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When Gestalt Processing Meets Low-Level Feature Integration

Introduction

Gestalt theory provides numerous examples arguing against the atomistic view according to which perception results from hierarchical computations proceeding from simple low-level to complex high-level features. For example, in Fig. 1A we have a stimulus composed of vertical, horizontal, and curved line segments. These segments are organized into two fundamental Gestalts: two periodic waveforms which are the mirror image of each other. When the distance between the elements is changed, as in Fig. 1B, the global organization produces two completely different Gestalts, a sine-wave in front of a square-wave. It is virtually impossible to perceive the Gestalts in Fig. 1B as a simple aggregation of the Gestalts in Fig. 1A. Similarly, Fig. 2B shows the initials of Max Wertheimer and the letters M and W are readily perceived. Yet by changing the spatial positions of these letters as in Fig. 2B, a new Gestalt emerges wherein the letters M and W are no longer perceived. These examples show how large-scale global factors can restructure perceptual organization to form "units" that cannot be predicted directly from local feature analyses. To explain factors that govern this organization, Gestalt psychologists proposed several "laws", such as grouping by proximity, similarity, closure, and good continuation (Koffka, 1935). In Fig. 3A, the dots are grouped into horizontal rows based on their similarity (gray vs. black). Changing the spacing between the dots (Fig. 3B) transforms perceptual grouping into vertical arrays based on the closer proximity of the dots to each other in the vertical versus horizontal direction.

GESTALT THEORY

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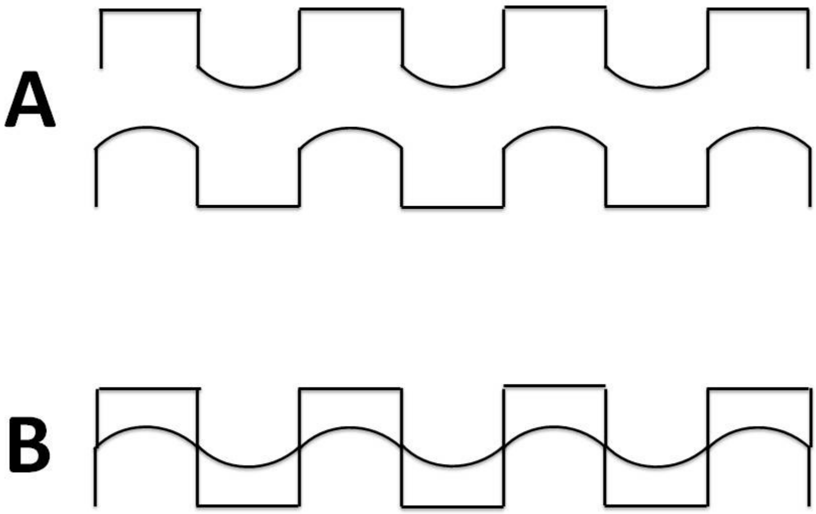

Fig. 1 Classical example. The stimuli in A and B are composed of exactly the same constituent vertical, horizontal, and curved line segments. The only difference is that the top and bottom parts in A are shifted so that they touch each other. The resulting Gestalts in A and B are drastically different.

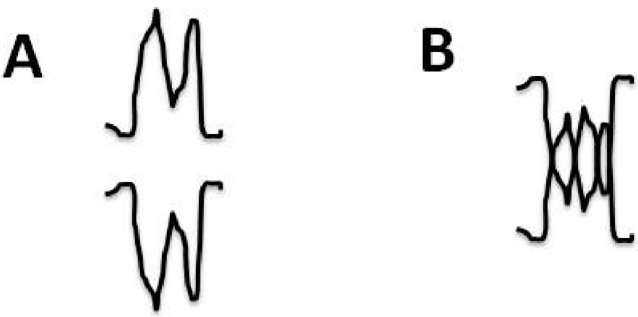

Fig. 2 In **(A)** the letters M and W are readily recognizable. In **(B)**, when these two patterns are superimposed on each other, a completely different Gestalt emerges. It is virtually impossible to see the parts M and W that make up this new pattern.

