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How to use individual differences to isolate functional organization, biology, and utility of visual functions; with illustrative proposals for stereopsis

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Abstract

This paper is a call for greater use of individual differences in the basic science of visual perception. Individual differences yield insights into visual perception's functional organization, underlying biological/environmental mechanisms, and utility. I first explain the general approach advocated and where it comes from. Second, I describe five principles central to learning about the nature of visual perception through individual differences. Third, I elaborate on the use of individual differences to gain insights into the three areas mentioned above (function, biology/environment, utility), in each case describing the approach advocated, presenting model examples from the literature, and laying out illustrative research proposals for the case of stereopsis.

Keywords

psychophysics; visual perception; vision; twin; factor analysis; utility; latent variable

Introduction

This paper has two catalysts, one historical and one recent. The historical catalyst is the somewhat perplexing tendency in vision and other behavioral sciences to study natural and laboratory experiments separately. The advantage of combining such efforts is well-illustrated by the following quote from Cronbach's classic paper, and American Psychological Association Presidential Address, "The two disciplines of scientific psychology" (1957).

> The well-known virtue of the experimental method is that it brings situational variables under tight control. It thus permits rigorous tests of hypotheses and confident statements about causation. The correlational method, for its part, can study what man has not learned to control or can never hope to control. Nature has been experimenting since the beginning of time, with a boldness and complexity far beyond the resources of science. The correlator's mission is to observe and organize the data from Nature's experiments. As a minimum outcome, such correlations improve immediate decisions and guide experimentation. At the best, a Newton, a Lyell, or a Darwin can align the correlations into a substantial theory. …both applied work and general scientific work…requires combined, not parallel, labors from [these] two historic disciplines.

In other words, Nature's experiments provide a rich source of information that can and should be exploited in combination with data from laboratory experiments. Indeed, since our theories must ultimately explain manipulations originating both inside and outside the laboratory, the traditional tendency in basic vision science to ignore the latter is scientifically perilous. I describe three basic vision science questions for which Nature's experiments can yield particular insights: 1) What is the organization of a given visual function? 2) What biological

and environmental mechanisms underlie that function? and 3) What is the utility of that function?

By Nature's experiments, I mean the full range of natural variation in an ability as shaped by each individual's unique genes and environment: individual differences. Individual differences based methods have yielded substantial insight into the functional organization and genetic underpinnings of color vision (e.g. Webster & Macleod, 1988; Neitz & Jacobs, 1986); however, such methods have rarely been applied to other visual functions, particularly those that rely more heavily on processing beyond the retina like stereopsis, motion perception and object perception. The goal of this paper is thus to provide an open door for greater use of individual differences in basic vision science.

The proximal catalyst for this paper was the lively online discussion that inspired both the present "unresolved questions in stereopsis" special issue and a symposium on individual differences that I ran at the 2007 Vision Sciences Society meeting. The discussion - on the 2,000-subscriber vision science email list Cvnet - followed my posted question "What are the consequences of good and bad stereopsis?" The 155 postings and direct responses I received indicated great interest in individual differences in stereopsis but little systematic data on them, and great interest in the underlying question "What is the utility of stereopsis?" but surprisingly little documented success in answering it (cf. Greenwald et al., 2005). The present paper, especially the section on "utility," is largely a call to fill the gap highlighted by that discussion.

Two chief methodological traditions provide inspiration and a foundation for greater use of individual differences in basic vision science. One is cognitive neuroscience's twin subfields of neuroimaging and patient-based cognitive neuropsychology. Neuroimaging has begun using individual differences to illuminate brain function by identifying aspects of brain activity that predict individual differences in behavior; however, despite initial successes (e.g. Yovel & Kanwisher, 2005; Epstein et al, 2005; Vogel & Machizawa, 2004) and burgeoning use in other content areas (Thompson-Schill et al, 2005), this technique remains largely untapped for vision research. Cognitive neuropsychology has succeeded in dissociating several high level visual functions (Farah & Feinberg, 2006); however, patient based methods have limited power of association (Caramazza, 1986), whereas individual differences based methods can simultaneously associate and dissociate visual functions (e.g. Wilmer & Nakayama, 2007).

