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Does Visual Modularity Increase over the Course of Development?

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Abstract

Early in postnatal development, the brain produces exuberant connections, some of which are later retracted, a process that is thought to play a role in the formation of functionally segregated modules in the brain. In the case of visual development, retraction between visual areas might underlie the known psychophysical and neural segregation of processing for different aspects of vision (e.g., color, motion, form, depth) known to exist in adults. This review covers the psychophysical evidence for increasing dissociation between visual modules over the course of development, and provides insight into the possible functions of this developmental alteration.

Keywords

development; color; motion; shape; synesthesia; parvocellular; magnocellular

Neuroanatomical evidence has shown that young animals possess transient connections between cortical areas that will subsequently be retracted.^{1-5,6} Although little is known regarding the behavioral consequences of this neurobiological phenomenon, it has long been conjectured that this transient period of *enhanced neural intermingling* will create for infants an unusual perceptual experience, with one of the earliest discussions proposing that the sensations of newborns “were mixed together like a bouillabaisse”.⁷ Since then, several papers have further discussed the potential for enhanced *sensory* intermingling in infants, both within and across sensory modalities.⁸⁻¹⁵

Although rich in theory, a major obstacle in providing evidence for the *enhanced sensory intermingling* hypothesis is that, while it may be relatively easy to show that young infants experience an intermingling of senses,¹⁵ it is far more difficult to show that the intermingling *dissipates* over the course of development. This is because demonstrating the dissipation requires using the same test at different ages, and then showing that older subjects (whether that be older infants, children or adults) exhibit *weaker* effects than younger infants, which for practical reasons (degree of attentiveness, cooperation, motor control, etc.) is an improbable outcome in a developmental study. Still, there has been some supporting evidence in the cross-modal domain, as follows. Preferential looking studies have shown that younger (3- to 4-month-olds), but not older (5- to 6-month-olds), infants look appropriately at a face (visual) that matches a voice (auditory).¹⁶ And, habituation studies have shown that younger (newborn to 3-month-olds), but not older (4- to 5-month-olds), infants show cross-habituation transfer from a tactile stimulus to its visual equivalent,¹⁷⁻¹⁹ although these findings should be viewed with caution as they are not entirely consistent²⁰ (note that the age-related effect observed in the above-mentioned studies reverses for visual-to-tactile transfer).

The current paper reviews some recent investigations of transient enhanced sensory intermingling in early infancy, and in addition, addresses what purpose it might serve in development. For this feature issue of IOVS, the discussion will be restricted to evidence from *within the visual system*, specifically, addressing the possibility that dissipation of sensory intermingling leads to increased visual modularity over the course of development. To help elucidate what function transient sensory intermingling might serve, it is perhaps important to distinguish between intermingling that is utilitarian versus that which is not. *Utilitarian* sensory intermingling can be considered that in which one sensory process provides a functionally appropriate input cue for another sensory process. A good example of this would be the extraction of a contour defined by a particular visual feature (e.g., color, luminance, depth) being used as an input cue to extract the *movement* of that contour. So defined, in young infants, there could be an exuberance of visual feature types that provide input to motion detectors, with the most efficient input types being maintained, and less efficient input types being retracted, over the course of development. This process could reduce redundancy, and in addition, could be shaped by visual experience, with more or less retraction occurring depending on the statistics of an individual's environment. By contrast, *non-utilitarian* sensory intermingling can be considered that which has no obvious benefit to the developing system. A good example of this would be “synesthesia”, a condition in which a single stimulus produces two sensations, one that is appropriate and one that is not, where it can easily be argued that it makes good sense to get rid of the inappropriate sensory response over the course of development.

This chapter begins with discussing evidence for enhanced *utilitarian* sensory intermingling in infancy, in particular, reviewing studies that report age-related decreases in the use of chromatic contour cues for motion processing. This is followed by recent evidence for enhanced *non-utilitarian* sensory intermingling in infancy, in particular, presenting studies that report age-related decreases in the strength of synesthetic-like associations between particular colors and shapes.

