



Human development of perceptual organization

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Abstract

Two relevant dimensions are revealed within which developmental patterns of perceptual organization might be investigated. Within the local–integrative dimension, employing a contour integration task, we found indications that spatial integration develops slowly. We also found reduced contextual modulation of a local target in children employing the Ebbinghaus illusion. Within the action–perception dimension, we hypothesize a relatively slow development of the perceptual system (mediated by the ventral visual stream), as compared to the development of the action system (mediated by the dorsal visual stream). Taken together, the data indicate that long-range neuronal connectivity supporting perceptual organization in the posterior pole of the brain, and in the ventral visual pathway is not fully developed in young children. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Contour integration; Development; Long range connections; Parallel visual pathways; Perceptual organization

1. Introduction

The purpose of the paper is to present our recent findings with respect to the development of perceptual organization (Section 2), and to provide a hypothetical theoretical context (Section 3) to those findings. Two relevant dimensions are investigated within which the developmental patterns of perceptual organization might be mapped (see Fig. 1). The first is the capacity to spatially integrate local features across the visual field in order to generate object boundaries. While local processes are known to be available at an early age, we found indications that spatial integration develops slowly. This will be referred to as the *local–integrative dimension*. The local–integrative dimension is associated mainly with posterior cortical areas in the occipital lobe, because this is where spatially limited receptive field sizes necessitate long-range spatial interactions for effective spatial integration. Our visual engagements in the world are mediated by at least two parallel neural systems that have been shaped by phylo- and ontogenetic pressures, and this defines the second dimension. A very early commitment of brain structures might be

required in the occipitoparietal or dorsal visual stream that mediates visuomotor control; while slower maturation, more flexibility, and later commitment might be permitted, or even favored in other cases, such as in environmentally cued classification of objects and events mediated by the occipitotemporal or ventral visual stream. This will be referred to as the *action–perception dimension*.

2. From local to integrative

A great deal of descriptive knowledge has been accumulating about visual development in the first year of human life. It is known, for example, that there is a very early preference for moving stimuli (Nelson & Horowitz, 1987), good flicker sensitivity from 2 months on (Regal, 1981), an ability to process complex motion information already at 4 months (Kellman & Spelke, 1983); reliable chromatic discriminations at 2–3 months (Teller & Bornstein, 1986); onset of stereopsis around 4 months (Braddick, Atkinson, Julesz, Kropfl, Bodis-Wollner & Raab, 1980); and rapidly increasing acuity during the first year (Teller, McDonald, Preston, Sebris & Dobson, 1986). Once the time of onset of a particular function is estimated, the assessment of subsequent

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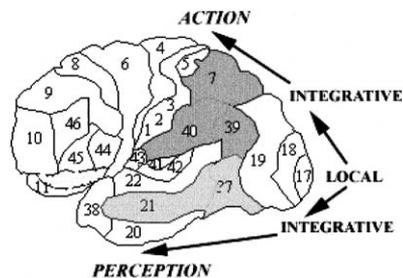


Fig. 1. The local–integrative (Brodmann areas 17, 18, 19) and action (7, 40, 39)–perception (21, 37) dimensions as they are related to brain regions. (The planar brain map is after Shankle et al., 1998a).

development should follow. This is, however, methodologically more complicated, because it relies on comparative behavioral, not on absolute (a certain function present or not) behavioral or physiological measures. Performance in a certain task has to be compared to that of an older age group, or adults. One of the difficulties is that the level of performance in children is particularly affected by non-visual factors, such as the lack of motivation or attention, and the comparability of their data with adult data is not always obvious. This might be one of the reasons why behavioral studies of human visual development beyond the second year of life are not so numerous, although the last decade brought about a few well-controlled studies. The best-studied function in these terms is visual acuity. It is now known that while stereo acuity (Ciner, Schanel-Klitsch & Herzberg, 1996), and grating acuity reaches adult levels by around 2 years of age, vernier acuity is not adult-like before 5 years (Zanker, Mohn, Weber Zeitler-Driess & Fahle, 1992; Carkeet, Levi & Manny, 1997). Recent studies also emphasize the importance of the temporal characteristics of the stimuli in determining developmental curves (Dobkins, Anderson & Lia, 1999; Ellemberg, Lewis, Liu & Maurer, 1999).

