Perceptual learning of spatial position in the visual domain

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視覚領域における空間位置の知覚学習

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要旨

本稿では、視空間イメージの特徴を我々の視覚システムがどのように処理するかを分析的に吟味する。筆者は、先ず、人の認知的行動における知覚、特に視覚における知覚学習の重要性を指摘する。続いて、視覚空間処理において我々が明らかにすべき基礎的問題を提起し、最後にこの問題を解決する上での新たな概念を述べる。過去数十年において、副尺視力に代表されるような視空間視力が多くの刺激要因によって影響を受ける事が明らかされてきた。それらの要因とは刺激サイズ・方位・輪郭・空間周波数・コントラスト・網膜位置などである。一方で研究者たちは、訓練の結果、皮質において神経細胞の感度変化が生じること、そしてそのような学習的変化は、神経細胞によって分け隔てなく、すべての視野内あるいは皮質内に与えられた負荷に応じて対等に生じるものと考えてきた。しかし、方位や運動方向の感度は方位・方向において均一ではない。また、網膜感度も視野内で均一でない。このため、視覚システムの感度や学習が視覚対象の位置関係、例えば副尺視力における２つの副尺の位置の相対性に関しても同等かどうかという問題が生じる。本研究では、この問題に関わる先行研究を慎重に吟味した上で、この課題の重要性と説明の可能性について論じる。そして、我々が今後行なうべき心理物理学的実験と議論の方向について解説する。

キーワード

空間知覚・副尺視力・位置の相対性

Introduction

Our everyday life goes through a countless number of difficulties and challenges. Through learning we develop cognitive and behavioral skills and strategies directed toward solving these difficulties and challenges. Learning in this age of brain competition can be considered as the best tool to attack our opponents and defeat enemies. What is learning then? Learning refers to a relatively permanent change in behavior and cognition as a result of practice or experience. It is undoubtedly one of the most important functions of our brain. Learning does associate not only with high-level things like math functions, rather it includes low-level perceptual (e.g., letter identification) and motor skills too (e.g., moving a finger). Perceptual learning results in changes in the ability to pickup information in a meaningful or appropriate manner. People perceive in order to understand, and their understanding leads to more and

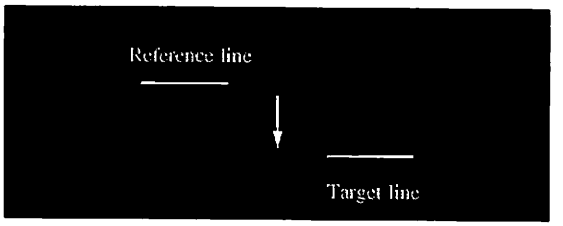
more efficient perception. Perception and action are related in that people act in order to learn about their surroundings, and they use what they learn to guide their actions. Perception becomes more skillful with practice or experience. As a result, perceivers come to notice the features of situations that are relevant to their goals although irrelevant features may also come into play of the process (Seitz & Watanabe, 2005 ; Watanabe, Nanez, & Sasaki, 2001). Perceptual learning can aid an animal with many things, like detecting preys or predators, and avoiding obstacles while running. In human activities, perceptual learning can help with arts, sports, music, piloting fast planes, and many other functions. For example, art students learn to differentiate different strokes, textures, and styles, and to classify paintings by period and artist.