The other tradition is latent variable modeling, developed by Spearman and Thurstone - with inspiration from Galton - to study intelligence (Spearman, 1904; Thurstone 1944, 1947; Galton, 1883). Latent variable techniques - such as factor analysis, structural equation modeling, and path analysis - isolate psychological mechanisms by identifying a limited number of categories that summarize individual differences across an array of tests or measurements. These methods have succeeded in dissociating several perceptual continua into distinct underlying mechanisms (e.g. Peterzell & Teller, 2000; Macleod & Webster, 1988); their potential for informing other aspects of vision remains largely untapped. Latent variable models provide the statistical basis for behavioral genetic studies and can be used quite generally to represent any individual differences based design.

While individual differences are routinely measured in basic vision science to produce stimuli that have the same effect on different observers, thereby experimentally eliminating these differences, I focus on harvesting individual differences for the information they contain. While individual differences may also be studied for their own sake, or to define normal vs. abnormal vision, I focus on using individual differences for basic vision science: to define the number and nature visual mechanisms.

The next section of this paper describes five principles central to the study of visual perception through individual differences. The last then elaborates on the use of individual differences to

gain insights into three issues - function, biology/environment, utility - in each case describing the approach advocated, presenting model examples from the literature, and laying out illustrative research proposals for the case of stereopsis.

Principles and methods

Five principles are central to individual differences based inference in vision science:

1) Consider both natural and laboratory experiments.

Since manipulations imposed within and outside the laboratory are independent in origin, they provide independent sources of confirmation or falsification for a theory. Both types of information should be used whenever possible. Indeed, an effective research strategy is to conduct hybrid studies that observes the effects of both Nature's manipulations and laboratory imposed manipulations concurrently (Kosslyn et al., 2002; Peterzell et al, 1993; Cronbach, 1957; Spearman, 1904). A single dataset may thereby produce two independent tests of a research hypothesis, adding power to one's research.

Meeting two conditions facilitates drawing inferences based on individual differences. First, enough participants should be tested to robustly detect associations or demonstrate non-associations. Vision and imaging studies commonly have few participants; for perspective, to detect an r=0.5 correlation 80% of the time at a p=0.05 level, one-tailed, 23 participants are needed. Second, one's measures should be assumed unreliable and invalid until demonstrated otherwise. Importantly, reliability/validity *for detecting differences between experimental conditions* does not imply reliability/validity *for detecting differences between individuals*, and may in some cases even imply the opposite (Omura et al, 2005).

2) Contrast remote associations with proximal dissociations.

Whether due to general ability, motivation, alertness, visual acuity, or a host of other general factors, performance on most cognitive tests correlates to some degree (Spearman, 1904). Though this is less true of vision tests (Pickford 1951; Burt, 1949), a lack of correlation between two similar tests - a proximal dissociation - is still impressive. Conversely, a sizable correlation between two dissimilar tests - a remote association - is also impressive. In general, any association is defined by the dissociations that accompany it, and vice versa. The more remote the associations and proximal the dissociations, the sharper this definition.

It is useful (Thurstone, 1947) to distinguish *within-domain* studies that emphasize proximal dissociation (e.g. Peterzell & Teller, 1996) from *between-domain* studies that emphasize remote association (e.g. Wilmer & Nakayama, 2007; Peterzell & Teller, 2000). A within-domain study attempts to isolate distinct mechanisms underlying a psychological continuum. For example, how many distinct temporal mechanisms process objects, or contrast, or binocular disparity? I refer to these as studies of functional organization. A between-domain study attempts to identify mechanisms shared across different functions or levels of analysis - tying, for example, biological and environmental factors to perception or perception to performance. I refer to these as studies of biology/environment and utility.

Importantly, within-domain and between-domain studies are not mutually exclusive. Indeed, finding two distinct *associations* between domains implies a *dissociation* within each domain. For example, Wilmer and Nakayama (2007) found two independent associations between visual motion processing and smooth pursuit eye movements, not only tying perception to pursuit but also fractionating both perception and pursuit into component mechanisms. One can similarly fractionate perception by identifying (at least) distinct or (more powerful yet) independent associations with genes, neural responses, or environmental factors.

3) Identify and account for noise.

