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Perceptual Dependencies in Information Visualization Assessed by Complex Visual Search

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A common approach for visualizing data sets is to map them to images in which distinct data dimensions are mapped to distinct visual features, such as color, size and orientation. Here, we consider visualizations in which different data dimensions should receive equal weight and attention. Many of the end-user tasks performed on these images involve a form of visual search. Often, it is simply assumed that features can be judged independently of each other in such tasks. However, there is evidence for perceptual dependencies when simultaneously presenting multiple features. Such dependencies could potentially affect information visualizations that contain combinations of features for encoding information and, thereby, bias subjects into unequally weighting the relevance of different data dimensions. We experimentally assess (1) the presence of judgment dependencies in a visualization task (searching for a target node in a node-link diagram) and (2) how feature contrast relates to saliency. From a visualization point of view, our most relevant findings are that (a) to equalize saliency (and thus bottom-up weighting) of size and color, color contrasts have to become very low. Moreover, orientation is less suitable for representing information that consists of a large range of data values, because it does not show a clear relationship between contrast and saliency; (b) color and size are features that can be used independently to represent information, at least as far as the range of colors that were used in our study are concerned; (c) the concept of (static) feature saliency hierarchies is wrong; how salient a feature is compared to another is not fixed, but a function of feature contrasts; (d) final decisions appear to be as good an indicator of perceptual performance as indicators based on measures obtained from individual fixations. Eye tracking, therefore, does not necessarily present a benefit for user studies that aim at evaluating performance in search tasks.

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1. INTRODUCTION

Information visualization helps to locate and understand patterns and relationships in large data sets by transforming them into sensory images. While a given data set can be mapped to an image in nearly infinite ways, not every mapping will be equally effective. One of the goals of information visualization research is to reveal the principles that determine whether a particular mapping is effective. As these principles depend on how the human brain processes and interacts with visual information, it has been recognized that the study of perceptual aspects should play a prominent role in visualization practices [Ebert 2004; Interrante 2004; Johnson 2004; Tory and Müller 2004; House and Ware 2002; Ware 2000; Bertin 1983].

A general approach for visualizing data sets is to map distinct data dimensions to distinct visual object features (such as color, texture, size, shape, and orientation). In line with traditional theories of visual search (e.g., Treisman and Gelade [1980], Desimone and Duncan [1995]) it is then often assumed that such features are judged independently of each other, in the sense that appearance of the one does not depend on that of the other(s).

There is, however, experimental evidence challenging this view of independent feature processing. In particular, color appears to be a very dominant feature. In previous experiments, we found that judgment of orientation and size in a basic search task was contingent on whether one simultaneously searches for color, while judgment of color did not show the reverse dependency [Hannus et al. 2006] (some details about this experiment will be provided in Section 2.4). Nothdurft [2000] found that adding color to an oriented visual object increases its visual salience more than adding orientation to a colored object. It has also been found that search for color is faster than search for shape [Luria and Strauss 1975]. Furthermore, Callaghan [1989] reported that judgment of shape-defined boundaries is affected by hue variation, but that the reverse is not true. A similar effect was reported by Snowden [1998], who found that irrelevant variations in color, depth, and combinations of color and depth produce detrimental effects in performance on texture-segregation tasks. Williams and Reingold [2001] found that subjects are more likely to fixate nontarget distractors that have the same color as the target than distractors that have the same shape and/or orientation. In addition to these psychophysical findings, there is a substantial amount of physiological evidence that indicates that features are multiplexed (e.g., chromatically tuned orientation selective cells), at least at the early stages of processing by strictly separated brain regions/cells [Gegenfurtner 2003; von der Heydt et al. 2003; Roe and Ts'o 1999; Yoshioka and Dow 1996]. Even though it is not clear how this relates to the more feature-specific processing that is assumed to be present in later stages of visual perception [Livingstone and Hubel 1988; Zeki and Shipp 1988], it has been suggested that processing at these early stages may determine feature salience and, as such, search performance [Li 2002].

Such perceptual feature dependencies may have implications for information visualization design. For example, information that is visualized by orientation or size could become less salient (and, therefore, more difficult to judge) when color-coded information is added or when color contrast is being changed. Effects such as these will make it hard for the visualization designer to predict and control the salience of displayed information and should, therefore, be avoided as much as possible.

Because of differences in complexity and duration of tasks and stimuli, one should refrain from straightforward generalization of findings from basic psychophysical experiments to the domain of information visualization applications. Low-level effects found by psychophysical experiments might, for example, be negligible in the problem-solving strategies that are used in information visualization tasks. The above cited findings should, therefore, be reassessed in a visualization context.