Perceptual skills occur across widely different domains such as visual, auditory and haptic (touch and kinesthetic) etc. Among these the visual domain is a greatly advancing area of scientific enquiry. We have focused here on spatial perception in this domain of our interest. Visual spatial perception provides us with information about the spatial environment. The way we perceive space and their position or orientation within that space can affect our gross motor skills. For example, good visual acuity, a measure of space perception, is necessary for skilled performance in spatially complex task such as in surgical procedure. However, studying perceptual learning in the visual domain scientists have demonstrated left vs. right and upper vs. lower visual field asymmetries in information processing. For example, spatial information such as orientation, localization, and size are processed more precisely in the left visual field and non spatial information (e.g., temporal processing) in the right visual field (Boulinguez, Ferrois, & Graumer, 2003 ; Corballis, Funnell, & Gazzaniga, 1999, 2002). The lower (south) visual field has been observed to be better for localization task, (Cameron, Tai, & Carrasco, 2002 ; Carrasco, Talgar, & Cameron, 2001), acuity (Carrasco, Williams, & Yeshurun, 2002), spatial resolution (Talgar & Carrasco, 2002), spatial memory (Previc & Intraub, 1997), global processing, near stereoscopic vision, color and orientation (Previc, 1990), and figure-ground segmentation (Rubin, Nakayama, & Shapley, 1996), whereas asymmetries in favor of the upper visual field have been reported for local processing, far stereoscopic vision, visual search, and apparent size (Ross, 1997) etc. The left-right visual field asymmetries have been attributed primarily to the functional differences of the two hemispheres (Heilman & Van Den Abell, 1980 ; Kinsbourne, 1970) whereas upper-lower visual field asymmetries do not have such kind of functional differences in the visual system. Researchers have also demonstrated that spatial acuity performance is higher for horizontal and vertical stimuli than for oblique stimuli (Furmanski & Engel, 2000 ; Li, Peterson, & Freeman, 2003). A few of the researchers have observed better vernier performance for vertical stimuli than for horizontal stimuli (Skrandies, Jedynak, & Fahle, 2001) indicating neural preference for a particular kind of stimulus orientation. Scientists have explained that this orientation preference might be associated with the everyday fact that we experience more vertical and horizontal than oblique stimuli and more vertical than horizontal stimuli causing differences in sensitivity (Gregory, 1997). However, in order to understand orientation and other feature based visual sensitivity and learning let us raise some basic question on the visual processing of spatial input and then critically analyze the relevant literature to find out the answers.

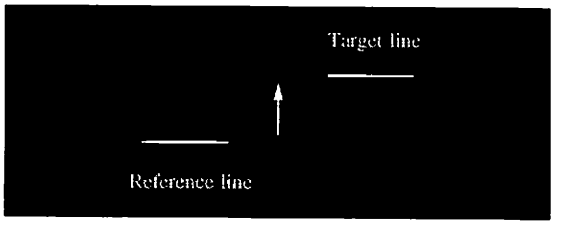
Visual spatial input: on the question of its processing

Visual perception refers to the process of interpreting

and organizing visual information (Kavale, 1982). To understand and organize the visual spatial environment visual discrimination is necessary. Visual discrimination involves the ability to recognize and identify a figure's distinguishing features and details, such as shape, size, orientation, position, and color etc. Good visual discrimination, in fact, refers to good visual acuity. Scientists have suggested several models to study visual acuity psychophysically. Among those vernier acuity model is a widely used one. It is a very sensitive measure to study perceptual learning based on cortical processing. In vernier acuity experiments scientists usually measure subject's discriminability of spatial position. That is, in a vernier discrimination task the subject usually judges the position of a target in relation to its reference. Consider a vernier stimulus comprising of two lines-a reference and a target (Fig. 1 - 2). A bright bar has a number of features that may be used for positional judgments. It has local features such as width, length, edges, orientation, position etc. In addition, it may have some other properties that we may ignore or do not take into consideration for scientific enquiry. For example, when the target bar is displayed above or below the reference/ comparison bar (constant) there is an asymmetry in relative position of the two image situations (Fig. 1 - 2). Rather than simply referring it absolute positions of the target bar we prefer to call it position relativity of the bars in the sensory map. In Fig. 1 we have displayed such situations of a vernier image comprising of two horizontal line features: a left reference (constant position) and a right target separated by some gap and displayed below or above the reference. These opposite target positions, in fact, give two comparable images: one image comprises of a left upper and a right lower lines (Fig. 1 (a)) and another one comprises of a right upper and a left lower lines (Fig. 1 (b)). When the left line is displayed as a target with a right reference a downward offset of the target gives an identical relative position of the image where the offset is upward for a right target and a left reference (Fig. 2 (a) and Fig. 1 (b)) and an upward offset gives an identical relative position of the image where the offset is downward for a right target and a left reference (Fig. 2 (b) and Fig. 1 (a)). That is, in our visual field there would be two comparable images irrespective of which bar is the target and which one is the reference. The criterion for such comparison is the position relativity of the vernier segments in their spatial configuration.