Because individual differences based inference requires contrasting association with dissociation (see principle #2), one must demonstrate that apparent dissociation is not due to measurement error. Such a demonstration is perhaps best accomplished via attenuation correction (Schmidt & Hunter, 1996; Spearman, 1904), a method that scales each correlation by the reliabilities of the two measures being correlated (dividing the correlation by the geometric mean of those two reliabilities). Since each measure's reliability (or correlation with itself) provides a ceiling for its correlation with other measures, this method controls for measurement error by expressing each correlation as a proportion of its maximum possible value. If a difference between two correlations does not withstand such scaling, then it can be explained purely by measurement error; if the difference remains, then measurement error cannot explain it. For most vision tests, reliability can be calculated simply as the mean Spearman-Brown corrected split-half correlation (Rosenthal & Rosnow, 1991).

4) Address questions of relation.

While laboratory-based manipulations are ideal for establishing causation, many of the important questions in vision are not questions of causation, but questions of relation. Examples of such relational questions are: whether or to what degree face and place perception, sustained and transient stereopsis, or action and perception are accomplished by overlapping or distinct mechanisms. Individual differences based methods are well-suited to answering such relational questions by harnessing the powerful, diverse manipulations that Nature imposes on such functions - indeed, an individual differences based correlation is essentially a tally of Nature's overlapping vs. distinct manipulations on a given aspect of vision. In addition, since relation is a precondition for causation, causal theories can be rendered plausible/implausible by a rigorous demonstration of individual differences based relation/non-relation (Underwood, 1975). Indeed, given limits on our ability to ethically manipulate human vision, individual differences based relation/non-relation may frequently be the best evidence we have regarding causation.

5) Assume similarity in form yet variation in efficiency

Individual differences based research extends the standard vision and cognitive science assumption that functions of interest exist in similar form across individuals (Caramazza, 1986), assuming in addition that these functions vary measurably in efficiency across individuals (Peterzell & Teller, 1996; Jones, 1957). In other words, this is the assumption of quantitative variation in a context of qualitative similarity. For functions where this assumption holds, individual differences based inference is possible; for functions where it does not hold, individual differences based analysis will yield inconsistent or null results.

Three areas amenable to individual differences based investigation

I elaborate below on the use of individual differences to address three questions about the nature of visual perception. Specifically, for a given aspect of perception: 1) What is its functional organization? 2) What biological and environmental mechanisms underlie it? and 3) What is its utility? In each case, I describe the approach advocated, present model examples from the literature, and lay out illustrative research proposals for the case of stereopsis.

Functional organization

The idea—A central goal in vision science is to determine the number and nature of mechanisms contributing to visual processing. More specifically, how many distinct mechanisms process a given continuum of stimuli, and what range of stimuli does each

mechanism process? The continuum of interest may be of any nature; fast to slow motion, green to red hue, face to non-face objects, high to low spatial frequency, and crossed to uncrossed stereopsis (aka stereopsis nearer than to farther than fixation), just to name a few. One attempts to "carve nature at its joints," determining which continua are processed by distinct or even independent mechanisms, and which by unitary mechanisms.

The answer to the question of distinctness is important for both basic and applied/clinical sciences. Should distinct mechanisms exist, the basic scientist may be well advised to study them separately, potentially learning more than she would by considering them as a unitary mechanism; similarly, the applied/clinical scientist may be confident that testing these mechanisms separately is a good use of precious time.

Individual differences are well-suited to probing for the presence of distinct mechanisms. Take the case of stereopsis for transient (brief duration) and sustained (long duration) stimuli. Previous evidence has raised the possibility that separate mechanisms process transient and sustained stimuli, but the evidence is not yet conclusive (see below). If separate mechanisms do exist, then Nature's manipulations may lead lead some individuals to have particularly sensitive transient mechanisms, and others particularly sensitive sustained mechanisms.

Thus if one tests a number of individuals with stereoscopic stimuli across several durations, one should observe clustering in the data whereby an individual with high sensitivity at a duration subserved by the transient mechanism will tend to show high sensitivity at other durations subserved by that same transient mechanism. Likewise, an individual with high sensitivity at a duration subserved by the *sustained* mechanism will tend to show high sensitivity at other durations subserved by that same *sustained* mechanism. Crucially, performance at two durations subserved by different mechanisms should predict each other to a lesser degree than performance at two durations subserved by the same mechanism.