Beyond visual acuity, there are studies indicating that visual segmentation and form identification based on texture- (Atkinson & Braddick, 1992; Sireteanu & Rieth, 1992; Rieth & Sireteanu, 1994), motion- (Giaschi & Regan, 1997; Hollants-Gilhuijs, Ruijter & Spekreijse, 1998a; Schrauf, Wist & Ehrenstein, 1999), color- (Hollants-Gilhuijs, Ruijter & Spekreijse, 1998b), and flicker-contrast (Barnard, Crewther & Crewther, 1998) are relatively slowly developing functions that emerge rather late and reach maturity beyond 2 years of age. Exactly what mechanisms are behind the poor performance of children in these tasks? All tasks seem to involve mechanisms beyond the local analysis of visual features, and rely on the integration of information across the visual field.

2.1. Contour integration

Integration of information across the visual field — one step beyond the local analysis of features, such as color, orientation, direction of motion, and depth — can be studied in a contour integration paradigm (Field, Hayes & Hess, 1993; Kovács & Julesz, 1993; Dakin & Hess, 1998; Braun, 1999; Hess & Field, 1999; Kovács, Kozma, Fehér & Benedek, 1999a; Kovács, Polat, Pennefather, Chandna & Norcia, 1999b; Pennefather, Chandna, Kovács, Polat & Norcia, 1999; Silverstein, Kovács, Corry & Valone, 1999). The local rules of neural interactions governing our ability to link contour segments together are determined by employing stimuli with a continuous path of Gabor signals embedded in noise (see Fig. 2). Gabor signals roughly model the receptive field properties of orientation selective simple cells in the primary visual cortex (V1), therefore they are appropriate stimuli for the examination of these small spatial filters and their interactions. The embedded contours cannot be detected by purely local filters, or by the know types of orientation tuned

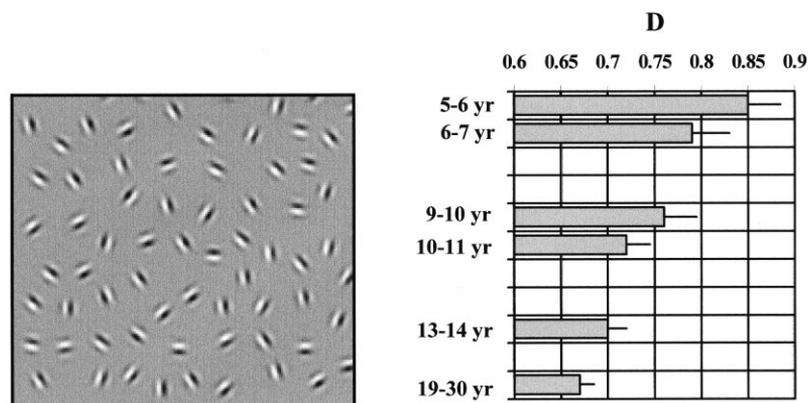


Fig. 2. The left panel shows an example of the orientation-defined contour stimulus. The closed contour in the middle of the panel is defined by orientation alignment of the Gabor elements. D at threshold is shown as a function of age in the right panel (these data were presented earlier in Kovács et al., 1999a; Kozma et al., 1999).

neurons with large receptive fields (see also Dakin & Hess, 1998; Hess & Field, 1999). The long-range orientation correlations along the path of the contour can only be found by the integration of local orientation measurements. The noise forces the observer to do these local measurements at the scale of the individual Gabor signals, and to rely solely on long-range interactions between local filters while connecting the signals perceptually. Thus, with these stimuli, long-range interactions subserving spatial integration can be studied in isolation.