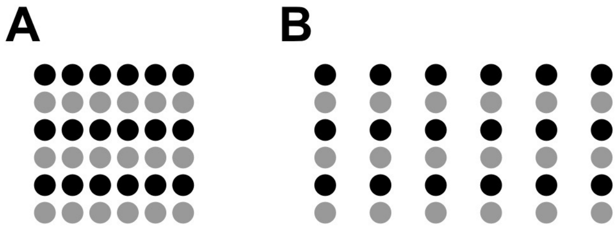

Fig. 3 **(A)** Grouping by similarity: The dots are perceptually grouped into horizontal arrays according to their gray levels. **(B)** Grouping by proximity. The dots are grouped into vertical lines because they are closer to each other vertically vs. horizontally. This figure also shows that perceptual grouping *per se* does not imply feature attribution. Regardless of which grouping occurs, the dots preserve their individual gray levels. Thus, perceptual grouping *per se* does not automatically imply non-retinotopic feature integration. Adapted with permission from Ögmen et al. (2006).

While the early attempts of Gestalt psychologists were criticized as being subjective, descriptive, and vague, subsequent research introduced additional laws, provided quantification of individual laws, and developed models and mechanisms for the interactions of multiple laws (e.g., Grossberg & Mingolla, 1985; Kayaert & Wagemans, 2009; Kubovy & Van den Berg, 2008; Palmer & Rock, 1994; Pinna, 2005; Quinlan & Wilton, 1998; Todorovic, 2008).

Notwithstanding these counter-examples and research efforts, the atomistic view of perceptual processing still remains prevalent in neuroscience, possibly due to findings that suggest a hierarchical organization in the visual system. Neurons in the early visual areas respond selectively to simple features while neurons in higher areas respond to progressively more complex features. It has been suggested that a hierarchical feed-forward architecture underlies the processing and categorizing of objects, at least when the stimulus is presented briefly (Serre et al., 2007). Only under longer, more natural viewing conditions are feedback and lateral long-range modulations supposed to interact with this "core hierarchical feed-forward model" (Roelfsema, 2006; Serre et al., 2007). One fundamental aspect of these hierarchical models is that early feature processing occurs locally and in retinotopic coordinates. In the retina, the lateral geniculate nucleus (LGN) in the thalamus, and in the early visual areas, elements which are nearby in the outer world are represented by neighboring neurons preserving the geometrical relations of the outer world elements. For example, two nearby dots are processed by nearby neurons. Processing of one dot can be influenced by the other one, for example, by lateral inhibition. A third dot which is more remote, however, cannot influence processing.

There is extensive evidence to support this view. For example, Westheimer and Hauske (1975) presented a Vernier flanked by two shorter lines, one on each side. Observers had to indicate the offset direction, i.e. left vs. right, of the Vernier. Performance was worst when the flankers were about 4' (arc min) apart from the

Vernier and improved when flankers were closer or further apart from the Vernier. The deterioration of performance was explained by local interactions between neurons involved in the Vernier offset discrimination. When the flankers fall on inhibitory regions, performance deteriorates because of increased inhibition. Performance improves when the flankers are outside the receptive fields or fall on excitatory regions.

However, observers are not stationary under normal viewing conditions (due to body, head, and eye movements) and many objects in the environment move as well. The implication of these dynamics is that the projection of the stimulus on the retina is not stationary. Thus, retinotopic neighborhood relations that influence processing of features, as observed under static viewing conditions, may not hold true in natural dynamic viewing conditions. In fact, using a Ternus-Pikler display, we have recently shown that retinotopic theories of feature processing fail to explain simple feature processing such as Vernier offset integration (Ögmen, Otto, & Herzog, 2006; Otto, Ögmen, & Herzog, 2008).

Non-Retinotopic Feature Processing and Integration

Given the insufficiency of retinotopic processing for dynamic stimuli, our hypothesis was that spatio-temporal grouping operations establish a non-retinotopic reference frame according to which features are processed. To test this hypothesis, we adopted a stimulus paradigm developed by the Gestalt psychologist Joseph Ternus. Ternus was interested in the "problem of phenomenal identity", viz., how the visual system maintains the identities of moving objects despite the fact that features defining these objects may change over time (Ternus, 1926). For example, when a familiar person approaches the observer, the size, location, orientation, luminance, shape, etc. of the image of the person's face may change continuously, yet the person can still be identified as being the same person, e.g., "cousin Mary". In order to address this problem, Ternus adopted a stimulus paradigm, previously used by Julius Pikler (1917), and investigated whether phenomenal identity of a stimulus is determined by its retinotopic position[1] or according to global Gestalt configurations.