Utilitarian Sensory Intermingling in Infancy

The use of chromatic contour information as a cue for motion processing is a particularly interesting case to study, since in adults a wealth of psychophysical data has documented the limited contribution of chromatic information to motion perception, a phenomenon that is thought to arise from minimal cross-talk between neural areas encoding object color versus object motion.²¹⁻²³ One particularly effective psychophysical paradigm that has been used to demonstrate limited chromatic input to motion perception is the “motion/detection” (*MOT/DET*) paradigm, in which contrast thresholds for *detection* of a moving grating stimulus (*DET*) are compared to contrast thresholds for *direction-of-motion discrimination* (*MOT*) for the same moving grating stimulus. For adults, *MOT/DET* ratios for luminance (light/dark) gratings are near 1.0 (i.e., luminance contrast levels sufficient for detection are sufficient for discriminating direction), indicating that luminance information provides strong and effective input to motion processing. By comparison, *MOT/DET* ratios for chromatic (equiluminant, red/green) gratings are significantly larger, ranging from 2.0 to 4.0 (i.e., chromatic contrast levels sufficient for detection are *not* sufficient for discriminating direction), indicating that chromatic information provides relatively ineffective input to motion processing.²³⁻²⁸ As described previously,²⁹ at the neural level, these adult *MOT/DET* results can be explained by supposing that, relative to the neural pathway that underlies luminance sensitivity (presumably the *Magnocellular*, *M*, retinogeniculate pathway), the neural pathway that underlies red/green chromatic sensitivity (presumably the *Parvocellular*, *P*, retinogeniculate pathway) provides weaker input (either fewer number of projecting neurons or weaker synaptic efficacy of those projections) to cortical areas involved in direction discrimination, like the middle temporal area, MT (see 30 for a review of MT). This neural input asymmetry is, in fact, supported by

studies in adult primates demonstrating weaker P- versus M-pathway input to MT,^{31,32} as well as studies showing that adult MT neurons' signaling of direction is significantly weaker for chromatic, than for luminance, stimuli.²³

For *infants*, the pattern of results obtained in the *MOT/DET* paradigm has been shown to be markedly different from that of adults. In these infant studies, the *MOT* threshold was obtained using a directional eye movement technique^{33,34} and the *DET* threshold was obtained using Forced-Choice Preferential Looking, FPL.³⁵ As shown in Figure 1A, in contrast to adults, the *MOT/DET* ratios of 3-month-old infants were nearly identical for luminance and chromatic (equiluminant, red/green) gratings.^{28,36} This result suggests that, for young infants, luminance (*M*-pathway) and chromatic (*P*-pathway) mechanisms provide equally strong input to cortical motion areas like MT. Presumably, over the course of development, the input becomes asymmetrical, with luminance (*M*-pathway) input dominating. Although the changing pattern of luminance versus chromatic *MOT/DET* ratios from infancy to adulthood suggests a reweighting of luminance versus chromatic input to motion processing, these effects could be mediated by one of two phenomena: 1) selective strengthening of luminance input to motion, and/or 2) selective weakening of chromatic input to motion, over the course of development. Only the latter scenario is in the spirit of enhanced color/motion intermingling in infancy, which to prove psychophysically, would require showing a genuine worsening of chromatic-motion performance with age. This could not be demonstrated in the above-described *MOT/DET* studies because, obviously, *absolute* chromatic MOT thresholds were lower, i.e., better, in adults than in infants, simply because adult contrast sensitivity is much greater than that of infants.

To investigate directly a possible age-related weakening of chromatic input to motion processing, a subsequent study measured absolute chromatic (equiluminant, red/green) motion performance across 2-, 3- and 4-month-olds, with the notion that age-related decreases in performance might be observed in this relatively short developmental period.³⁷ Using the directional eye movement technique, infants' percent correct performance in discriminating motion direction was compared across ages, separately for a chromatic-motion, versus a luminance-motion, stimulus. As shown in Figure 1B, the results of this study revealed that, while there was a clear and significant increase in luminance-motion performance between 2 and 4 months of age, for chromatic-motion, there was no age-related improvement, or if anything, there was a slight worsening of performance. This lack of age-related improvement in chromatic-motion performance cannot simply reflect a lack of increase in chromatic contrast sensitivity over the same developmental period, since chromatic sensitivity (outside the domain of motion) shows a robust and significant increase between 2 and 4 months of age.³⁸⁻⁴² To reconcile the lack of age-related improvement in chromatic-motion performance in the face of clear improvement in chromatic sensitivity, one can suppose a selective weakening/retraction of chromatic (*P*-pathway) input to cortical motion detectors within the first few months of life. Interestingly, developmental studies in primates have provided neuroanatomical support for substantial retraction of *P*-pathway input to area V1 in the first few months (in terms of spine numbers and axonal branching,^{43,44} leaving open the possibility that the same is true for input to cortical motion areas, a possibility that has yet to be explored. Such selective *P*-pathway retraction would be expected to lead to increased modularity between color and motion processing throughout development.