The strength of evidence for distinct mechanisms can therefore be assessed simply by looking at a correlation matrix where performance at each duration is predicted by performance at each other duration. The diagonal of such a matrix will show correlations between adjacent durations. Dips in correlation along this diagonal will be evident at points where a transition between mechanisms occurs.

Various statistical techniques exist for systematically characterizing the evidence for such underlying mechanisms (Loehlin, 2004). A general term for such techniques is latent variable modeling, and the most popular of these is factor analysis. The need to determine the robustness and replicability of an observed result is common to all these techniques: resampling methods such as bootstrap may be used to attach confidence limits to an observed result (Morrone et al., 1999; Efron & Tibshirani, 1993), and monte carlo simulation may be used to determine the probability of obtaining the observed result from simulated data with or without an imposed structure (Peterzell et al, 1993).

Examples—The most extensive line of research of the type just described is that by David Peterzell and colleagues (Peterzell et al., 2000, 1995, 1993; Peterzell & Teller, 2000, 1996; Peterzell & Kelly, 1997). In a series of studies, Peterzell and colleagues map out the developmental trajectory and adult form of color and luminance contrast sensitivity. They do so by assessing the degree to which an individual's contrast sensitivity at one spatial frequency predicts their sensitivity at other spatial frequencies. They find selective dips in correlation for certain adjacent spatial frequencies (as mentioned above), which move along the spatial frequency continuum with increasing age, indicative of an increase in the number and range of contrast sensitivity mechanisms over the first years of life and through to adulthood. The

statistical technique used by Peterzell and colleagues to characterize their results is factor analysis.

Several other researchers have used latent variable modeling techniques to isolate contrast sensitivity mechanisms (Dobkins et al, 2000; Billock & Harding, 1996; Mayer et al., 1995; Sekuler et al, 1984). Such methods have also contributed to our knowledge of the functional organization of color vision (Bimler, Kirkland & Jameson, 2004; Gunther & Dobkins, 2003; MacLeod & Webster, 1988; Webster & MacLeod, 1988; Burt, 1949; Jones, 1948) and motion perception (Morrone et al, 1999). In addition, individual differences based studies have yielded insights into the functional organization of color vision (Malkoc et al., 2005; Webster et al., 2000a,b, 2002; Pickford, 1951), stereopsis (van Ee & Richards, 2002; van Ee, 2003; Scharff, 1997; Regan et al., 1986; Richards & Lieberman, 1985; Richards & Regan, 1973), and shape from shading (Adams, 2007) without explicitly using latent variable models. While the studies mentioned above test specific hypotheses of functional organization, an approach referred to as "confirmatory," individual differences based techniques are also valuable for so-called "exploratory" analysis when no such hypotheses exist (Thurstone, 1947, 1944).

Applications to stereopsis—The described approach - using individual differences to assess the presence of distinct mechanisms underlying a continuum - is limited only by the identification of continua of interest. For stereopsis, two continua of consistent interest have been between a) stimuli closer than or further than fixation ('crossed' and 'uncrossed' binocular disparity respectively) and b) short and long durations of inspection ('transient' and 'sustained' durations respectively).

Depth from crossed vs. uncrossed binocular disparity: Individual neurons may be sensitive either to crossed disparities, uncrossed disparities, or to disparities near fixation (Poggio, 1991). Thus, the raw materials certainly exist for separate perceptual mechanisms. However, these types "are abstractions in terms of standard prototypes," and "probably exist on a continuum" (Howard & Rogers, 2002). Thus the classification systems used to describe them may be more heuristic than inherent. Of course, it is also nontrivial to make strong predictions about perception from proposed physiological distinctions (DeAngelis, 2000). Evidence more direct for establishing distinctness of mechanisms at the level of perception comes from studies of individuals specifically lacking one of these mechanisms. Individuals have been identified who have selective deficits for perceiving depth from crossed, uncrossed, or zero disparity; such deficits are in fact common (30%) in the general population (Patterson & Fox, 1984; Jones, 1977; Richards, 1971, 1970) when tested with transiently presented stimuli. Such studies, in determining that a specific deficit can occur in either of two proposed mechanisms, establish that such mechanisms are at least marginally distinct (Caramazza, 1986). Yet these studies still do not determine the degree of distinctness. A final source of evidence comes from psychophysical case studies of normal adults and children. Such studies have suggested different temporal (e.g. Patterson, et al., 1995) and spatial (e.g. Manning, et al., 1987) limits, tolerances for polarity reversal (Pope, et al, 1999), and rates of development (Birch, Gwiazda, & Held, 1982), for various such mechanisms. However, such findings have also been interpreted as consistent with a model that does not posit distinct disparity pooling mechanisms (Landers & Cormack, 1997). Given the limitations for using each of these methods to assess the distinctness of perceptual mechanisms, an additional approach seems warranted. The individual differences based method described above provides a heretofore untapped approach that allows the distinctness of perceptual mechanisms to be assessed.

