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Review Article

Theories and Experiments on Perceptual Filling-in at the Retinal Blind Spot: A Survey

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Abstract

Flow of sensory signal between our eyes and brain is one of the most significant biological communications by which the brain gets several times less compressed information than that received by the eyes. Blind spot, the part of photoreceptor free area of retina from where optic nerves emerge out to convey visual information to brain, is a natural physical limitation of our retinal strata because of which we are unable to get full information of the outer reality. Perceptual filling-in is one of the significant attributes of monocular vision which turns up when a light stimulus appears at blind spot. As this important interpolation process procures a visual compilation without any such oddity, the cardinal mechanism behind it is an interesting and paramount topic of exploration. To model this process computationally and to decipher the underlying neural mechanism, research concerning the designing of various psychophysical experiments is on the rise, presently. Numerous experiments that demarcate the significant roles played by different biological and environmental factors (i.e., visual attention, surround information etc.) in filling-in process, in turn enhance the modelling and understanding of this biological phenomenon. Our article produces a holistic description of filling-in mechanism for deciphering the complex integrated mechanism accomplished by the parts of human visual system including eyes, brain, various ocular cells and visual pathways. With this highly congruent intricacy we can perceive the reality despite missing some actual information. The historical study of systematic realization of visual world 'without reality', in combination with former and recent explorations to measure neural activity has yielded a rich source for guiding neurobiological and computational frameworks and experimental investigations that have been systematically presented in this survey paper.

Keywords: *Filling-In; Monocular Vision; Photoreceptor; Scotoma*

Abbreviations

CMF: Cortical Magnification Factor; HPC: Hierarchical Predictive Coding; PE: Predictor Estimator; ISI: Indian Statistical Institute; CSRI: Cognitive Science Research Initiative; DST: Department of Science and Technology

Introduction

To let humans navigate through the world successfully, the photoreceptors (rods and cones) of the retina of our eyes send back visual signals to the brain through various intricate visual pathways. Still, the visual information we perceive is not entirely complete. Each human eye has a blind spot (See figure 1), angled about 15° in the nasal retina and subtended approximately 6° to 8° visual angle. It is the photoreceptor free zone of retina from where optic nerves come out together and thus physical information cannot be received by this area. Astonishingly, we can comprehend the visual world uninterruptedly both in monocular and binocular vision. Perhaps in binocular vision, the region for one eye's blind spot in visual area of brain is complemented by the usual retina of the fellow eye. In case of monocular vision, though we are supposed to perceive a discontinuity in our vision, we do not perceive any such discrepancy at all. Many researchers are involved to unbox the mystery of how the brain organizes the whole mechanism so that our vision is free of any oddity in spite of having such a limitation of retinal anatomy. In the present study, different evolving techniques those are implemented in variegated dimensions of optimizations in filling-in scenario have been explored extensively. After assessing different research studies related to perceptual filling-in at blind spot a brief survey has been performed for future reference so that it would act as a catalogue for recent development in this area. Existing research works related to perceptual filling-in at blind spot are categorically explained by citing relevant literature based on the following three research domains:

- Experimental findings on blind spot filling-in.
- Explanations of perceptual filling-in at blind spot in the light of possible neural mechanisms.

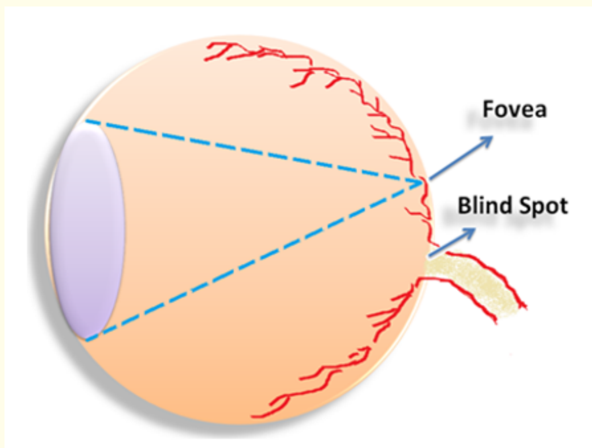

Figure 1: *Position of blind spot in human eye.*

- Explanations of perceptual filling-in at blind spot on the basis of computational modelling.

