neurons, should be less tuned to visual features. Meanwhile, SC neurons at different locations suppress each other; this suppression enables a WTA competition in the saliency map copied from V1 to select the most salient location[14**]. Visual orienting towards the most salient location can be made by the activation of SC neurons in its deeper, motor-related, layers. These SC neurons project to the brainstem, and directly or indirectly to the spinal cord, to shift gaze and/or to turn head and body[13**, 26•, 7] to the selected location.

If SC is lesioned in monkeys, saccades can be directed via a longer route through FEF, which can bypass SC and guide saccades itself directly via the brainstem[26•]. Consequently, a SC lesion prolongs RTs to saccade to a highly visible object that suddenly appears on a blank screen, and eliminates the so-called express saccades that have the shortest RTs[27•]. This is because the lesion

impairs the exogenous, reflexive, control route realized by the SC. On the other hand, lesions in FEF, which is associated with endogenous attentional guidance, only weakly affect such saccadic RTs[27•] since reflexive orienting via SC is sufficient for such easy tasks. Conversely, FEF lesions make memory-guided saccades (which are endogenous and non-reflexive) difficult[28]. Primate retina also projects to SC; however this appears not to constitute a saliency map (at least in normal circumstances). This is because lesioning V1 while leaving the retina intact makes monkeys unable to make visually guided saccades[26•] for at least several weeks[29•]. Furthermore, V1 lesions make monkey SC neurons in the (motor-related) deeper layers non-responsive to visual inputs[26•].

Since neurons in V1 are only tuned to simple features like bars and edges, one may wonder whether saliencies at locations of complex visual objects such as faces may require at least partial contributions from extrastriate visual areas such as V4 and IT. Faces are indeed likely to attract attention by a combination of both fast and transient exogenous attraction and slower and longer lasting endogenous factors[30, 31]. However, exogenous attentional attraction does not require object recognition, thus not having face detectors in V1 cannot be an argument against V1's role in the saliency of a visual location on a face. A case of looking or attending before seeing or recognizing the visual object at the attended location is dramatically demonstrated in the strong saliency of the eye-of-origin singleton whose unique eye-of-origin feature is not recognized[20••].

Not only is recognition unnecessary for saliency, recognition of visual object by itself is insufficient to account for saliency. Fig 1b demonstrates that a cross among bars is more salient than a bar among crosses; this would not be the case if saliency depended on recognizing the bar, the cross, and thus the difference between the bar and cross, since this difference is the same in both images of Fig 1b. Instead, V1 saliency hypothesis suggests that the location of the unique cross is salient not because any V1 neuron detects or recognizes the cross, but rather because the neurons responding to the unique horizontal bar in the cross escape iso-orientation suppression and respond more vigorously than neurons responding to the other (vertical) bars in the image.

It has also been shown that behavioral RTs to the feature singletons like those in Fig 1a can be fully and quantitatively accounted for by the predictions from the V1 saliency hypothesis without evoking any extrastriate contribution[9]. For example, the color-orientation singleton (unique in both color and orientation) in Fig 1a is so salient that the RT to detect it is shorter than the RT to the color singleton and the RT to the orientation singleton (each unique in only one feature dimension) in Fig 1a. Furthermore, this RT to the color-orientation singleton is also shorter than predicted by a statistical facilitation between two independent processes, one for the RT to the color singleton and the other for the RT to the orientation singleton[32, 33•]. This finding manifests the existence of V1 neurons tuned simultaneously to both color and orientation[34]. Furthermore, it also manifests that such V1 neurons must have sufficient activations (compared to the single-feature tuned V1 cells) and exhibit iso-feature suppression in both feature dimensions such that their responses to their preferred input features are highest when this input feature is a feature singleton in both feature dimensions[33•, 35].

A saliency map in the optic tectum for archer fish

Archer fish hunt by shooting water from their mouths at insects flying above water. Recently, Ben-Tov *et al.* [36••] found evidence for a saliency map in OT of this species. Singletons in motion direction or motion speed feature (analogous to the color or orientation feature in Fig 1a) apparently pop-out for archer fish such that these fish preferentially orient to singletons rather than background items and their orienting RTs are independent of the number of background items.