Non-Utilitarian Sensory Intermingling in Infancy

Perhaps the most well known example of non-utilitarian sensory intermingling is “synesthesia”, a condition in which a stimulus evokes not only the appropriate sensation, but also another (inappropriate) sensation of a different character.^{45,46} (Although, in principle, synesthesia has no obvious benefit, i.e., it is non-utilitarian, there has been suggestion that

synesthesia is associated with enhanced abilities on, or proclivity for, creative tasks, as well as enhanced memory function⁴⁷⁻⁵⁰). It has been proposed that synesthesia is a normal stage in early infancy, with only a small percentage of individuals retaining this unusual condition into adulthood.^{12,14,15,46,51} More specifically, the idea is that synesthesia originates from the normal circumstance of exuberant connections between brain areas in early infancy, yet, unlike the normal circumstance in which these connections retract over the course of development, in synesthetes, they do not. Within the *visual* domain, there is a form of synesthesia, “grapheme-color” synesthesia (seen in ~2% of adults⁵²), wherein a particular letter/number is associated consistently with a particular color (e.g., the letter “w” may evoke the color “pink”). In line with the “lack of retraction” hypothesis (*above*), data from recent diffusion tensor imaging (DTI) studies in grapheme-color synesthetes suggest abnormally high connectivity between their grapheme and color areas of visual cortex (53, and see ⁵⁴ for similar conclusions based on fMRI). Although little is known about the development of grapheme-color synesthesia, it has been shown to exist in 6- to 7-year-old children at about the same prevalence as seen in adults, although unlike the consistency seen in adult synesthetes, the grapheme-color associations of child synesthetes appear to be more chaotic, taking years to stabilize.⁵⁵ (There is also evidence for remnants of synesthetic-type pairings in *typical* children and adults, some of which could be learned associations.^{56,57} A full discussion of this topic is outside the scope of this review).

Very recently, the possibility of grapheme-color synesthesia in young infants has been investigated by Wagner & Dobkins,⁵⁸ in a study that used FPL to measure infants' looking preferences in response to combinations of colors and shapes, with the notion that “shapes” are developmental precursors to “graphemes”. The stimulus, shown in Figure 2, consisted of a field of black shapes (triangles or circles) on a saturated colored background, the left and right halves being equiluminant red and green, respectively (or vice versa). For each infant, the number of trials on which the red versus the green half of the background was preferred was statistically compared between the two different shape conditions, triangles and circles. The prediction is that if an infant perceives triangles as one color and circles as another color (consistent with a synesthetic experience), these “colored” shapes will interact with the red and green background colors in such a way that the preference for the red versus green background differs between the triangle and circle conditions. Moreover, this interaction is predicted to decrease with age. In line with these predictions, the results of this study revealed significant shape-color interactions for 2-month-olds, but not for 3-month-olds or 8-month-olds. Such findings are consistent with the possibility of exuberant connections between color and shape (later, grapheme) areas early in infancy, which under typical conditions later get retracted, a phenomenon that would lead to increasing modularity between color and shape processing throughout development.

Concluding Remarks

While neuroscience has shown that typically developing brains produce exuberant connections, some of which are later retracted, little is known about the functional or behavioral consequences of this developmental phenomenon. In a somewhat bold exposition, Gerald Edelman⁵⁹ proposed that the developmental exuberance/retraction is a type of “neural darwinism”, whereby the developing brain starts out with a smorgasbord of neural connections and processes, with only those most fit for the environment surviving. Along these lines, the above-described age-related decrease in strength of chromatic input to motion processing could be driven by relatively less fit input cues from the Parvocellular (P, chromatic) pathway, as compared to the Magnocellular (M, luminance) pathway, for motion processing. One should not jump to conclusions, however, that the ineffectiveness of the P-pathway input is related to its chromatic properties, *per se*. Instead, it may be that other response properties of the P-pathway, i.e., its relatively low temporal and high spatial resolution,⁶⁰ are not well matched