The concluding remarks are presented thereafter.

Experimental findings on blind spot filling-in

A seminal work on blind spot

According to some early scientists, our brain simply ignores the blind spot but Ramachandran [1] steered away from the existing belief of ignoring the image information at the blind spot area to assert that perceptual filling-in involves some computational mechanism in the brain. According to him, perceptual filling-in in natural blind spot (See figure 2) is obtained by surface interpolation. He mainly emphasized the characteristics of filling-in process and suggested that this process is not cognitive, it happens early in visual processing and a clearly described outline contributes the most for the proper establishment of filling-in mechanism. By another experiment he concluded that our brain performs filling-in before detecting motion.

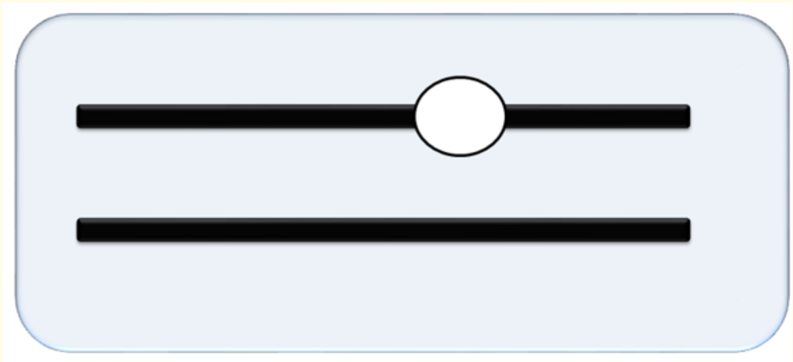

Figure 2: *Filling-in by bar stimulus at blind spot.*

Perceptual filling-in at artificial scotoma

Ramachandran and Gregory studied the spatio-temporal characteristics of filling-in phenomenon for artificial scotoma [2]. They proved that different kinds of filling-in procedures exist for the static and dynamic background. They also observed that filling-in mainly depends on the adaptation of the neural detectors that extricate the contour information of the object placed in the scotoma region. One of their experiments ascertained that due to filling-in when a stimulus gets disappeared in the scotoma region, placing it either side of its previous position seem to create a motion. The scientists concluded that though the disappearance of the object is a contribution of the dorsolateral area, the processing of motion is done in the middle temporal zone. Another finding of them suggested the time-varying neural characteristics of filling-in through which the dynamic nature of perception can be realized. They described that filling-in can take place for textured background as well and that texture has an impact on the nature of the filled-in surface. In case of retinal scotoma, the filling-in occurs only with congruent colors and static noise. According to them, the converging process starts from the edge of the blind spot area and the illusory contours effect the filling-in process.

Contribution of binocular rivalry in blind spot filling-in

In dichoptic vision, binocular rivalry makes some existing objects invisible whereas in blind spot filling-in process some non-received information becomes substituted by the surrounding one. He and Davis [3] investigated the extent to which this filled-in illusory information of one eye takes part in the contention with the perceived real information of the fellow eye. The rivalry between two real information and between a real and a filled-in information were measured to compare their performances in this biological competition. If no object was placed in the blind spot of one eye, the other eye's object experienced Troxler type fading [4]. If an annulus was placed around the blind spot of one eye, the other eye's stimulus was perceived at the center of the annulus due to inter ocular lateral suppression. But when a solid stimulus was placed on the blind spot a filled-in information was perceived and the degree of rivalry became less because the total number of appearances of the other eye's stimulus got reduced. Various studies states that filling-in occurs in between striate cortex and extra striate cortex whereas rivalry occurs in extra striate cortex and this fact indicates that filling-in occurs before rivalry. The observations of this study concluded that filling-in has a strong suppressive effect on rivalry. According to Chen., *et al*. [5], in spite of absence of local image conflict, filling-in rivalry has some common attributes with other types of perceptual rivalry.