These relatively low-level interactions seem to be sensitive to factors of perceptual organization. We found superiority of closed paths over open paths in terms of maximal separation between adjacent elements in this task (Kovács & Julesz, 1993), and enhanced local contrast sensitivity within closed contours (Kovács & Julesz, 1994). We also found indications for the existence of an object-centered shape representation at the level where these interactions are located (Kovács & Julesz, 1994; Kovács, 1996; Kovács, Fehér & Julesz, 1998). These results indicate the participation of the interactions in object-related processing.

Integration of orientation information across space in the contour-detection task (Field et al., 1993; Kovács & Julesz, 1993; Kovács, 1996; Dakin & Hess, 1998; Kovács et al., 1999b; Pennefather et al., 1999), and in a less complex configuration employing a lateral masking paradigm (Polat & Sagi, 1993, 1994; Polat & Norcia, 1996) has been related to long-range facilitatory interactions between orientation-tuned spatial channels. Anatomically, integration across space can be mediated either by horizontal connections within each cortical representation of the visual field, by the increasing receptive field sizes at higher level cortical areas, or by modulatory feedback connections from them. A possible anatomical substrate of the psychophysically defined long-range interactions is the plexus of intrinsic horizontal connections of the primary visual cortex (Rockland & Lund, 1982; Gilbert & Wiesel, 1983; Gilbert, 1998). There might also be contribution in the contour task from feedback connections that originate in extrastriate cortex and mediate top-down influences. In a recent neuropsychological study (Giersch, Humphreys, Boucart & Kovács, 2000), a visual agnostic patient with intact V1, but severely damaged occipital areas beyond V1 has shown normal contour integration performance. This might indicate the sufficiency of V1 in mediating contour integration.

Illusory contours are interesting with respect to the anatomical correlates of contour integration in our task because (1) they are similar to the Gabor-contours in that they also involve the integration of orientation information across large spatial distances in the absence of luminance cues; (2) there is information with respect to their anatomical substrates. Single cell studies indi-

cate V1 (Grosf, Shapley & Hawken, 1993) and V2 (von der Heydt, Peterhans & Baumgartner, 1984) responses to illusory contours. Recent fMRI accounts of illusory contour processing seem to indicate the participation of higher-tier areas, such as V3A, V7, V4v, and V8 (Mendola, Dale, Fischl, Liu & Tootell, 1999).

In a series of recent experiments, we directly tested the *development of visual spatial integration* in children, and the *effect of abnormal visual input* in adults by employing the contour integration task. We found significant improvement of performance in children between 5 and 14 years in this task (Kozma, Kovács & Benedek, 1997; Kovács, Kozma, Fehér & Benedek, 1999; Kovács et al., 1999a), and a deficit in performance of adults who had abnormal binocular visual experience early in life (Kovács et al., 1999b; Pennefather et al., 1999). We have also started to investigate very young subjects (3-month-old babies, Gerhardstein, Ditre & Kovács, 1999; Gerhardstein & Kovács, 2000), and different patient populations with a possibility of perceptual organization problems (Giersch et al., 2000; Silverstein et al., 1999). In these studies we used a card-test version of the contour detection task (introduced by Kovács, Polat & Norcia, 1996; Kozma et al., 1997, 1999; Kovács et al., 1999a,b; Pennefather et al., 1999) to study the human developmental pattern of spatial integration. The card version is more suitable for children and for clinical settings, and it also allows us to test a large number of children and patients. Similarly to Fig. 2, a contour integration card consists of a closed chain of colinearly aligned Gabor signals (contour), and a background of randomly oriented and positioned Gabor signals (orientation noise). The task is to identify the path of the contour. To estimate the actual strength of long-range interactions in each observer, relative noise density is varied across the set. Relative noise density (D) is defined as the ratio of average noise spacing over contour spacing (see Fig. 3). D is varied between 0.5 and 1.2 in steps of 0.05, resulting in 15 cards per set. When $D > 1$, the contour can be detected by using element density information, because the contour elements are closer to each other than the noise elements. However, when $D < 1$, this cue is not available, and it is impossible to detect the contour without orientation specific long-range interactions (see Fig. 3). The value of D at threshold (D_{\min}) defines the strength of the long-range interactions in an individual observer. The smaller this number the stronger the interactions.