(a) Building blocks for creating and utilizing the saliency map for exogenous guidance of attention

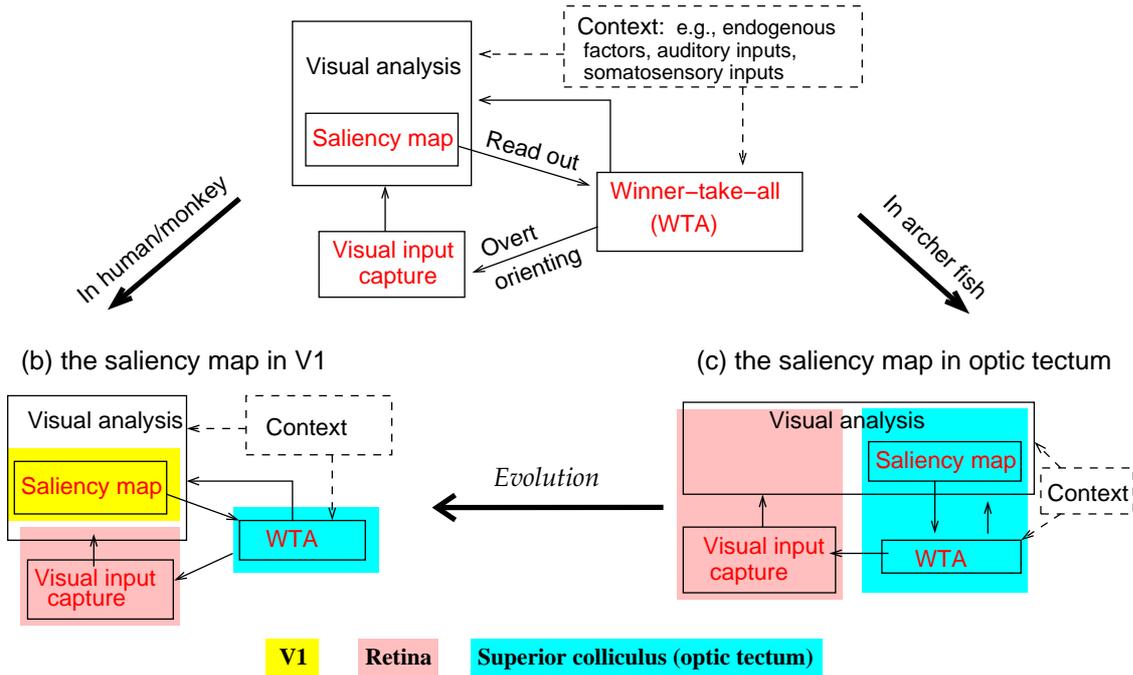


Figure 2: Building blocks for the creation and utilization of the saliency map in the brain (a) and its implementations (b) and (c) in animal species. The pink, yellow, and cyan colored regions denote retina, V1, and SC/OT, respectively.

Furthermore, a direction-speed singleton, unique in both motion direction and motion speed, is even more salient than a singleton unique in only direction or speed[36••].

The OT neurons in archer fish, like V1 neurons in monkeys and cats, are tuned to orientation and/or motion direction[37], and, based on their tunings to spatiotemporal frequencies[37], some neurons should also be tuned to motion speed. Focusing on the feature dimensions of motion direction and motion speed, Ben-Tov *et al.* [36••] found that many OT neurons in archer fish showed iso-feature suppression. OT neural responses to their preferred feature are higher when this feature is a singleton rather than a background item, and, for some neurons, this response is higher still when the singleton is unique in both feature dimensions[36••]. These OT neural properties are analogous to those in primate V1 which has cells tuned (for example) to color, orientation, or both and exhibits the corresponding iso-feature suppression. The link between visual search behavior and V1 physiology in primates mirrors that between behavior and OT physiology in archer fish, although, for archer fish, whether the extra degree of saliency in the direction-speed (double-feature) singleton is beyond that due to a statistical facilitation between the two feature dimensions has yet to be determined. Taken together, these findings suggest that the OT of archer fish performs the sort of saliency computation that V1 does in primates.

Could the saliency map in OT be inherited from a V1 homolog in fish? Fish lack a neocortex; and it is not known if there is any homolog of V1 in fish forebrain, which is typically concerned much more with olfaction than vision[7]. We suggest that it is also unlikely that the saliency map in OT is inherited from the fish retina, because of the feature selectivities of the OT neurons. To see this, note first that, in primates, the saliency map in V1 is copied to the SC, whose neurons are

mostly untuned to visual features[13**]. In other words, while feature-tuned neurons help build a saliency map, copying this map from one brain region to another does not require copying the feature-tuning properties. Not only are the OT neurons in fish feature-tuned, but it has also been found that, in zebrafish at least, feature tuning in OT can be very different from that in the retina (although it can also be inherited from that in the retina)[38, 39*, 40]. This suggests that neural feature tuning in fish OT serves its own purpose, perhaps particularly to create a saliency map.

Neural processes for saliency computation across different vertebrates

Based on the observations in the previous sections, we consider the hypothesis that monkey and fish lie at the two ends of the vertebrate phylogenetic scale, with saliency maps in V1 and the upper layers of OT, respectively, see Fig. 2bc. To evaluate this hypothesis, we examine the trend across vertebrates of visual processing leading to the saliency map.