Effect of attention on blind spot filling-in

Lou and Chen tried to prove that visual attention plays an important role in filling-in phenomenon [6]. They observed that width of the bar plays a significant role in filling-in process. They also noticed that in case of diffused attention, filling-in occurs at a great extent.

The superiority of feature mixing during the process of perceptual filling-in

According to Hsieh and Tse, for retinal stabilized images the foreground features are not lost due to the merging of the foreground and background attributes [7]. The authors used both static and dynamic stimuli to analyze this color mixing. For static stimuli, the perceived color is biased to the color having high luminance and expansion and the merging procedure is a linear one. For non-static stimuli, the perceived feature depends on the direction of motion and the foreground-area. In balanced situation, the perceived motion is a conglomeration of the movements of fore-parts and back-parts.

Studies of similarities among different kind of filling-in mechanisms

Durgin., *et al*. [8] reported the similarities among blind spot filling-in, amodally completed objects concerning surface segregation and perceptual interpolation of hindered objects while viewing them by peripheral retina. To explain some blind spot upshots, the authors used zero crossing techniques along with edge information extraction mechanism that emphasizes those parts of the image which have a vivid dissimilarity in luminance with the other parts. The temporal alliance between the filling-in and motion awareness results in same perception for blind spot filling-in and amodal completion.

Impact of perceptual filling-in in natural blind spot on pupillary light reflex and dynamic filling-in process

Miyamoto and Murakami [9] showed that both the large and the small disk stimuli adjacent to the blind spot (i.e. extrinsic to the blind spot) produce same amount of reflex whereas intrinsic stimuli generate no reflex at all. They proved that pupillary light reflex is influenced by the perceptual filled-in surface and not by the area of the suddenly appeared stimulus. They also stated that some high sensitive mechanisms are involved in pupillary light reflex. Maus and Whitney [10] explained the motion-induced position shifts to describe dynamic filling-in process which uses spatiotemporal information from the motion system to extrapolate visual percept into the scotoma.

Nature of the filled-in surface of blind spot and contribution of one-sided stimulus in filling-in scenario

Baek., *et al*. [11] conducted some experiments to relate the perceptual nature of physical surface with the neuronal interpolated one which is generated either from monocular or from binocular filling-in process. According to the researchers, when two bars, having parallel or orthogonal gratings to their orientations with different angles, were placed on the opposite fringes of the blind spot, the filling-in mechanism involved same contour-integration mechanism as the general surface interpolation. According to Araragi., *et al*. [12] a line segment presented on either side of blind spot also takes part in filling-in paradigm.

Relating psychophysics to retinal topography regarding the analysis about the effect of awareness on blind spot filling-in

As the combination of intrinsic and extrinsic stimuli helps the observers to become aware about filling-in process at the blind spot, some researchers [13] placed a horizontal bar inside blind spot region as an intrinsic stimulus. When the length of the bar got increased a bit at both the sides, only two blobs became visible at the ends of the bar. Further increment in the length of the bar helped to perceive a hazy bar with two prominent blobs at the ends and this kind of hazy bar with two prominent blobs at the ends was described as "ghost center". Eventual enlargement in the length of the bar helps in perceiving an entire filled-in bar (See figure 3).

Brightness suppression in binocular vision controlled by different parameters

Paradiso and Nakayama [14] explained the process of binocular vision with respect to brightness suppression while viewing two different objects with monoptic and dichoptic vision. According to them, the shape of the object plays an important role to subdue brightness. The spatiotemporal properties of the object are also very significant for brightness suppression when the object is viewed by monoptic or dichoptic vision. Brightness suppression occurs to a large extent in the dichoptic vision, in simultaneous presentation of objects and in the situation where mask is present after the target. With the increasing spatial difference between the target and the mask, the time required for brightness suppression also increases. The authors suggested that brightness spreads towards the center of the target and is interrupted by the contour of the mask. Thus, brightness of the target gets suppressed. The propagation speed of lateral brightness is