Depth from transient vs. sustained binocular disparity: This dichotomy was suggested by Ogle (1952). More recently, Clifton Schor and colleagues have conducted a systematic characterization of our sensitivity to depth from transient and sustained disparity (Schor et al., 2001, 1998, 1984; Edwards et al., 2000, 1999a b; Pope et al., 1999). These studies have shown

different 1) spatial tuning, 2) tendency to depth-alias, 3) orientation tuning, 4) sensitivity to spatial envelope size, and 5) tolerance for opposite polarity, for long vs. short duration depth stimuli. While these studies clearly show a coarser processing of short-duration stimuli than long-duration stimuli, this does not necessarily suggest the presence of distinct underlying mechanisms. It could be, as was suggested by Richards and Kaye (1974), that stimuli are processed by a single mechanism that simply gains in the quality of its representation over time. Further evidence consistent with the idea of distinct transient vs. sustained mechanisms comes from the studies of stereoanomaly cited above. The vast majority of such anomalies exist only for transiently presented stimuli. However, as yet no cases have been reported with the opposite deficit (sustained impaired, transient intact). Therefore, it could simply be that transiently presented depth stimuli are harder to process, and thus are a "higher bar" for a unitary mechanism to reach. In short, the question as to whether distinct mechanisms exist for processing transient vs. sustained stimuli is still very much an open one. The individual differences based approach described above can provide a novel source of information for helping to resolve this question.

Biological and environmental mechanisms

Recently, several studies have used individual differences to tie perception to neural and genetic/environmental factors (see below), and Kosslyn and colleagues have highlighted essential theory for such an enterprise (Kosslyn et al., 2002; Plomin & Kosslyn, 2001). The techniques I will describe focus on establishing associations between perception and underlying biological/environmental mechanisms; I refer to these above as "remote associations." If multiple distinct remote associations are found between biology/environment and perception, this is also evidence for dissociation within perception.

Neural factors

The idea—A neural circuit can be implicated in perception by finding that a focused measure of brain processing predicts an individual's perceptual performance relative to other individuals. Indeed, any experimental study that links perception to brain processing and has both enough participants and sufficiently reliable and valid measures can have its findings independently tested by such an individual differences based approach.

Examples—There has been a recent push in the neuroscience community to take individual differences into account when tying human behavior to brain function. A 2005 special issue of *Cognitive, Affective, & Behavioral Neuroscience* included examples of such efforts (Thompson-Schill et al., 2005); a symposium at the 2004 *Society for Neuroscience* meeting also focused on this approach. The following three examples illustrate the power of applying this method to vision.

Yovel and Kanwisher (2005) found two face-selective brain regions that showed a higher response to upright than inverted faces, indicating potential involvement in the behavioral "face inversion effect" (FIE - the disproportionate drop in recognition of upside-down relative to upright faces). These two regions were the fusiform face area (FFA) and the face-selective region of the superior temporal sulcus (f_STS). However, only for the FFA did an individual subject's drop in neural activation to inverted faces predict the size of their FIE. Together, these findings isolate the FFA as a likely neural source of the FIE and illustrate the benefits of a hybrid study design that considers the effects of both Nature's manipulations and laboratory imposed manipulations.

Vogel and Machizawa (2004) used a similar hybrid design for a study of event-related potentials (ERPs) and visual working memory. The authors reported a lateralized ERP measure that increased in amplitude with visual memory load, reaching an asymptote at the mean visual

memory capacity for the group of individuals tested. This finding alone provides reasonable evidence that the measure may reflect processes involved in visual working memory. However, additional evidence for this idea was provided from the same data by showing that an individual's measurement on the ERP index was highly predictive of their visual working memory capacity.