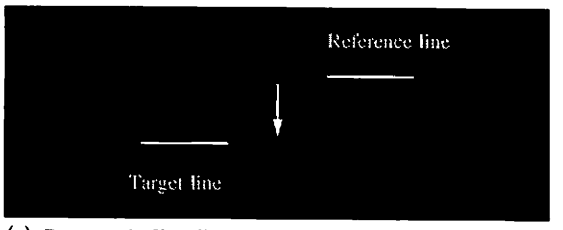


(a) Downward offset direction

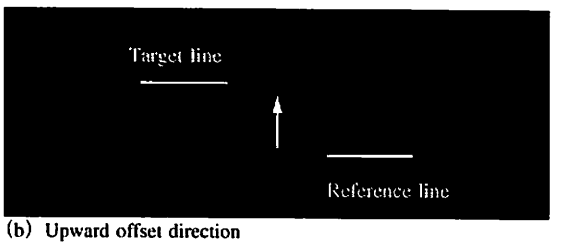


(b) Upward offset direction

Fig.1. Position relativity of the segments of a horizontal vernier stimulus comprised of a right target and a left reference



(a) Downward offset direction



(b) Upward offset direction

Fig.2. Position relativity of the segments of a horizontal vernier stimulus comprised of a left target and a right reference

However, any stimulus gives rise to a distributed pattern of light on the retina, and it is from such a distribution that the visual system must determine the nature of the stimulus. So, a general and basic question is : what particular features of the vernier stimulus are being located by the visual system?

Looking for answers into the literature

Scientists have tried to answer the question from a number of views. For example, Geisler proposed an ideal observer model which predicts that vernier acuity improves proportionally with the square root of stimulus energy (Geisler, 1984; Geisler & Davila, 1985). If neural mechanisms can integrate spatial information perfectly, measurements from a real observer should parallel those of the ideal observer (Cohn, 1990). Some of their efforts have explained vernier or hyperacuities (a spatial localization task) for a closely spaced (abutting) target feature as to rely on contrast sensitive spatial filter mechanisms (Wilson, 1986, 1991). According to their model, the responses of an appropriate class of spatial filters represents the vernier target as a point in complex space, which has dimensions such as orientation, spatial frequency, and contrast. The location of this point is then compared to a reference point in the same N-dimensional space based either on an internal norm, or a normative value established from the filter responses to a set of null (zero-offset) stimuli. A non-zero value from this comparison process indicates the presence of vernier offset. The role of contrast in spatial-position perception has been supported by several other studies too (Fendick & Swindale1994; Watt & Morgan, 1983 ; Wehrhahn & Westheimer, 1990; Westheimer & Pettet, 1990). Westheimer and Pettet (1990), for example, showed that both vernier and stereoacuity thresholds decreased with increasing contrast, but the stereo function was shifted as though the effective contrast for stereo were half the contrast for the vernier configuration.

Vernier acuities for widely separated (non-abutting) target feature usually have been attributed to local-sign mechanisms responsive to differences in stimulation of individual receptive fields (Wang & Levi, 1994). This theory explains that each point or direction in the visual field can uniquely activate only one point on the retina. This activated retinal point may serve as an internal position or direction tag, and is called a local sign. To achieve hyperacuity, the visual system may average the positions of local signs along the length of a spatial feature to minimize the uncertainty created by the structure of the visual system (Wang & Levi, 1994). Local mechanisms seem to be involved in hyperacuities for bisection and vernier alignment of stationary patterns, where the component features must be separated by no more than a few minutes of arc. McKee, Welch, Taylor and Bowne (1990) and Westheimer and McKee (1979) suggested that spatial position is an essentially local property, encoded by visual mechanisms tagged with local signs of retinal position. McKee et al. (1990) acknowledged that optimal acuities for binocular disparity and relative motion require a spatial reference feature, and they suggested that such cues may serve to eliminate positional uncertainty caused by eye movements. Watt, Morgan and Wardt (1983) showed that location is assigned to some widespread property of a retinal light distribution rather than a local feature but they could not rule out the possibility of using perceived edges or boundaries as the position cue in a vernier acuity task. After demonstrating the perceived location of such an edge cue as a function of the whole light distribution they concluded that the position of a bar is determined by its edges if available and by some total measure of centrality in the retinal light distribution if no edges are available (Watt et al., 1983).