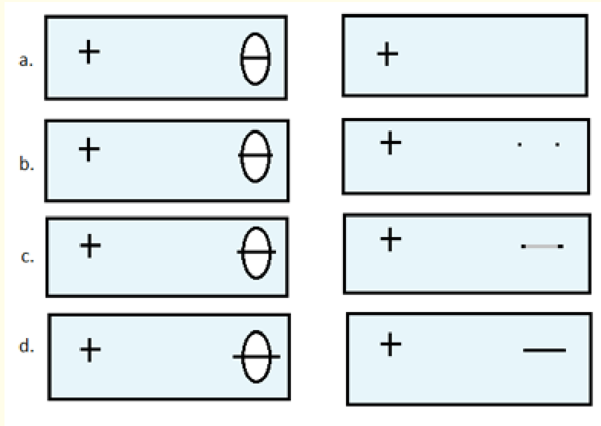

Figure 3: *Panel a shows that no perception is there for fully intrinsic stimulus. Panel b shows the stimulus is little bit outside of the blind spot and the perception of 2 blobs. Panel c shows the length of stimulus is a bit bigger than the previous one and the perception of ghost center. Panel d shows the length of the stimulus is larger than the previous cases and perception of total filling-in [13].*

different for different subjects. If the mask is smaller than the target, brightness suppression occurs to a greater extent. Mask with broken contour can suppress brightness at a less extent. Using brightness-matching experiments Saito., *et al*., [15] found that blind spot stimulation affects visual perception and enhances pupillary light reflex. According to these researchers, a photo-sensitive mechanism inside the optic disk influences our image-forming vision and helps to calibrate the perceived brightness of visual objects.

Domination of visual sides in filling-in depending on CMF

Li., *et al*. [16] explained the role of CMF with respect to blind spot filling-in. This factor determines the dominance of the nasal visual half over the temporal one in filling-in process when the object is placed in the purview of blind spot. They used bi-chromatic rings with primary color constituents as stimuli. At a particular width, both the nasal and the temporal region produce same influence in filling-in and after a certain width, the color of temporal visual half overpowers the color of nasal half. According to the study, high CMF has high contribution in filling-in. While rotating the bi-chromatic ring by 90° both the colors present in the upper and lower part of the annuli contribute equally in filling-in.

Importance of Information Theory and CMF in filling-in for surrounding color gradient stimuli

Mukherjee., *et al*. [17] performed some psychophysical experiments in the light of the work of Li., *et al*. [16] with their own augmentation. Li., *et al*. [16] recommended that the filling-in pattern follows a retinotopic rule which suggests that the color in the nasal half highly dominates the color in the temporal visual half. Here, the authors used black and white along with the primary colors in the stimuli and got some interesting results. They observed that when white or black belongs to the nasal visual half, almost symmetrical filling-in was observed and when primary color is present in the nasal visual half nasal priority is observed (See figure 4) [17]. They proposed a new hypothesis which encircles the importance of Information Theory and CMF in filling-in. According to the authors, as our brain generally tries to remain in a low entropy state [18] it tends to provide primary colors with higher priority than white or black during any contention. That the spatial organization of photoreceptors [19] (See figure 5) also plays an important role in filling-in mechanism, has also been indicated.