Figure 4A shows an adapted Ternus-Pikler display as used in one of our studies (Ögmen, Otto, & Herzog, 2006). The first frame contains three lines which, after a variable Inter-Stimulus Interval (ISI), are shifted by one position to the right in the second frame. Hence, two of the lines are presented at identical locations in the two frames. Consider now the central line of the first frame. If identity were determined based on retinotopic locations, it should be associated with the leftmost line in the second frame that is presented at the same retinotopic location.

[1] In these experiments, the observer was stationary and the stimuli were presented on the frontal plane. As a result, there is a one-to-one relationship between retinotopic and spatiotopic locations of the stimuli.

Therefore, it should appear stationary (Fig. 4B, "element motion"). However, if identity were determined according to global Gestalt rules, the central line of the first frame should be associated with the central line in the second frame that is presented at the same position within the group of lines. As a result, instead of appearing stationary, the central line of the first frame should be perceived to move, together with the group, by one position to the right (Fig. 4C, "group motion"). Experimental studies showed that the percept in this stimulus depends on several stimulus parameters (e.g., Alais & Lorenceau, 2002; Aydin, et al., 2011; Dawson, Nevin-Meadows, & Wright, 1994; Kramer & Rudd, 1999; Kramer & Yantis, 1997; Pantle & Petersik, 1980; Pantle & Picciano, 1976; Petersik, 1984; Scott-Samuel & Hess, 2001; for a review, see Petersik & Rice, 2006). For example, when the ISI is short, the overlapping elements appear stationary and the leftmost line appears to move to the rightmost line (Pantle & Picciano, 1976). For longer ISIs, the three lines appear to move together as a single Gestalt.

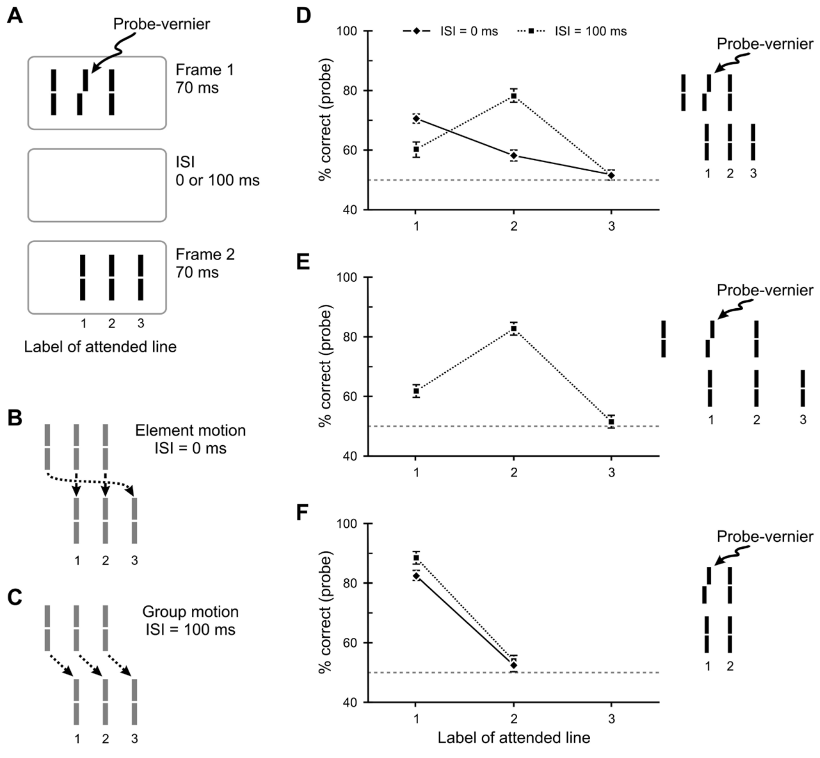

Fig. 4 Non-retinotopic processing. (**A**) In this Ternus–Pikler display, three lines were presented in the first frame, followed by a blank inter-stimulus interval (ISI) of 0 or 100 ms, followed by a second frame of three lines shifted by one position to the right (e.g., the central element in frame 1 is presented at the position of the leftmost element in frame 2). A small Vernier offset (the probe) was inserted in the central line of the first frame only. The direction of the probe offset (left or right) was chosen randomly in each trial (an offset to the left is shown). At the beginning of a block, observers were instructed to attend to one of the elements in the second frame (labeled as 1, 2, and 3). Observers were asked to report the direction of the offset (left or right)