It has been demonstrated that improvements with practice on tasks such as vernier acuity and texture discrimination are highly specific for retinal locus, stimulus orientation, size and the trained eye (e.g., Ahissar & Hochstein, 1993, 1996; Gilbert, 1994; Karni & Sagi, 1991; Schoups, Vogels, & Orban, 1995). There are some experiments showing little transfer of vernier improvements when changing the target in its orientation or position or is presented to the untrained eye (Fahle, 1994 ; Fahle & Edelman, 1993 ; Poggio, Fahle, & Edelman, 1992). A few recent behavioral studies tell the same story that perceptual learning can be highly specific to the trained stimulus features like retinotopic location (Crist, Kapadia, Westheimer, & Gilbert, 1997 ; Watanabe, Nanez, Koyama, Mukai, Liederman, & Sasaki, 2002), visual orientation (Schoups, Vogels, Qian, & Orban, 2001) and direction (Watanabe et al., 2002). Such specificity has been also observed for stimulus context and configuration learned during training. For example, training on a three-line bisection task does not transfer to a vernier discrimination task the visual field, trained position and orientation being the same. Hyperacuity learning with line stimulus does not transfer to a hyperacuity task composed of dots (Poggio et al., 1992). The lack of transfer, however, has been taken as evidence that learning might be mediated by cells in the primary visual cortex (Fahle, 2005, Watanabe et al., 2002). That is, all the specificities undoubtedly refer to the corresponding cellular changes in the early visual cortex thus indicating the involvement of neural mechanisms in the process. Saarinen and Levi (1995) revealed a close correspondence between improvement in vernier acuity and a specific narrowing and downward translation of the orientation tuning curve. Their results implied that neural plasticity in the early visual pathway is a possible key mechanism for perceptual learning of vernier acuity (Kirkwood, Rioult, & Bear, 1996; Saarinen & Levi, 1995). The past studies have shown that orientation and spatial frequency tuning are two of the most prominent features of neuronal selectivity in V1, the primary visual cortex (De Valois & De Valois, 1990). The receptive fields of neurons with different orientation preferences and slightly differing receptive field positions are clearly able to discriminate between a straight vernier and an offset one, or between an offset to the left and an offset to the right (cf., Wilson, 1986). Perceptual learning relies on an improvement in processing by the neurons in area 17 best suited to discriminate between vernier offsets in opposite directions (Poggio et al., 1992). In such discrimination a higher cortical level may also involve. The dependence of learning on attention and error feedback (although there are some exceptions) proves the importance of top-down influences from higher cortical centers. As Fahle (2004) reported, the neurons on higher levels of processing may use more complex features to discriminate vernier offsets to the right from those to the left. Through training they would learn which input neurons on preceding or lower levels of cortical processing are best suited to discriminate between those two classes of neurons. Learning would consist, at least partly, in assuring a higher impact of these neurons on the discriminating neurons in the higher level and, hence, in changing the receptive fields of these neurons in a task-specific way (Fahle, 2004). In short, the discrimination of a leftward vernier offset from a rightward one is done by the neurons in primary visual cortex under top-down control.

As we have seen above scientists in the last several decades have investigated a variety of stimulus factors underlying visual spatial perception. These factors include stimulus size, edges, orientation, retinal locus, spatial frequency, context and contrast etc. All the researchers have demonstrated a common fact that the changes that occur as a result of training in cortical cells are specific to the stimulus features.

They have undoubtedly made significant contributions in the said area of perception. However, the scientists know what they know but there may be things that they don't know. That is, there may remain some unresolved issues despite their land mark contributions. For example, they never tried or even thought to explore the effect of position relativity of the image features on visual spatial judgment. That is, the question of position relativity of the vernier segments has been attacked neither experimentally nor theoretically till today. It is, therefore, necessary to address the issue experimentally that will advance our understanding of the visual processing of spatial objects. However, in this review we would like to be confined to displaying our own hypothetical views on position relativity issue of visual spatial processing.