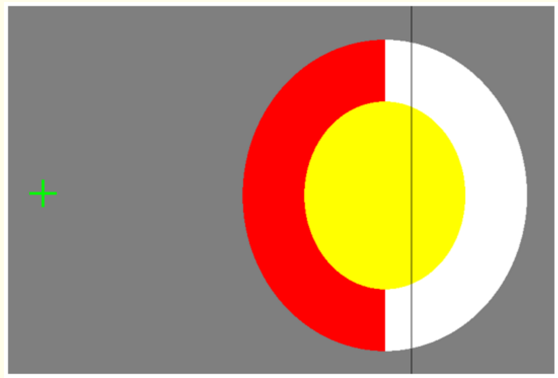

Figure 4: *A visual stimulus used in [17].*

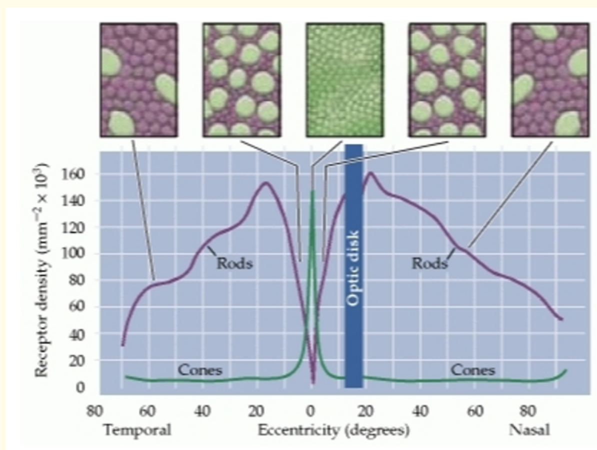

Figure 5: *Anatomical distribution of photoreceptors throughout the retina [19].*

Explanations of perceptual filling-in at blind spot in the light of possible neural mechanisms

Responses of cells in monkey in perceptual filling-in

Like human beings, monkeys are also able to perceive filled-in visual information. Though for cats, filling-in occurs after several minutes suggesting that the receptive fields get expanded in due course of time, for human beings the filling-in occurs almost within no time. De Weerd., *et al*. [20] experimented on Rhesus monkey for the phenomenon of neurological activities involved in filling-in of an image with hole and compared these activities for a no-hole image. With the help of physiological recordings of V2 and V3 areas for with-hole and no-hole images, they asserted that after a certain interval, both the corresponding recordings of the images tend to align with each other and this proves that perceptual filling-in is the resultant minimization of the difference of neurological activity of with-hole and no-hole images. During the time of artificial filling-in, the receptive field does not increase; rather filling-in occurs dynamically when the receptive field is in excitatory state and its surround receives inhibitory signal. With the same line of reasoning, the authors [20] predicted that the blind spot filling-in phenomenon for human being is instantaneous due to the adaptive nature of surround inhibition.

Filling-in of visual phantoms in human brain

This paper by Meng., *et al*. [21] is not directly related to the experimentation on blind spot, though it deals with the incident of filling-in at human brain. The researchers used low-contrast moving grating objects separated with a gap of almost 10° to create filling-in effect in the brain. This filling-in occurrences, described by the authors as visual phantoms, have the similar kind of spatial format as of the surrounding inducers and they are actively mapped in the brain. Meng., et al. [21] used fMRI studies to understand the biological significance of the visual phantom. The vertical grating produces stronger brain activity than the horizontal one which does not create any phantom feeling. They considered the retinotopic area from V1 to V4 as region of interest and showed that filling-in occurs at V1 and V2 areas automatically irrespective of the attentional locus. The involvement of higher visual areas like V3 and V4 in filling-in may be less or detection of filling-in at higher visual brain areas may be difficult to register due to point-spread function. The main conclusion of this paper [21] is that the enhanced activities in the lower visual brain areas (i.e. V1 and V2) contribute the most in the filling-in process.

Explanation of filling-in procedure in retinal scotoma

Zur and Ullman [22] did not directly use blind spot region or any kind of artificially induced scotoma for filling-in purpose rather they took some patients having retinal scotoma. The psychophysical stimulus designed by them had 1-dimensional and 2-dimensional patterns. Perceptual completion increases as the width of the bar placed at central retinal scotoma increases and this perception is more vivid than that of the artificial scotoma cases. The researchers also showed that filling-in does not ignore the image information in damaged area of retina, but it actively manipulates cortical neural activities at various visual levels and produces a kind of virtual reality. They hinted at the blind spot filling-in from a different angle and according to them, blind spot being a special anatomical feature normal to every eye, may have a separate filling-in mechanism in higher visual areas.