Finally, Epstein, Higgins and Thompson-Schill (2005) found that the extent of an individual's fMRI adaptation in putative scene processing areas to repeated viewpoint or place information predicted their self-reported navigational ability. This finding not only bolsters evidence, provided in the same study, that these brain areas are important for scene processing, but supports the further hypothesis that the scene processing associated with these areas is important for navigation.

Other studies have used similar individual differences based methods to investigate the brain bases of vernier acuity (Duncan & Boynton, 2003) and visual expertise (Gauthier et al. 2005). However, such methods remain underutilized for vision research.

Applications to stereopsis—As seen in the examples given above, the search for neural correlates of perception is aided by the identification of a neural index that mirrors a particular behavioral phenomenon such as the face inversion effect or visual working memory capacity. A similar behavioral phenomenon in stereopsis is the existence of both a minimum and a maximum binocular disparity for evoking a depth percept. Indeed, brain areas that show a reduction in activity with the breakdown of perception at these extremes have been identified (e.g., Backus et al, 2001). Since these disparity limits vary substantially between individuals, a similar individual differences based approach to that used in the cited examples could be applied to stereopsis. That is, the disparity value at which a given neural index shows a sharp change in activity for a given individual could be used to predict that same individual's disparity limit of stereopsis. A correlation across a number of observers would provide crucial additional evidence for a tie between that brain index and stereoscopic depth perception, whereas a lack of correlation would call such a tie into serious question.

Genetic/Environmental factors

The idea—Given the success that the neurosciences have had tying individual visual functions to specific neural areas, for example motion processing to the middle temporal area (MT) and face processing to the fusiform face area (FFA), can similar success be had in tying individual visual functions to specific genetic or environmental influences? The benefits of such an enterprise are twofold. First, we gain insight into genetic and developmental bases of perception. Second, we tap a new source of information about mechanisms shared and distinct between different aspects of perception, potentially improving our knowledge of the functional organization of perception. A consideration of individual differences is central to such research for two reasons. First, the environmental and (especially) genetic manipulations that can be imposed on humans in the laboratory are severely limited. Second and conversely, it is difficult to assess higher level perception in the animals whose genes and environments *can* easily be controlled and manipulated.

A classic twin study is an effective first step in the search for genetic and environmental influences on human perception (Plomin et al., 2008; Falconer & Mackay, 1996; Galton 1883). The heart of the classic twin study is to compare MZ (monozygotic/identical) to DZ (dizygotic/fraternal) twins on a measure of interest. MZ twins share on average twice as many genes (100%) as DZ twins (50%). Assuming that MZ and DZ twins share environments to roughly equal degrees, if MZ twins' scores predict each other more than DZ twins' scores, this is evidence for genetic influence. If certain assumptions hold - for example, absence of genetic dominance effects - some elegant inferences can be made from such data. First, the percent

variance in a measure due to genes can be estimated by doubling the difference between MZ and DZ correlations (2*(rMZ-rDZ)). The influence of environmental effects shared between twins can be estimated by subtracting half of the genetic effect from the DZ correlation (rDZ-(rMZ-rDZ)). Since measured differences between MZ twins can be due either to environmental effects not shared between twins or measurement error, the combined influence of these two sources of variance can be estimated by subtracting the MZ correlation from one (1-rMZ). If the reliability of a measure is known, this can be used to estimate the effect of measurement error alone, enabling the parsing of measurement error from effects of environment not shared between twins.

Once the relative influence of genetic and environmental factors as a whole have been estimated, further research can identify the specific factors involved. If environmental influence is high, one can use developmental methods to isolate important environmental factors. If genetic influence is high, one can study familial inheritance patterns, which, if simple, indicate a small number of influencing genes, and if complex, indicate a larger number of influencing genes. Given a sufficiently small number of major influencing genes, one can use genetic linkage studies to identify those genes. All of these methods - twin, developmental, family, and linkage studies - rely squarely on the assessment of individual differences.