perceived at the attended element. (**B**) With a short ISI (0 ms), the percept of "element motion" is elicited. Arrows depict the established motion correspondence. (**C**) With a longer ISI (100 ms), the percept of "group motion" is elicited. (**D**) A Ternus–Pikler display with an inter-element separation of 13.3' was presented. In every block, observers attended to one element of the second frame. Performance above 50% (dashed line) denotes that observers' responses agreed with the direction of the probe offset in the first frame. Means and standard errors for seven observers. (**E**) We repeated the experiment but with an inter-element separation of 26.7' and for an ISI of 100 ms only. Performance is very similar to D. Hence, the distance between lines, at least within certain limits, does not matter for Vernier offset integration. (**F**) Static control experiment. We displayed only the elements that overlapped in the two frames (i.e., the leftmost element of the first and the rightmost element of the second frame of the stimulus shown in D were not displayed). No motion percept was elicited. When the ISI is 100 ms and line 2 is attended, there is clearly no non-retinotopic feature integration. Adapted with permission from Ögmen et al. (2006).

In order to study whether feature processing and integration take place according to a retinotopic or non-retinotopic frame of reference, in the first frame, we presented one offset Vernier flanked by two aligned Verniers for 70 ms (Fig. 4A; Ögmen et al., 2006). An inter-stimulus interval (ISI) of either 0 or 100 ms followed. Then, in the second frame, three aligned Verniers shifted by one position to the right were presented for 70 ms. ISI values of 0 ms and 100 ms produced element and group motion percepts, respectively. If feature integration depends only on local retinotopic interactions, Vernier offset integration should be independent of the ISI and the central Vernier offset in the first frame should integrate with the leftmost Vernier in the second frame only. To test this prediction, we asked observers, in a block design, to attend to one of the three aligned Verniers in the second frame and to indicate the perceived Vernier offset direction.

When the ISI was 0 ms, indeed, the Vernier offset was predominantly perceived at the leftmost aligned Vernier (Fig. 4D). This result is well in line with a local integration mechanism because the offset central Vernier of the first frame overlaps spatially and retinotopically with the aligned leftmost Vernier in the second frame. When the ISI was 100 ms, the result changed contrary to what is expected from a retinotopic, local mechanism. Now, the offset was predominantly perceived in the central Vernier of the second frame even though the two Verniers overlapped neither retinotopically nor spatially (Fig. 4D). Moreover, the central element in the second frame was 13.3' apart from the probe in the first frame, i.e. outside the range where flankers interacted with the Vernier in the study by Westheimer and Hauske (1975). This result is well in line with the group motion percept and the Gestalt principle of common fate. Additional experiments show that non-retinotopic feature processing does not depend, at least within certain limits, on retinotopic distances (Fig. 4E) but strongly on the global motion percept (Fig. 4F). Moreover, when a corresponding Vernier in the second frame is offset as well, the two offsets integrate. For example, when the first frame offset is leftward and the second frame offset is rightward, the two offsets can cancel each other out (Ögmen et al., 2006, their Figure 5). In summary, our findings show that features of elements can be integrated when they are grouped by Gestalt principles.