Relative emphasis between retinthalamic and retinotectal pathways

From lower to higher vertebrates, the percentage of resources devoted to SC/OT compared with that devoted to V1 is reduced. One way to quantify this is via the ratio between the volume of SC and that of LGN, which relays retinal input to V1. This decreases from lower to higher mammals: it is 3:1 in hamster, 2:1 in rats, and 1:8 in rhesus monkey[13**]. In mammals, the projection to the SC from the forebrain is often more extensive than that from the retina, but such projections are sparse in non-mammalian species[13**]. Meanwhile, from lower to higher mammals, the percentage of retinal ganglion cells that project to the SC/OT decreases[13**], from almost 100% in rabbit[41] and rat[42], and at least 70% in mouse[43], to about 50% in cats[44**], and about 10% in primates[45**, 44**].

Degree of visual feature tuning in tectum neurons

Meanwhile, in higher vertebrates, feature tuning in SC/OT neurons appears weaker. The OT of fish, amphibians, and reptiles are replete with pyramidal cells with extensive basal and apical dendritic arborizations that allow these cells to sample retinal inputs for visual analysis[13**]. However, in mammals, the SC of cat does not have either pyramidal cells or cells with extensive dendritic arbors[13**]. Consistent with this, single cells in the colliculus show more specificity for patterns in fish, amphibians, and birds than in higher mammals[13**, 46]. OT/SC cells tuned to orientation have been seen in ground squirrel, tree shrew[13**], and mouse[47, 48], but not in cat or monkey[13**]. Direction selectivity in SC cells is rare in monkeys but present in pigeon, mouse, hamster, and cat[13**, 47]. After removing inputs from V1 to SC, this direction selectivity in SC cells persists in mouse[47] but is reduced in cats[13**, 45**], suggesting that this feature is partly inherited from V1 in cats. Upper layer SC neurons in mouse also display tuning to the feature of direction-independent motion, looming motion, speed, and size[49].

That OT/SC neurons are feature tuned perhaps helps them to compute saliency through the mechanism of iso-feature suppression, and iso-feature suppression is consistent with neural response properties observed in archer fish[36**]. However, although feature singletons such as those in orientation, color, motion direction, and eye-of-origin features are highly salient for humans, in monkeys it is V1 and not SC cells that are tuned to these features[22, 13**, 45**], suggesting that saliencies for these singletons are calculated in V1 before being projected to SC.

Retinal ganglion cells and their central projections

In cats and monkeys, the majority of retinal ganglion cells (RGCs) are X and midget cells respectively. They have spatially center-surround receptive fields, respond linearly to inputs, and are not tuned to complex spatiotemporal features like orientation and motion direction. They project to LGN en route to V1 and do not project to SC[44••]. Accumulating evidence supports the idea that these RGCs code visual input information efficiently for transmission to the brain[50, 11]. The second most numerous type of RGC cells is the Y or parasol cells for cat or monkey, respectively. These are similar to the X or midget cells, but are more sensitive, have nonlinear and more transient responses to inputs, have larger receptive fields, and they project to both LGN and SC[44••]. One suggestion is that they send the minimum necessary amount of information to the brain as fast as possible[51].

However, lower vertebrates have some dozens of other types of RGCs[44••], and RGCs of these other types collectively comprise an increasing percentage of the total number of RGCs. Many of these RGC types have complex spatiotemporal receptive fields and respond nonlinearly to inputs, such that they can be viewed as detectors for such spatiotemporal features as orientation, motion direction, foreground motion, and local edge contrast[44••, 52, 53, 40, 54]. Let us call them the feature-detector RGCs. They tend to have larger receptive fields and project to SC/OT[13••, 44••, 55••]. They only comprise a few percent of RGCs in monkeys[55••], but are often in the majority in lower vertebrates[44••, 40, 52, 54]. For example, in the mouse retina, about 50% of the RGCs are feature detectors for motion direction, orientation, or local edge contrast[56•], and there are 20 or more RGC types, depending on the methods of classification[54, 52, 56•]. Birds, whose visual system is dominated by the retina-to-OT rather than the retina-to-thalamus pathway[57, 58], also have a heterogenous collections of RGC types, as characterized by the morphology of dendritic fields of the RGCs[58, 59]. Furthermore, the bird RGCs that project to the thalamus tend to have the less complex, center-surround, structure for their receptive fields[58, 59].

Hence, in vertebrates, feature-detector RGCs tend to project to SC/OT while RGCs of simpler (e.g., center-surround) receptive fields tend to project to thalamus, with a trend for an increasing emphasis on the retina-to-tectum pathway in lower vertebrates. This is consistent with the idea that the saliency map is built in SC/OT in lower vertebrates, based partly on the ready-made feature maps from retina and partly from additional analysis by SC/OT's own feature detectors (e.g., in pigeon[60•] and zebrafish[39•]). Meanwhile, although RGCs that project to thalamus have simpler receptive fields, monkey V1 receiving these efficiently coded visual inputs can use them to construct neurons tuned to many different features, and thereby build a richer saliency map[11].