2.2. Normal development of contour integration

Over 400 children with normal vision were tested with the contour-integration cards (Kozma et al., 1997, 1999; Kovács et al., 1999a). The children ranged in age from 5 to 14 years. As shown in Fig. 2, children in the

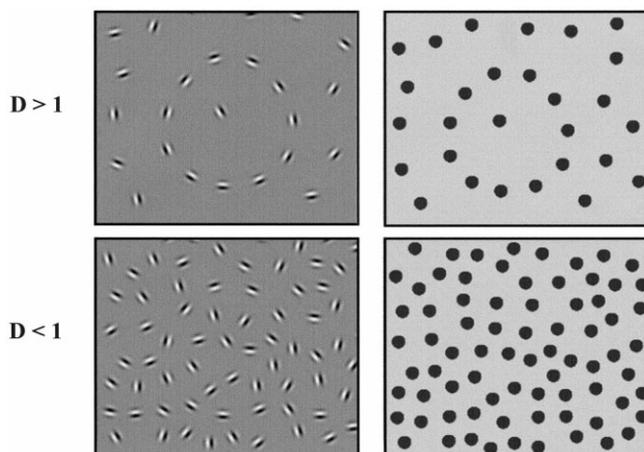


Fig. 3. Examples of contours with different D values. Top, $D = 1.4$; bottom, $D = 0.85$. In the right panels, Gabor elements were replaced by disks. Without orientation cues, the contour remains invisible at $D < 1$.

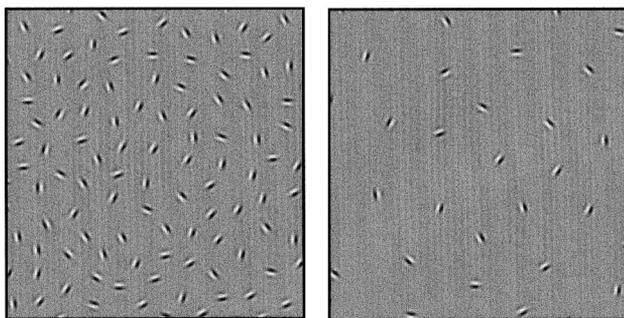


Fig. 4. Examples of contours with different contour spacings (left, 4.5λ ; right, 9λ , where λ is the wavelength of the Gabor signal). $D = 0.85$ in both cases. Adult performance does not depend on contour spacing, only on D . Children integrate large-spaced contours with greater difficulty.

13–14 year old group were able to see most of the contours in the set ($D_{\min} = 0.7$), while 5–6 year old children missed the contours in about half of the cards ($D_{\min} = 0.84$). This is a great difference in contour-integration performance between the two age groups. There is gradually increasing performance, and adult-like levels are not reached until after adolescence in this task.

In order to see whether the surprisingly slow development that we found is due to the immaturity of perceptual skills, or to the lack of motivation or attention, we looked at the effect of practice and at the specificity of learning (Kozma et al., 1999; Kovács et al., 1999a). We used a new set of cards, where the path of the contour was defined by color instead of orientation. The locations of the contour and background elements were the same as in the orientation-defined set. Contour elements were red, and the background was mixed red and green. Luminance contrast and the size of the elements were randomized in order to ensure that the contour was purely defined by color similarity. The difficulty