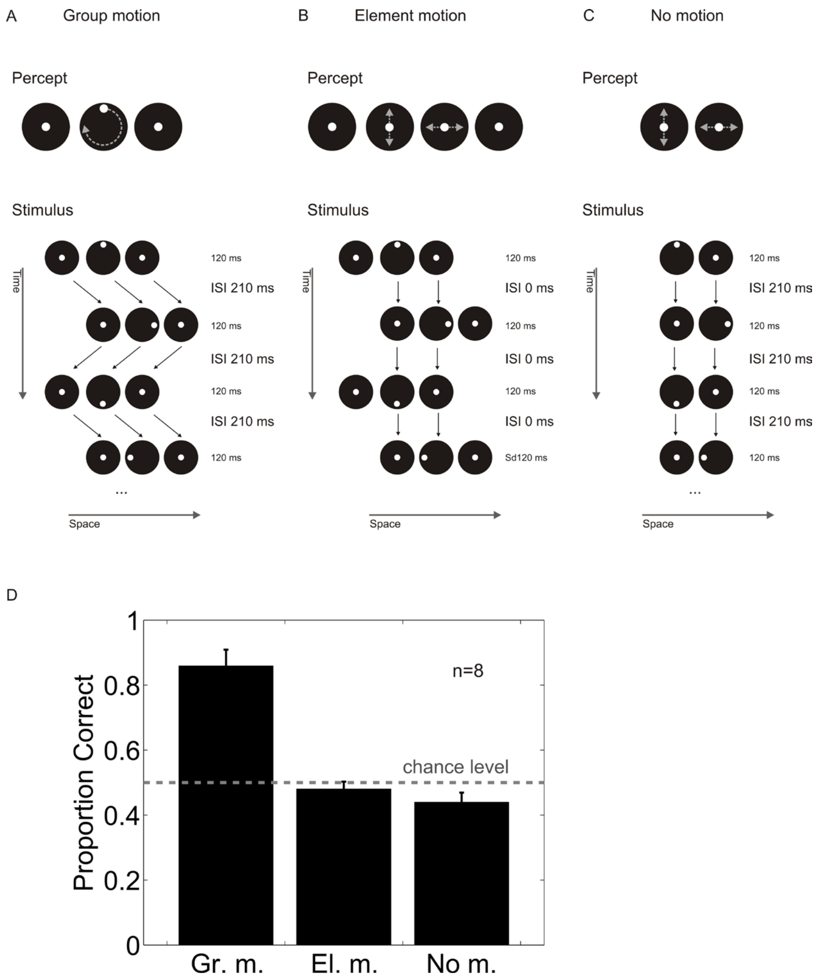

Fig. 5 Non-retinotopic motion. (**A**) We presented Ternus-Pikler displays with black disks (instead of Verniers as in Fig. 1). The outer disks of each frame contained a white dot in the center. In the central disk the white dot was shifted frame by frame along a clockwise rotation trajectory. With an ISI of 210 ms, the disks elicit the percept of group motion. In the central disk, the white dot appears to rotate clockwise (see Boi et al., 2009, their Videos 4 and 5). The apparent rotation can only be detected by motion detectors operating on non-retinotopic coordinates. (**B**) With an ISI of 0 ms, the disks elicit the percept of element motion. The white dots in the stationary central disks appear to move linearly up and down (left central disk) or right and left (right central disk; see Boi et al., 2009, their Video 6). (**C**) Only two overlapping disks are presented. As with element motion (B), the dots are perceived to move linearly (see Boi et al., 2009, their Video 7). (**D**) Observers were asked to discriminate the rotation direction of the central dot that was randomized (clockwise vs. counter-clockwise). When group motion was perceived ("Gr. m.", see A), performance was significantly better than in the other two conditions ("El. m.", "No m."; see B and C, respectively). Adapted with permission from Boi et al. (2009).

It is important to note that we do not propose that feature integration occurs whenever there is grouping. This is clearly not the case (Fig. 3). Still, our results show that, under appropriate conditions, features integrate according to non-local and non-retinotopic principles. It remains an open question when features are integrated depending on Gestalt factors and when they are not.

Importantly, our findings are general in that non-retinotopic, non-local feature processing and integration are not restricted to Vernier offsets but occur for a wide range of features. For example, local position information can be integrated into a global motion percept (Fig. 5; Boi et al., 2009). Likewise, visual search (Boi et al., 2009) and ambiguous motion (van Boxtel et al., 2009) can occur in a non-retinotopic coordinate frame.

Application of the Paradigm to the Study of the Micro-Structure of Grouping Processes