Our views on position relativity issue: importance and possibilities

Stimulus context plays a vital role in processing visual images. The importance of context has been demonstrated in several studies. A neuron's response to a given stimulus depends not only on the parts of the stimulus within the classical receptive field but on the context too (Herzog, Schmonsees, & Fahle, 2003). The contextual influences play a central role in the process of integration of information from different parts of a scene (Gilbert, 1998). In learning experiment context can be introduced in a variety of ways. Every different kind of stimulus, in fact, may serve as a particular context and in psychophysical experiments contextual difference can be introduced by simply changing any local features of the visual image. So, like other local features of a visual image position relativity may also be important for visual processing. As mentioned earlier visual spatial acuity is finer for horizontal and vertical stimuli than for oblique stimuli (Furmanski & Engel, 2000; Li et al., 2003) and so is for vertical stimuli than for horizontal stimuli (Skrandies et al., 2001). This indicates the neural preference for a particular kind of stimulus orientation. This orientation preference has been attributed to the everyday fact that we experience more vertical and horizontal than oblique stimuli and more vertical than horizontal stimuli causing differences in sensitivity (Gregory, 1997). We think that such preference may also occur for a particular stimulus configuration thus creating sensitivity difference to the vernier images of opposite target position in the same orientation. In addition, as the two opposite vernier targets have relative positional difference in the spatial configuration there is a possibility of learning specificity because a vernier target lying below the reference gives a context different from the context given by a vernier target lying above the reference. That is, perceptual learning with upper vernier target may not transfer to lower vernier target or vice versa. Similar arguments can be given for vertical and other tilted vernier images. This argument gets indirect support from the evidence that perceptual learning is context specific (Poggio et al., 1992) and that the primary visual cortex may modify its input signals in a stimulus or task-specific way under top-down control (Fahle, 2004). Although Poggio et al. (1992) introduced completely different kinds of task or stimulus as the contexts in their study our argument is that context can be introduced within the same kind of task just by changing some stimulus features such as position relativity in this case.

Another argument is that the attention paid to the image features'one relative position may be stronger than to another as per learning or experience in early development. As a consequence, spatial judgment (vernier acuity) for one position relativity of the image features may be more precise than for another. The subjects need to be aware of and focus their attention on a stimulus feature for that feature to be

perceived and learned (Ahissar & Hochstein, 1993) although there are some exceptions (Watanabe et al., 2001). The various influences on receptive field properties interact with attentional mechanisms and attention can have a stronger effect on contextual influences than on the target stimuli themselves (Ito, Westheimer, & Gilbert, 1996). These effects are reflected in the activity of neurons in V1 (Ito & Gilbert, 1997). However, attention to spatial position and higher order representations of vernier image may be fed back toward cortical areas processing the incoming sensory input. Although receptive fields in higher level (for example, in area V4) are larger, and would be expected to carry less specificity about spatial position, it is possible to effectively reduce receptive field size by attention (Moran & Desimone, 1985). It is clear from psychophysical studies that discrimination of simple attributes is influenced by attention to stimulus position and that interpretation of form is influenced by anticipation of stimulus configuration (Gilbert, 1998). Moreover, a fundamental feature of the anatomy of cortical pathways is a feedback of information from higher order cortical areas to areas that are closer to the input from the periphery. It is likely, therefore, that one would influence the response properties of cells at early stages in sensory pathways by attention.

The primary visual cortex (V1) has the smallest receptive fields, most highly organized visuotopic maps, and sharpest orientation selectivity (Crist et al., 1997). Furthermore, the smallest area of retinal illumination from an easily visible point of light has a diameter of several arcmin, stimulating a dozen or so neighboring photoreceptors. As a consequence, a small change in location of the target may produce widespread changes in the relative stimulation of neighboring photoreceptors and neurons. This leads to the assumption that two different groups of neurons are tuned if subjects are exposed to two comparable positions of the vernier target in relation to its reference. Yes, depending on eccentricity from the fovea there may be some neurons common to making these differential responses. However, two comparable vernier images as we showed earlier have many identical local features such as orientation, edges, offset size, gap size etc. But, they must differ in position relativity in their spatial configuration and this may send different kinds of messages to the cortical processing. In this situation, some neurons may prefer to respond only to a particular kind of vernier configuration whereas other neurons to other kind of configuration. If this is the case their response strength may also be different depending on their early experience or attention. Thinking along this line we would like to assume that perception and or perceptual learning of vernier acuity may vary as a function of image features'position relativity and accordingly be specific to that stimulus configuration.

Some scientists have plainly stated that V1 neurons are best suited to discriminate between vernier offsets in opposite directions. For example, for vertical vernier stimuli neurons can discriminate between an offset to the left and an offset to the right (Fahle, 2004; Poggio et al., 1992). Our argument here is that such discrimination may depend on the position relativity of the stimulus segments or on the relative configuration rather than on offset direction. That is, we prefer to call it responding to position relativity in the spatial configuration rather than to offset direction because the target feature itself has no direction at all. Yes, in the sense that the reference feature's position is constant and the target feature is changed leftward or rightward the concept of offset direction is acceptable but in behavioral terms or in terms of response selectivity the term position relativity of the features is more appropriate. Because, response selection is not made solely on the basis of the target feature rather selection depends on the relative position of

the target and reference features. So, the point should not be concerning offset direction rather it should be concerning position relativity of the image features and this argument may be true at least for still vernier targets.