One excellent example of the latter is that cells in the monkey retina that are tuned to color (the midget cells) do not project to SC[13••, 44••]. However, color singletons enjoy a substantial saliency. According to our scheme, this saliency necessarily depends on V1 inputs to SC.

V1 processing

While there is no known V1 homolog in fish, V1's role in visual processing increases in higher vertebrates. Selectivities of V1 neurons to orientation, motion direction, and scale are present across mammals such as monkeys[22], cats[61], and mouse[62, 63], while visual acuity in monkey is 100 times higher than that in mouse. In mice, although selectivities in orientation and direction features are already prevalent in retina, recent data suggest that these selectivities are further refined in V1 so that the cortical neurons exhibit sharper tunings and have a greater diversity of preferred features[64].

In visual Wulst, which is the homolog of V1 in birds, orientation selectivity has been observed in chickens[65], and selectivity to orientation, motion direction, and even binocular disparity have been observed in owls[66]. The size of the receptive fields in chicken Wulst is huge, in the range of 20–45°[65], slightly larger than those in mouse[63], but receptive field sizes in owls are heterogeneous with some as small as about one degree[66].

Effects of lesion in V1 or SC/OT

In birds, OT lesions produce deficits in visual discrimination, localization, and reflex orientation[13**] without recovery (in pigeons) even after extensive postoperative training[67]. In frogs, an OT lesion makes the animal blind except for ballistic escape behavior[13**]. In fish and amphibians in general, ablating OT causes substantial deficits in visual pattern perception[13**, 26*]. By contrast, in mammals such as cats, a SC lesion mainly affects orienting[13**, 26*]. Cats become less easily distracted, although there are some reports of deficits in pattern perception[13**]. In monkeys, as already mentioned, a SC lesion does not noticeably affect behavior except for eliminating the short latency reflexive saccades[27*].

The opposite trend arises for lesions or disruptions in V1. In monkeys, as mentioned, they render deep layer SC cells unresponsive to visual inputs[13**, 26*] and make the animal unable to make visually guided saccade for at least weeks[26*, 29*], although the animal can still fixate when the input is sufficiently intense[13**]. In mice, V1 lesions mainly reduce visual contrast sensitivity and acuity in visual discrimination tasks[68, 69]. While SC neurons in monkeys are mostly untuned to visual features[13**], disruption of the V1 to SC pathway reduces or eliminates direction selectivity in SC (upper layer) neurons in cats and hamsters[13**, 49] but not in ground squirrels[13**], rabbits[13**], and mice[47, 49]. These findings collectively suggest that visual orientation involves SC/OT in all animals, while visual analysis relies more on SC/OT and V1, respectively, for lower and higher vertebrates.

Concluding remarks

In summary, it appears that through the evolutionary expansion of the forebrain, visual analysis increasingly migrated from the optic tectum to the forebrain, in particular to V1[13**]. This was accompanied by decreases in the percentage of retinal ganglion cells that project to the tectum. It was also accompanied by increases in the percentage of retinal ganglion cells which, like the midget cells in monkey, are not special feature detectors, but rather encode visual information efficiently for transmission via the thalamus to the forebrain to enable visual analysis. With the migration of visual analysis to V1, the computation of the saliency map also migrated from the tectum to V1 in monkeys. This saliency map is then read out by the tectum to execute WTA for attentional selection.

Could some vertebrates have a saliency map in retina? This is perhaps unlikely. In higher vertebrates, the saliency map could not be built in the retina from the limited feature analysis that is present there. The retina of lower vertebrates does include much richer feature analysis. However, building a saliency map in the retina before copying it to the tectum would only make sense if no substantial visual feature analysis was additionally needed in the tectum. However the tectum in lower vertebrate occupies a larger fraction of the brain and performs substantial visual feature analysis.

In traditional wisdom for primate vision, V1 has been seen as too lowly to play a significant role in guiding attention, a task presumed for the frontal and parietal brain areas[3]. It is helpful

to note that, from the perspective of a frog, who could be easily fooled to attack an imitation fly in its visual field, V1 could be seen as an overkill for guiding its visual orienting. This perspective reminds us that, despite our common sense, exogenous attentional guidance does not require visual object recognition.

This paper assumes that the drive behind essential behavior of visual orienting in lower vertebrates has basically the same nature as exogenous attentional guidance in humans and monkeys. This assumption predicts that the benefits of attentional guidance manifested in the cueing effects observed in humans and monkeys[1•, 2, 12] should be similarly present in lower vertebrates such as frogs. This prediction can be readily tested, and is consistent with recent observations in birds[70].

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A review that visual cortical neural responses exhibit contextual influences, in particular, iso-feature suppression

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