The approaches just described for identifying genetic and environmental influences on visual perception are ‘top-down,’ in that they begin at the level of perception. One can also use a ‘bottom-up’ approach that begins with a specific ‘candidate gene’ or ‘candidate environmental factor’ and determines whether it has an effect on a given aspect of perception. In animal studies (mainly conducted on mice), candidate genes can be “knocked out” to determine if removing them affects function or “knocked in” to determine if adding them affects function. Indeed, a recent study created novel color discrimination capacity in mice by “knocking in” a human long-wavelength-sensitive (L) cone photopigment gene (Jacobs et al, 2007). In humans, determining the role of a candidate gene requires associating different gene variants with individual differences in the function of interest (Plomin et al., 2008). While virtually no candidate genes currently exist for higher level perception, given that a number of specific genes are known to affect neural and cognitive function (Zechner et al., 2001), and that the genetics of color vision has been fairly well mapped out (Nathans et al., 1986ab), such candidate genes may be within reach.

Examples—The genetics of color vision has been a topic of active and ongoing investigation (Nietz & Jacobs, 1986; Nathans et al, 1986a, b). Studies of natural and laboratory experiments in color vision have historically been undertaken in concert, leading to complementary insights about both the genes that encode color photopigments and the variations in them that lead to colorblindness and color anomalies (Jameson, Highnote & Wasserman, 2001; Pickford, 1951).

I am aware of only two top-down studies of genetic and environmental influences on perception outside the realm of color vision. One is a twin study by Drayna and colleagues (2001) that found that musical pitch recognition ability is “primarily due to highly heritable differences in auditory functions not tested by conventional audiologic methods.” The other is a small twin study showing evidence for a “fairly strong genetic component” to susceptibility to a well-known motion illusion (Fraser & Wilcox, 1979).

Enormous progress has been made in understanding the genetics of the eye itself and of ocular disorders, through both top-down and bottom-up approaches. Perhaps the most no success is the recent association of two specific genes with age-related macular degeneration (Chamberlain et al, 2006). Interest in the genetics of vision has burgeoned in recent years, even as frustration is being expressed with the difficulty of tying complex traits and diseases (e.g.

personality, schizophrenia) to individual genes (Zondervan & Cardon, 2004). It could be that the genetics of visual perception will provide an attractive, relatively tractable next step in attempts to tie behavior to underlying genetics. However, since efforts to tie genes to behavior are currently focused largely on major public health issues (Zondervan & Cardon, 2004), justifying such efforts will require evidence that discrete perceptual functions contribute importantly to quality of life (i.e. that they have utility in the broadest sense; see "utility" below).

Applications to stereopsis—Stereopsis exhibits anomalies that are as common, and nearly as distinct, as those seen in color vision (Hong & Regan, 1989; Kohly & Regan, 1999; Regan et al., 1986; Richards & Regan, 1973; Richards, 1970, 1971). In a small family study, Richards (1970) provided preliminary evidence that stereoanomalies for briefly presented stimuli appeared to follow an autosomal dominant inheritance pattern (a pattern of inheritance similar to that exhibited by brown eye color). Twin studies are needed to rigorously determine the relative contribution of genes and environment to stereopsis. Evidence for genetic influence would motivate genetic linkage studies to identify specific stereopsis-involved genes, whereas evidence for environmental influence would motivate developmental studies to identify specific stereopsis-involved environmental factors. Simply knowing the relative contribution of genes and environment to different aspects of stereopsis informs therapeutic interventions; isolating specific genetic/environmental mechanisms may guide such interventions still further.

Utility

The idea—A visual function is defined, in large part, by its utility. In other words, to fully understand an aspect of vision, one must understand what it is used for. In the case of stereopsis, while we know much about how it works, we still know little about its utility (Land, 2006; Howard & Rogers, 2002). Much of what we do know comes from cross-species comparisons. For example, it has been hypothesized that the tendency for predators to have highly developed stereoscopic vision results from stereopsis' utility in breaking prey camouflage (Julesz, 1971). If inter-species correlations teach us about a visual function's utility, then intra-species, individual differences based correlations should teach us even more, since insights derived most directly from humans apply most directly to humans. Specifically, two classes of utility-related questions can be tested using individual differences. While in practice both are often tested simultaneously, it is useful to distinguish them conceptually.

The first class of questions - which I will call "common influence" questions - ask to what degree common mechanisms influence (demonstrate utility for) different functions. This question is central, for example, to the issue of whether common signals are used for perception and action. Indeed, if an aspect of perception correlates across individuals with an aspect of motor control, these functions must share one or more common mechanisms, and the nature of these mechanisms can be isolated with appropriate comparisons and controls. While many dissociations between perception and action have been reported (Goodale & Westwood, 2004), there is to date surprisingly little evidence for shared mechanisms (Krauzlis, 2004), perhaps because the majority of perception and action studies have been designed to dissociate. A valuable opportunity thus exists to tie perception and action using individual differences based methods.