level of each color-defined card was matched to the difficulty level of orientation-defined cards. This was achieved by varying the percentage of red elements in the background, and measuring the performance of adult observers. We found significant learning after a few days of practice both in children and in adults, and the learning was specific to visual cues of orientation and color. Performance in various low-level visual tasks has been shown before to significantly improve with practice (e.g. hyperacuity — Poggio, Fahle & Edelman, 1992; visual discrimination — Fiorentini & Berardi, 1980; pop-out — Karni & Sagi, 1993; visual search tasks — Sireteanu & Rettenbach, 1995). Although these tasks involve a variety of visual stimuli, most of them seem to be specific for stimulus parameters, and some of them even for retinal location. A high degree of stimulus specificity usually suggests that the plastic neuronal changes of learning took place at early cortical levels where the basic stimulus dimensions are still separable. The lack of transfer of learning across orientation and color in the contour-detection task indicates that the involved mechanisms are perceptual mechanisms with access to relatively low-level perceptual representations. Since there are no luminance cues in these cards, integration within specifically tuned mechanisms — such as the orientation and color processing ‘channels’ — is required to solve the tasks. The lack of transfer indicates that the dynamic changes during learning must have occurred within these channels.

Why do young children perform poorly in the contour integration task? The development of horizontal connections in layer 2/3 of the primary visual cortex of humans has been shown to extend well into childhood (Burkhalter, Bernardo & Charles, 1993), and a delayed postnatal development of feedback connections between V1 and V2 has also been indicated in humans (Burkhalter, 1993). In order to see whether absolute cortical distances spanned by lateral interactions are limiting performance in the contour-integration task, we conducted an experiment where we varied the spacing among contour elements while we kept the relative noise level constant (see Fig. 4). We found that D_{\min} in adults is independent of contour spacing (see also Braun, 1999). This indicates that adults are only limited by display parameters (signal-to-noise ratio) in the tested range, and not by the absolute range of cortical interactions. In children, however, we found better performance at smaller contour spacings, and the difference between children and adults in contour detection performance was greater at larger contour spacings. At 9λ contour spacing, where λ is the wavelength of the Gabor signals, performance was poorer in a group of 30 relatively practiced children ($D_{\min} = 0.85$) than at 7λ ($D_{\min} = 0.8$; $P < 0.01$; two-tailed t -test). We concluded that long-range interactions span a shorter spatial range in children than in adults. The result also

indicated that it is not some kind of search (Sireteanu & Rettenbach, 1995) deficiency that limits children's performance, because that should result in an opposite tendency (improving performance with decreasing number of distractors). And the third implication is that our effect is probably truly perceptual because motivational factors (such as perseverance in completing a difficult task) or cognitive mechanisms (such as search strategies) would not be expected to generate different tendencies among children and adults in terms of contour spacing.

Taken together, these data raise the possibility that the development of related visual mechanisms could be understood in terms of local neural circuits. Based on the existing data, it seems that those circuits that process local visual features mature first, while circuits integrating the local features into coherent scenes come about later. Further behavioral experiments will have to address integration of other visual features, such as motion.

2.3. *Abnormal visual development and contour integration*

Along with preprogrammed maturation, perceptual experience is also shaping the development of perceptual organization. Developmental insults caused by abnormal perceptual input/experience will depend both on the developmental timing of the system, and on the onset of abnormal input (as it has been dramatically demonstrated by visual deprivation experiments, e.g., by Wiesel, 1982). It might be expected that early insult to an early maturing system should result in irreversible losses, while to a late maturing system it should be much less dramatic because of the plasticity of the system at the time of the injury. Late insult — unless it is extremely selective and extensive — should leave the early maturing system relatively intact, and bring about more serious impairments in a late maturing system. If perceptual organization in the contour-integration task were a late maturing function, one would expect that it would be most affected by insults with a relatively late onset.