For a target located within the receptive field of a simple cell, changes in target contrast, orientation and position can all produce equivalent changes in the cell's response. If spatial performance can be associated with upper-lower visual field location having no corresponding functional difference in the brain why not the position relativity difference in such performance? The position relativity concept as we introduced earlier in this paper has a particular gap orientation which may give important information for the line-alignment task. The argument is that cortical neurons respond not only to the bars but also to the gap between them. While comparing the positions of the bars the subject's attention may be focused on the ending point (position) of one bar and starting point (position) of another bar. If we connect these two points by some straight line the orientation of that line for one position relativity will be different from its opposite position relativity. That is, we want to mean that by focusing attention on the points of comparison the subject will form an imaginary line in between the comparison bars and the orientation of this imaginary line will indicate whether the comparison bars are aligned or misaligned. If the imaginary line is collinear with the comparison two a non-offset response will be delivered otherwise an offset response will be made by the subject. Although the two comparable vernier images are iso-oriented the disparity in their gap orientation and or relative position may make difference in neural tuning or response selection. Neural mechanisms are able to integrate spatial information but it may not be equal for the two comparable positions especially for widely separated vernier features having asymmetry in gap orientation because neural response is influenced by its preference, attention and or early experience etc.

Our final argument is also a neural one. Vernier acuities for widely separated (non-abutting) target feature can be attributed to local-sign mechanisms responsive to differences in stimulation of individual receptive fields (Wang & Levi, 1994). The precision of the local sign may be influenced by neural experience during early development. As the activity of most neurons are more strongly modulated by positional difference than by orientation difference (Nelson, Kato, & Bishop, 1977) there may be corresponding dissimilarity in perceptual performance for the two vernier targets that have asymmetry in position relativity in the spatial configuration. Scientists have revealed the fact that receptive field properties, most notably visual topography and receptive field size, can be influenced by visual experience throughout life (Crist et al., 1997). That visual experience can change receptive filed properties in the primary visual cortex leading to the possibility that a group of cells develops preference for the image's one relative position but not for another. That is, some people may have preference for a vernier image comprised of an upper left line and a lower right line while others may have preference for a vernier image of an upper right line and a lower left line. Although adult cerebral cortex has been proved to be considerably dynamic the amount of plasticity and readiness for evoking learning processes is significantly greater during early development. During early development some neurons may be functionally enhanced and others be deprived. As a consequence some neurons may become dominant over others showing disparity in response strength.

Conclusion

Because we see the world with our eyes visual per-

ception plays a central role in our daily activities and working life as well. We have very powerful visual perceptual learning with many surprising properties. Those properties have a long history of investigation. However, in order to understand those properties we raised a basic question on visual spatial processing. Reviewing meticulously the studies so far done and documented on visual psychophysics and visual neurology in the recent past we find some answers but not all. For example, scientists have demonstrated that improvements with practice on tasks such as vernier acuity and texture discrimination are highly specific for retinal locus, stimulus orientation, size and the trained eye (e.g., Ahissar & Hochstein, 1993, 1996; Gilbert, 1994 ; Karni & Sagi, 1991; Schoups et al., 1995). In addition with the role of these low level features on visual processing we have introduced here a novel concept : the concept of position relativity and argued how this low level feature of a visual image can influence response selectivity in a visual spatial judgment task like vernier acuity. We have explained that the presentation of an image comprised of more than one component feature may give those stimulus segments different comparable positions on the visual field. This position relativity of the component features may be important for processing the incoming information. This might be especially true for visual spatial judgment where the perceiving individual's task is to locate the position of an image segment in relation to another of the same. We have argued that as a stimulus context position relativity of the image segments may have influence on visual spatial judgment and that this influence may be caused by attention, gap orientation and or neural preferences developed during early development.

This review is the first hypothetical thinking of the position relativity effect on neural selection for visual spatial judgment. It has not yet been explored or thought to explore even after a great achievement in vision research in the near few decades. So, a new challenge for the vision scientists should be to investigate position relativity effect of the visual input having two or more elements of varying positions in the sensory map. As a first step of that effort we would like to address this issue in our future empirical studies thus leaving it here with some explanatory statements only.

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