We propose that non-retinotopic feature processing can be used to understand the micro-structure of grouping processes. Consider the example with four Verniers in the first frame but only three in the second frame, which creates an ambiguous motion (Fig. 6A; Otto, Ögmen, & Herzog, 2008). What are the resulting motion correspondences between individual Verniers? With classical techniques, such as subjective reports of the perceived grouping, the microstructure of these correspondences is difficult to determine. We tested motion correspondences between individual Verniers using non-retinotopic feature integration as a "perceptual marker". The idea is that the strength of feature integration reflects the strength of underlying grouping relations. For this, only one of the four Verniers in the first frame was offset (Fig. 6A). We asked observers to attend to one of the three aligned Verniers in the second frame. High performance indicates strong feature integration (Fig. 6B), and therefore strong grouping between the offset Vernier in the first frame and the attended Vernier in the second frame (Fig. 6C). With this technique, we could, for example, show that edge elements in the first frame are mapped onto edge elements in the second frame even though the sheer distance between the elements predicts a different motion grouping (Otto, et al., 2008). Edge element grouping is a feat of perceptual organization because "edgeness" is in the eye of the beholder presupposing the grouping of elements into objects. For example, in the Ternus-Pikler display, the four Verniers in the first frame must be grouped before they can be mapped onto the group of Verniers of the second frame. Hence, again, global Gestalt grouping determines low-level feature integration.

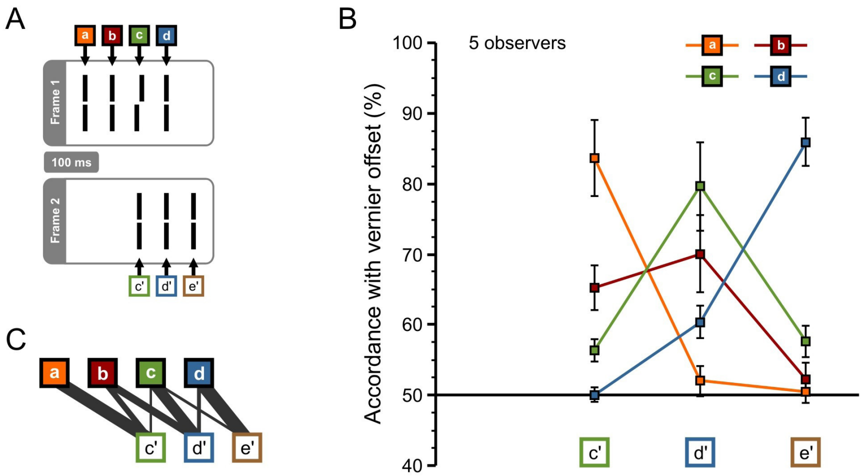

Fig. 6 Non-retinotopic feature integration reveals the microstructure of motion correspondences. (**A**) We presented a display with four lines in the first and three lines in the second frame. One line in the first frame was offset (line *c* here). Observers attended to one line in the second frame. (**B**) Percentages of responses in accordance with the offset in the first frame as a function of the attended line in the second frame. Offsets presented at the outer lines *a* and *d* are primarily perceived at the outer lines *c* and *e* in the second frame. The offset of line *c* is primarily perceived at line *d*, whereas the attribution of the offset of line *b* does not follow a clear trend. Interestingly, a vernier offset at line *a* attributes much stronger to element *c'* than a vernier offset at *b* even though *b* is closer to *c'* than *a*. (**C**) To visualize the strength of vernier offset integration between elements in the first and second frame in a compact manner, we represent the performance levels shown in B as line width in a correspondence diagram. Adapted with permission from Otto et al. (2008).

Discussion

In order to implement global distributed effects and interactions, early Gestalt theorists adopted the concept of "field" (e.g., electrical, gravitational fields) and "forces" within these fields (Koffka, 1935). Their *principle of isomorphism* implied that correlates of such fields and forces should be found in the operation of the nervous system. For example, the perception of apparent motion was explained by an energy transfer from the first point of stimulation to the second as a "short-circuit" within the field. As modern neuroscience replaced fields by networks of neurons, researchers started conceiving these long-range global interactions in terms of signals that propagate via lateral and recurrent connections (e.g., Craft et al., 2007; Grossberg & Mingolla, 1985; Roelfsema, 2006; Zhaoping, 2005)[2].

The optics of the eyes maps, by perspective projection, the distal stimulus into a proximal stimulus that preserves neighborhood relations. The projections from

[2] In theory, any input-output mapping can be approximated by a feed-forward network after carefully training the network with the desired mappings. However, since these networks cannot be trained with all possible input-output pairings, there is no guarantee that they will generate correct "generalizations" for untrained inputs. Nor do they provide a natural explanation for why the Gestalts emerge the way they do. Recurrent networks offer a more natural way of expressing the dynamics of context-dependent formation and modulation of patterns.

retina to early visual cortical areas are such that these neighborhood relations are preserved at least at the early levels of cortical representations. In addition, physiological studies suggest a hierarchical organization in the visual system such that progressively more complex features are extracted as processing moves from retina to higher visual cortical areas. Inspired by these findings, the aforementioned models implement their interactions within and between retinotopic representations. Based on these physiological and theoretical observations, one would expect the processing of relatively simple features, such as small spatial offsets, to take place relatively early in the visual system according to retinotopic relations.