It has been shown that abnormal binocular input not only leads to reduced visual acuity (usually in one eye only: the condition of amblyopia), but to reduced contour-integration performance as well (Kovács et al., 1996, 1999b; Pennefather et al., 1999), and that performance in the contour-integration task depends on the type of amblyopia (Hess, McIlhagga & Field, 1997; Hess & Demanins, 1998), and also on the type of the treatment patients received (Chandna, Pennefather, Wood, Polat, Kovács & Norcia, 1998). Our results also show that even in the absence of amblyopia, a history of abnormal binocular input can lead to reduced contour-integration performance in both eyes (Kovács et

al., 1999b). While strabismic amblyopes are at the 6–7 year old performance level in the contour-integration task as measured by the card test, strabismic patients without amblyopia perform at the 10-year-old level (Kovács et al., 1999b). The conclusion of these studies was that there is a complex picture in terms of visual deficits following abnormal binocular input, and the type and severity of the deficit depends not only on the type and timing of input abnormality, but on the treatment history of the patients as well. A longitudinal study looking at the perceptual organization abilities of children with early and late onset eye problems (e.g. strabismus or anisometropia) would be extremely interesting.

2.4. *Is contextual integration less efficient in children?*

We assume that context mediating neural interactions of the primary visual cortex (Gilbert, Das, Ito, Kapadia & Westheimer, 1996; Gilbert, 1998) are responsible for integration in our contour integration task. Since these interactions seem to span shorter distances in children than in adults (Kovács et al., 1999a; Kozma et al., 1999), we predict reduced susceptibility for contextual influences in children. Perceptual contextual influences can be estimated by measuring the contextual modulation of the percept of a local target. Geometric optical illusions provide a good paradigm for this type of measurement. There is indication that the 'strength' of a size contrast (Ebbinghaus) illusion varies across different age groups, and that young children succumb less to it (Weintraub, 1979; Zanutti, 1996). In order to verify this tendency, we determined the magnitude of a size contrast (Ebbinghaus) illusion in 4–5 year old children, and in adults (Káldy & Kovács, 2000). First we tested whether children can reliably perform a simple size-comparison task. We used the method of constant stimuli. Observers were asked to compare two disks displayed side by side, and point to the larger disk. One disk was kept at a constant size of $d = 38$ mm across all conditions. Comparison disks were varied in size in equal steps in a range of 32–42 mm of diameter, with eight different comparison sizes. Within one block of trials each comparison size was presented five times, and the order of presentation was randomized. Under these conditions children performed like adults (Fig. 5, left two bars). Notice, however, that this only indicates that children are able to carry out precise size discrimination when the size difference is about 3–4%. The result does not indicate that children are as good at size discrimination as adults, because we did not look at smaller differences where adults might be performing better. In the next experiment we added large inducing disks to the constant size disk, and repeated the measurement. The results are shown in Fig. 5, right two bars. While adults

were significantly affected by the context of the inducers, and underestimated the size of the comparison circle significantly, children were only minimally affected. This pattern of results supports the prediction with respect to reduced contextual influence in young children.

These results also provide an interesting link between the local–integrative, and action–perception dimensions. Supporting evidence for the action/perception distinction also came from studies on normal subjects where the magnitude of the Ebbinghaus illusion was estimated in two different conditions: (1) the perceptual system of adults was subject to the illusion in a size estimation task; and (2) the action system was not affected by the context in a grasping task (Aglioti, DeSouza & Goodale, 1995; Marotta, DeSouza, Haffenden & Goodale, 1998; Goodale & Haffenden, 1998; Haffenden & Goodale, 1998). The reduced illusion in young children therefore might be attributed to the immaturity of the perceptual system.

3. From action to perception

It has become clear from primate physiology, anatomy, and from human psychophysical and lesion studies that there are at least two major specialized subsystems of vision. According to earlier accounts, the dorsal (occipitoparietal) stream specializes in spatial vision, and the ventral (occipitotemporal) stream specializes in form vision (Ungerleider & Mishkin, 1982; Hubel & Livingstone, 1987). Goodale and Milner