Neural mechanism of perceptual filling-in

What Meng., *et al*. [21] found biological region for the visual phantom in the brain, Komatsu also reached the same kind of conclusive brain region i.e. the lower visual cortical areas where filling-in occurs [23]. He described filling-in as surface interpolation process. fMRI based neuro-imaging technique has shown that when filling-in happens, the lower visual brain areas (i.e. V1) become highly activated and these neural activities are congruent with perception. The biological evidence different from the established "Cognitive Theory" predicts that filling-in occurs at higher visual areas and isomorphic theory fails to achieve proper experimental veracity. According to the authors, filling-in happens when the neurons in the deep layer are selectively activated based on the kind of stimulus. The main finding of this paper is that the selection of particular types of deep layer neurons in V1 area are dependent on the requirement of the visual stimulus such as in the case of bar stimulus present in the blind spot region, the neurons which are biased towards long bars are chosen by the brain for activation and this may be the key to the filling-in incident.

Analysis of cortical representation of the region surrounding the blind spot

According to Awater., *et al*. [24], blind spot filling-in may occur due to the spatial propagation of signal from the periphery to the center of the blind spot region i.e. the blind spot surrounding receptive neurons are re-mapped in the corresponding blind spot region of the brain.

Amount of spatial information required for filling-in

Otte., *et al*. [25] suggested that homogeneous primary colored frames of width 0.26°and textured frame of width 0.43° encompassing the blind spot produces complete filling-in. Later, Spillmann *et al*. [26] tried to measure the minimum width of the colored and textured annuli required for spontaneous filling-in. The colored image boundary with minimum width of 0.05° completes the perceptual filling-in for 40% cases and for the textured image patterns the minimum width required for filling-in is 0.17°. The authors' results agree with Komatsu's logic [23] of spreading the neural signals from the edge of the blind spot and while comparing the results with the outcomes of De Weerd's Monkey experiment [20], the instantaneous filling-in of the blind spot region happens they concluded is, because the process is not hindered by the signal transmission from periphery. They also hinted towards another mechanism where binocularly activated color and pattern specific neurons may contribute in activating the filling-in process.

A new classification of perceptual filling-in

Our brain performs a number of different tasks of filling-in in various circumstances but till now none of the mechanism is properly explained. Weil and Rees [27] beautifully compartmentalized different kinds of perceptual filling-in in their work with respect to the characteristics of various stimulus and time duration required for perceiving filling-in. Some of them are stimulus dependent and some are not. Some of the illusions like blind spot filling-in, retinal scotoma filling-in, illusory contour and surfaces and amodal completions (See figure 6) are instantaneous and some like Troxler fading [4], artificial scotoma filling-in etc. are not instantaneous. They explained a

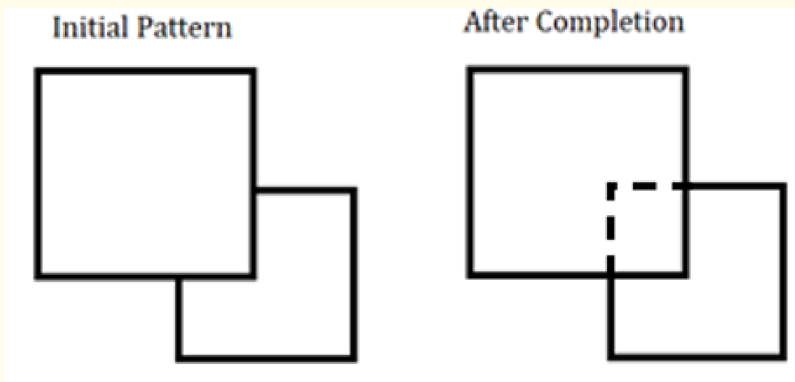

Figure 6: *An example of Amodal Completion.*

generalized view describing the fact that the activation of filling-in phenomenon may be related to real image contour. If the real boundary is not present, filling-in occurs instantly.