Although the aforementioned prediction seems to be well supported by known physiology of the primate visual system, it does not agree with the Gestalt view that rejects the atomistic approach. In addressing this problem, we noted that, under normal viewing conditions, due to the movements of objects and the observer's eyes, head, and body, the proximal stimulus is highly unstable in terms of retinotopic coordinates. In other words, the proximal stimulus does not remain long enough in the receptive fields of early cortical neurons in order to allow meaningful computations. Perceptual data also show that a retinotopic stimulus is neither sufficient nor necessary for form perception. Insufficiency of a retinotopic representation in generating form perception can be demonstrated by metacontrast masking, where a "mask stimulus" can render invisible a "target stimulus" without any retinotopic overlap (revs. Bachmann, 1994; Breitmeyer & Ogmen, 2006). In anorthoscopic perception, one views the stimulus through a very narrow slit (rev., Rock, 1981) and thus, at any time, there is no spatially extended retinotopic image of the stimulus. Yet, we perceive the figure as a spatially extended whole instead of a temporal succession of tiny fragments, demonstrating that a spatially extended retinotopic image is not necessary for form perception. Also for static stimuli, recent investigations showed that Gestalt rather than low-level interactions explain crowding. For example, the deleterious effects on vernier offset discrimination by neighboring lines can be undone when the lines become part of a good Gestalt, e.g. being part of a rectangle (Sayim, Westheimer & Herzog, 2010).

Given these observations, we modified a stimulus paradigm, introduced by Gestalt psychologists Ternus and Pikler, in order to investigate whether processing and integration of simple features, such as Vernier offsets, take place in retinotopic or grouping-based non-retinotopic coordinate systems. As reviewed in this paper, our results favor the non-retinotopic processing hypothesis. Based on these findings, we support the view of cortical visual computations as a highly distributed and interactive non-retinotopic system, rather than a strict feed-forward retinotopic hierarchy.

Summary

Atomistic views of perception remain prevalent in neuroscience. It is often believed that visual processing proceeds from low to high levels of analysis and that low-level features are processed retinotopically. Furthermore, this low-level retinotopic processing is often assumed to be local, i.e. only neighboring elements "influence" each other. For example, the processing of two Verniers is subject to mutual interference only when the two Verniers are presented within a few minutes of arc. Here, based on a paradigm developed by the Gestaltists Ternus and Pikler, we show that global Gestalt rather than local low-level mechanisms determine feature processing and integration. Vernier offsets are integrated non-retinotopically when the Verniers are grouped by motion correspondences. These motion correspondences are determined by Gestalt grouping that emerges from contextual elements and the timing of the stimulus.

Keywords: Non-retinotopic processing, Ternus, Pikler, motion, feature inheritance.

Zusammenfassung

Wahrnehmung wird vornehmlich durch atomistische Theorien beschrieben, in denen die visuelle Informationsverarbeitung erst in niedrigen, dann in höheren retinotopen Verarbeitungsstufen stattfindet. Die Informationsverarbeitung ist darüber hinaus lokal in dem Sinn, dass sich nur die Verarbeitung räumlich benachbarter Elemente beeinflussen kann. Zum Beispiel „interagieren" zwei Nonien nur dann, wenn sie innerhalb weniger Winkelminuten präsentiert werden. Wir zeigen hier jedoch, dass eher globale als lokale Mechanismen Merkmalsverarbeitung bestimmen. Dafür nützen wir ein Paradigma, das von den Gestaltpsychologen Ternus und Pikler entwickelt wurde. Noniusversätze werden integriert, wenn die Nonien durch Bewegung gruppiert werden. Bewegungsgruppierung wird durch Gestaltprinzipien bestimmt, die sich aus dem raum-zeitlichen Kontext ergeben.

Schlüsselwörter: Nicht-retinotrope Verarbeitung, Ternus, Pikler, Bewegung, vererbte Eigenschaft.

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