(1992) give a modern reinterpretation of the functional dissociation: the two streams carry out different transformations on the object and location information they both receive. The transformations of the dorsal stream mediate the control of visually guided actions, while the transformations of the ventral stream permit perceptual and cognitive representations of objects and their significance (Goodale & Milner, 1992; Goodale, 1993; Milner & Goodale, 1995). The earlier approaches (Ungerleider & Mishkin, 1982; Hubel & Livingstone, 1987) concentrated on the division of labor between the two streams in terms of visual attributes (such as movement and location in the dorsal, versus orientation, color, size and shape in the ventral stream), and assumed that the outputs of the streams contribute to a single representation of the environment subserving both action and conscious perception. Goodale and Milner place less emphasis on the parallel processing of different visual attributes, and focus more on the phylogenetically relevant functional aspects. They suggest that the two parallel streams might have evolved because visually guided locomotion/action requires different types of representations than the phylogenetically much younger visual perception. The representations are obtained through different transformations carried out by the streams. The action system has to encode object properties as they change from moment to moment with respect to the observer, therefore, it is on-line, uses egocentric coordinates, and has a very short memory-span. The perception system has to encode object identity for further use by the cognitive system, therefore it employs object-centered descriptions, and relies on long-term storage. The outputs of the streams contribute to *two parallel 'visual worlds'*, one — largely unconscious — underlying the control of action, and the other providing us with conscious visual experience of constant object properties.

If the two visual streams have evolved to carry out different transformations on the input for the purposes of goal-directed action and perception, any possible developmental dissociations between them should be best revealed in stream-specific tasks addressing that dimension. The ideal study would establish psychophysical tasks that are selectively engaging the ventral or dorsal visual streams, and it would investigate their developmental speeds, subpatterns, and possible dissociations. With selective tasks, the ventral and dorsal developmental curves could be compared. This goal, however, is very difficult to achieve, because most of the existing psychophysical techniques are related to ventral stream function. Please note, that according to the theoretical framework (Goodale & Milner, 1992), the functional dissociation is beyond 'Where' versus 'What' (Ungerleider & Mishkin, 1982), or 'motion' versus 'form' (Hubel & Livingstone, 1987; and a developmental consideration in Atkinson, Braddick, Lin, Curran,

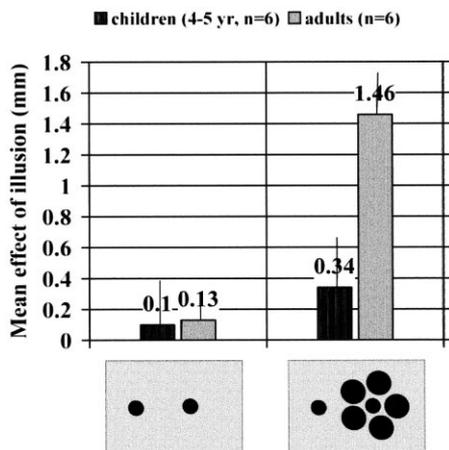


Fig. 5. The magnitude of the Ebbinghaus illusion was estimated with the method of constant stimuli. The task was to compare the size of two disks, and decide which one is larger. The figure shows performance in two conditions: the control task without inducers (bars on the left, and the condition illustrated below); the task with large inducer disks (bars on the right). Children, as well as adults, are performing well in the control task, and children experience much smaller illusions when the inducers are added (these data are presented in Káldy & Kovács, 2000). The error bars show 1 SE.

Guzetta & Cioni, 1999; Braddick, O'Brien, Wattam-Bell, Atkinson & Turner, 1999). The distinctive features of the two streams are along the 'action' versus 'perception' dimension, and the ultimate goal is to address that dimension.

How can ventral stream function be best addressed? 'Transformations carried out in the ventral stream permit the formation of perceptual representations that embody the enduring characteristics of objects and their relations' (Goodale, 1998). The most relevant cortical area within the stream is the inferior temporal (IT) cortex. IT is thought to be important in maintaining object identity, size and location invariance and short-term memory (Miller, Li & Desimone, 1991; Lueschow, Miller & Desimone, 1994), and has been studied extensively in a delayed matching-to-sample (DMS) task in behavioral, and combined lesion studies. Based on our findings on the limited range of perceptual spatial integration, and reduced contextual integration in children (Kovács et al., 1999a), it is predicted that perceptual representations that are important in the DMS task will be more vulnerable in young individuals. And indeed, it takes 2 years of maturation before macaque monkeys can solve a version of the task (delayed nonmatching-to-sample, DNMS) with adult proficiency (Bachevalier, 1990). It has also been found that human infants up to 32 months of age required prolonged training and maturation before learning a DNMS task (Overman, 1990; Overman, Bachevalier, Turner & Peuster, 1992), although it has been argued that some of the effects are related to non-visual task demands (Diamond, Towle & Boyer, 1994).