Explanations of perceptual filling-in at blind spot on the basis of computational modelling

Prototyping human blind spot using a new multi-scale Gaussian interpolator

With the help of the idea of edge detection and surface interpolation in human visual system as propounded by David Marr, Ghosh., *et al*. [28] modelled a non-classical receptive field of retinal ganglion cells where the edge detection algorithm has been used for interpolation purpose. Considering a linear combination of three zero-mean Gaussian equivalence to bi-Laplacian of Gaussian, they tried with a combination of a four Gaussian (Zero-Mean Gaussian) interpolator model. With the mechanism of edge detection, they showed that like the edge detection process blind spot surface interpolation also happens in the early visual areas.

Rationalizing the filling-in mechanism with the help of the predictive coding

Rao and Ballard are the pioneers in devising the theory of HPC (See figure 7) which is gaining more and more impetus nowadays by the leading scientists to analyze the Bayesian brain in cognitive neuroscience [29]. Raman and Sarkar [30] assumed that it is not the neural ignorance but some neural computation which is involved in the mechanism of blind spot filling-in even though the exact phenomenon is still unknown. They tried to illuminate this mechanism with the help of HPC and considered the top-down and bottom-up approach as described by Johan and Iris. Different visual areas like V1, V2 etc. were treated as the PE modules which have the primary task of predicting the spatio-temporal intensity of the signals of neighboring points and these predictions from the higher visual areas are fed back to the lower PE modules which send the differential error signal between the real and predicted value to the higher PE modules. Blind spot has

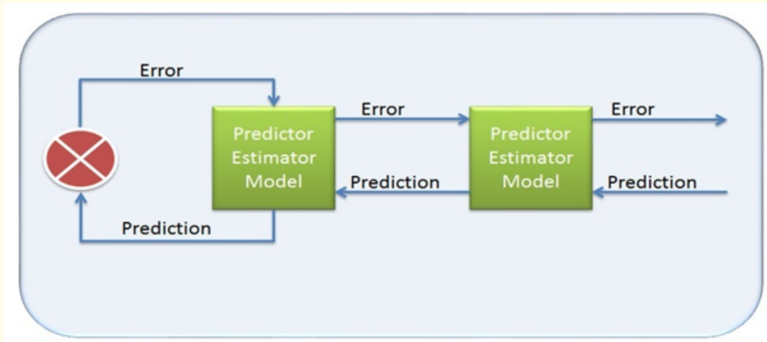

Figure 7: *HPC Model.*

the special arrangement where the feed-forward error signal has no role to play as the blind spot is devoid of the real retinal inputs. With the help of the bar experiment reproduced from Komatsu's paper [23] and also from another bar alignment experiment, it was concluded from the HPC network output that V2 region is the most probable region of the blind spot filling-in which is also biologically plausible from the earlier evidence of fMRI techniques. But this study could not reject the hypothesis that there exist some alternative feed-back and feed-forward pathways in V1 which may also be involved in filling-in mechanism without going into higher visual level (V2).

Computational analysis of a Bayesian brain using predictive coding approach

Kwisthout and Rooij [31] used top-down and bottom-up predictive coding approach to analyze the computational intractability of a Bayesian brain with three respective activities - prediction, error computation and hypothesis updating.

Dynamic predictive coding performed by retina

Hosoya., *et al*. [32] utilized the concept of dynamic predictive coding by retina while conveying the visual information from retina through optic nerve to visual areas of the brain. According to them, when a signal comes to a retinal receptive field, the retina manipulates spatial and temporal intensity of surrounding points and differentiate the values from the real image information. Due to this differential property of the signals those are to be transmitted by the ganglion cells, varied range of dynamicity can be maintained with minimum neural sparks.

Conclusion

A substantial amount of research work is being done to decipher the salient mechanism underlying the blind spot filling-in. With the objective to help in an extensive development in this area and also to aid in exploring the presumptions and rationale produced in the previous studies through new experimental validations, our accomplished survey of related research works, which is sectioned into three different approaches, will support future scientists to further proceed towards the research arena of human blind spot psychophysical studies.

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Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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