The second class of questions - which I will call "direct causation" questions - ask which abilities depend directly on a given function. For example, is stereomotion perception relied on for vergence, reaching, table tennis, slalom skiing? Since relation is a precondition for causation, causal theories can be rendered plausible/implausible by a rigorous demonstration of individual differences based relation/non-relation (Underwood, 1975). Indeed, given limits

on our ability to ethically manipulate human vision, individual differences based relation/non-relation may frequently be the best evidence we have regarding causation.

By establishing common influence and providing constraints on theories of direct causation, individual differences based methods help us understand the nature and utility of visual functions. In turn, such an understanding suggests their influence on our daily life and provides clues as to how they may have evolved.

Examples—We provide two representative examples of studies that answer questions of utility. The first ties perception to action, the second ties distinct perceptual mechanisms to each other.

Wilmer and Nakayama (2007) found evidence for independent influences of two distinct visual motion processing mechanisms on two different periods of smooth pursuit eye movements. Specifically, correlating moment-to-moment measurements of smooth pursuit over time with two psychophysical measures of speed estimation during fixation, they found two independent associations across individuals. Low level (motion energy based) speed estimation predicted pursuit acceleration before the initial catch-up saccade, and high level (position tracking) speed estimation predicted pursuit precision after the initial catch-up saccade. These results suggest that independent links exist between low level motion processing and presaccadic acceleration on the one hand, and between high level motion processing and postsaccadic precision on the other hand.

Hibbard and colleagues (2002) found that an individual's sensitivity to differences in stereoscopic slant about the vertical and horizontal axes were predicted respectively by their sensitivity to spatial frequency and orientation differences. These results "support the notion that surface inclination and slant perception are in part limited [respectively] by the sensitivity of orientation and spatial frequency mechanisms."

Applications to stereopsis—While the examples described above focus on establishing 'remote,' or 'between domains' associations, the multiple distinct associations found in these studies also provide evidence for 'within domain' dissociation.

Analogous work could search for ties between stereopsis (e.g. stereomotion thresholds, stereoacuity, depth estimation precision) and diverse measures of performance (e.g. vergence control, image segmentation ability, table tennis skill). Given how little is known about the utility of stereopsis, initial studies might be relatively broad-based and exploratory, with later follow-ups asking more focused questions.

Conclusions

Basic vision science has been slower to identify and make use of Nature's experiments than have other areas of psychology and neuroscience. In considering why this is so, observe the following quote from Susan Barry's contribution to the online discussion mentioned at the beginning of this article. Barry gained stereopsis by way of prism glasses and optometric vision therapy after several decades of being stereoblind.

> A person who has normal binocular vision cannot view the world as a stereoblind individual even when they close one eye. Their brain will use a lifetime of stereovision experiences to fill in the missing stereo information. In an analogous way, your brain fills in color in your peripheral visual field and fills in the gap in your vision produced by the blind spot even when you're looking with just one eye. So this brings up a paradox. A normal binocular viewer cannot imagine vision without stereopsis and a stereoblind viewer cannot imagine vision with stereopsis.

Perhaps we have downplayed and failed to make full scientific use of the myriad visual differences that exist between us partially because it is so difficult to imagine a visual world different from the one we personally perceive. Alternatively, perhaps the mantra "correlation is not causation" has inspired in us a blanket skepticism of (cor)relations, causing us to overlook the fact that many of the important questions in vision are not questions of causation, but questions of relation.

Whatever the origin of this missed opportunity, the information contained in perceptual differences persists as a substantial untapped resource for learning about vision. I have argued that three issues are particularly amenable to investigation through individual differences: functional organization, underlying biological and environmental mechanisms, and utility.

While this paper has focused on individual differences as a tool for basic vision science, such research directly enables the study of normal or clinical differences for their own sake by defining normal performance and validating measures for the detection of differences. An active science of individual differences in visual perception could thus play an integral role not only in illuminating basic visual mechanisms, but also in bridging basic and applied/clinical vision sciences.

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