How can dorsal stream function be best addressed? Transformations carried out in the dorsal stream 'utilize moment-to-moment information about objects within egocentric frames of reference' (Goodale, 1998). According to the recent view, the function of the posterior parietal cortex (PPC) is to integrate sensory information for action planning (Andersen, Snyder, Batista, Buneo & Cohen, 1998). In PPC, target locations are coded in multiple coordinate frames, such as eye, hand, body, and world (Colby & Duhamel, 1996; Andersen et al., 1998; Snyder, Grieve, Brotchie & Andersen, 1998). Sensory signals from other modalities are combined there with visual signals, and integrated to provide motor coordinates for goal-directed movements (Andersen, Snyder, Bradley & Xing, 1997). Effective motion coordination probably also requires maturation and learning within these structures, however, the nature and temporal course of their development is not known yet.

Do the parallel streams mature at the same rate? In the lack of data allowing for direct comparison between the two streams, one may still formulate a working hypothesis to be tested. We hypothesize that the development of the ventral visual stream mediating percep-

tion is delayed with respect to the dorsal stream mediating action. The hypothesis is based on the following considerations: (a) there is anatomical indication for the slower functional development of the occipitotemporal pathway compared to the occipitoparietal pathway in macaque monkeys (Bachevalier, Hagger & Mishkin, 1991; Distler, Bachevalier, Kennedy, Mishkin & Ungerleider, 1996); (b) there is human anatomical indication for slower establishment of long-range connectivity in the ventral compared to the dorsal stream (Kovács, Fehér, Shankle, Hara & Fallon, 1999c) based on the analysis of the Conel database (Conel, 1939–1967; Shankle, Landing, Rafii, Schiano, Chen & Hara, 1998a; Shankle, Romney, Landing & Hara, 1998b; Shankle, Rafii, Landing & Fallon, 1999; Landing, Shankle & Hara, 1998a; Landing, Shankle & Boyd, 1998b); (c) the dorsal stream is phylogenetically older (Pandya, Seltzer & Barbas, 1988), which might suggest more genetic preprogramming, and faster maturation; (d) during ontogeny, there might be a greater need for early availability of structures mediating the visual control of action (dorsal stream) than for those representing object identity (ventral stream); (e) if the ventral stream is mediating perceptual representations that are part of a high-level cognitive network enabling us to understand the environment, a protracted developmental course with plasticity preserved beyond the earliest ages would be desirable.

4. Summary

Although important visual functions emerge during the first year of life, the completion of visual development seems to extend until the end of childhood. Development of different visual functions and the maturation of neuroanatomical circuits participating in visual information processing is not homogenous. We revealed two relevant dimensions within which developmental patterns of perceptual organization can be investigated. We employed a contour integration task to study the local-integrative dimension. The data show that long-range spatial interactions — subserving the integration of orientation information across the visual field — span a shorter spatial range in children than in adults, and become adult-like only towards the end of childhood. The developmental pattern of this important integrative function predicts that contextual integration should be underdeveloped in young children. That was confirmed by reduced contextual modulation of a local target in children (employing the Ebbinghaus illusion). The visual performance of 4–5-year-old subjects studied in our experiments resembles that of those adults with ventral visual stream dysfunction (Farah, 1990; Milner & Goodale, 1995): relatively advanced visuomotor coordination, but difficulties in perceptual organiza-

tion. Taken together, our data indicate that *long-range neuronal connectivity* supporting perceptual organization within the posterior pole of the brain, and in the ventral visual pathway *is not fully developed* in young children.

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