to the statistics of moving objects in the environment.⁶¹ To test this, future animal studies could investigate whether manipulating the spatiotemporal (and other) properties of motion signals in the environment influences the strength of P- versus M-pathway input to cortical motion areas (effects of environment on development of *general* response properties of cortical motion detectors⁶²⁻⁶⁶). Interestingly, Nassi et al.³² recently reported that the P-pathway provides more input to motion area MT than originally reported,³¹ but perhaps the difference between the original and more recent studies can be explained by differences in the animals' environment (e.g., cage-reared versus wild-caught animals are likely to be exposed to different motion statistics during development). Such differences could lead to the development of more or less P-pathway input to motion area MT, which, in turn, would affect the degree of modularity between color and motion processing.

But what purpose could the synesthetic links between colors and shapes in early infancy serve? Unlike the example of M- and P-pathways competing to provide the most effective input cues for motion processing, forming arbitrary links between colors and shapes (infants)/graphemes (children and adults) does not appear beneficial in any obvious way. Perhaps such links should be considered part of the neural darwinian process, existing to allow plasticity in the face of potential *atypical* sensory experience. That is, maybe early exuberant connections between shape/grapheme and color areas of the brain allow one region (i.e., the “shape/grapheme area”) to serve a different function (i.e., color processing) in the event that form information inputting to the shape/grapheme area is deficient (e.g., in the case of blurred vision from congenital cataracts). In fact, this scenario is a popular one in the *cross-modal* domain. Specifically, animal studies have shown that early in development, there exist transient connections between neural areas representing different sensory modalities, such as vision and audition, which normally get retracted over the course of development.⁶⁷⁻⁷⁰ In the case of early sensory deprivation (congenital deafness or blindness), however, these transient connections are believed to be maintained as a way of allowing neural areas originally appropriated for the absent sensory modality (e.g., vision areas, in the case of blindness) to be usurped by another intact sensory modality (e.g., audition), a hypothesis that is supported by neural imaging data from blind and deaf humans.⁷¹⁻⁷⁹ In sum, the results from these studies of atypical development, together with those of typical development, suggest that the developing brain, while on a course towards increasing modularity, is able to re-chart in a manner that adapts to the environment.

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Figure 1.

Data Showing Age-Related Decrease in Chromatic Input to Motion Processing. **(A)** Mean Log₁₀ MOT/DET Threshold Ratios for Luminance Stimuli (*black bars*) and Chromatic Stimuli (*white bars*): Adults (*left*) vs. 3-Month-Old Infants (*right*). Error bars denote standard errors of the means. Adults were tested with standard 2-AFC psychophysical techniques. For adults, but not infants, there is a significant difference between MOT/DET ratios for luminance vs. chromatic stimuli. [Note that the log MOT/DET ratios are normalized so that the mean log MOT/DET ratio for luminance is 0 (i.e., linear mean = 1.0), the purpose of which is to facilitate comparison between the two age groups. This is justified because the MOT task in infants, which relies on detecting small eye movements, tends to be inherently more difficult than the DET task in infants, which is based on detecting relatively large head rotations/saccadic eye movements, and this difference likely biases the MOT/DET ratio. Thus, the most fundamental outcome measurement is the comparison of MOT/DET ratios *between* luminance and chromatic stimuli, and not the absolute value of MOT/DET ratios *per se*. The data in this figure are adapted from Dobkins and Teller, 1996. Non-normalized MOT/DET ratios as well as absolute threshold values can be found in this earlier manuscript]. **(B)** Infant Percent Correct Performance on a Luminance-Motion (*black circles*) and Chromatic-Motion (*white circles*) Task as a Function of Age. Error bars denote standard errors of the means. While there is a clear and significant increase in luminance-motion performance between 2 and 4 months of age, for chromatic-motion, there is no age-related improvement, or if anything, there is a slight (but non-significant) worsening of performance. These changes in motion performance with age cannot simply be accounted for by changes in contrast sensitivity with age (*see text*).

Figure 2. Stimuli Used to Test for Shape-Color Synesthesia in Infants. The number of trials for which an infant preferred the red versus the green half of the background was compared between the two different shape conditions, triangles (*left*) and circles (*right*). The red background was either on the left half of the display (*shown here*) or on the right side (*not shown*).