Currently, the issue of feature interactions is not well understood [Ebert 2004] and remains unexplored by most visualization scientists. One exception to this concerns the work of Healey and colleagues,

who have conducted psychophysical experiments to test for possible perceptual interactions between the features they visualise their data with. For example, Healey and Enns [1998] used psychophysical methods to test for interference between the dimensions (texture height, density, and regularity) of the perceptual texture elements (“pexels”) that were used to visualize their data. They found that height, regularity, and density of background pexels interfered with short, dense, and sparse pexels. In a later study, it was assessed whether color could be added to pexels without interfering with one of the other pexel dimensions [Healey and Enns 1999]. It was found that variations of height and density had no effect on color segmentation, whereas random color patterns interfered with texture segmentation. Discriminability of features was not matched in these studies, however. As a result, it is possible that, for example, variations in height and density were of different (perceptual) magnitude than the variations in color. If this was, indeed, the case, then the interference effect might be explained by a design asymmetry and could possibly be removed by reducing color contrast (or increasing height and density contrasts).

Here, our primary question is whether previously found feature judgment interactions have potential relevance for information visualization. We experimentally assessed this using a relatively complex and visualization-realistic visual search task (many objects, a large range of feature values, and relatively long task duration). As color, size, and, to a lesser extent, orientation are frequently used features in information visualization and most evidence points toward color as a potential interfering feature, the experiments were carried out with combinations of color and size and combinations of color and orientation. Prior to the experiments, we matched discriminability of the features in order to avoid design asymmetries, as well as bias of the subjects’ attention toward a feature with higher salience than the others.

2. METHODS

2.1 Subjects

Six subjects participated in the color/size experiment (three females and three males, one of them author RB). Four of these subjects also participated in the color/orientation experiment. All participants had normal or corrected-to-normal visual acuity and normal color vision.

2.2 Apparatus

Stimuli in the form of node-link diagrams were presented on a 22-inch monitor at a resolution of 2048×1536 pixels and with a refresh rate of 75 Hz. For display of the diagrams, we made use of the force-directed graph layout algorithm of Cytoscape (<http://www.cytoscape.org>; [Shannon et al. 2003]). Stimulus presentation and data collection were done using Matlab in combination with the Psychophysics and Eye-link Toolbox extensions [Pelli 1997; Brainard 1997; Cornelissen et al. 2000]. Eye movements were recorded with an Eyelink II eye tracker (SR Research, Ltd., Mississauga, Ontario, Canada) with a temporal frequency of 250 Hz. Subjects viewed the stimuli at a distance of about 45 cm. A chin-rest assisted them in reducing head movements as much as possible.

2.3 Stimuli

2.3.1 Conjunction Search Stimuli. The stimuli consisted of a cue followed by a node-link diagram made up of 50 nodes and 70 (task-irrelevant) edges (Figure 1). Nodes were either discs with a particular color and size (color/size conditions) or bars with a particular color and orientation (color/orientation conditions). In each trial, one of the nodes was randomly chosen to be the target and was assigned a random color and size or orientation (for details about the colors, sizes and orientations used, see below). The other 49 nodes were distractors and were also assigned a random color and size or orientation, with the restriction not to be identical to the target (and thus a distractor could, for example, have a different

Fig. 1. Example stimuli.

Fig. 2. Cues in single feature search conditions. Cues in conjunction search conditions were identical to the target.

size, but the same color as the target). The cue was identical to the target and was shown in the center of an otherwise blank screen for 2 s. The target and distractors had a luminance of approximately 9.3 cd/m^2 and were viewed against a grey background (approximately 7.1 cd/m^2).

2.3.2 Single-Feature Search Stimuli. Stimuli for single-feature search conditions were exactly the same as the conjunction-search stimuli, except for the cues. In single-feature search conditions, the cues contained only information about the feature to be searched. Size information was removed by using cues as the one displayed in Figure 2a; color information was removed by using cues as those displayed in Figures 2b and 2c.

2.4 Definition and Matching of Contrasts

Color contrasts were created by increasing (decreasing) the output luminance of the red monitor channel and simultaneously decreasing (increasing) the output luminance of the green channel with respect to base color. This was done in such a way that luminance was held constant across search items. CIE coordinates of the default range (see below) ranged from ($x = 0.271$, $y = 0.311$; green) to ($x = 0.286$, $y = 0.305$; red). Size contrasts were created by increasing or decreasing the diameter of the nodes with respect to the base size (approximately 0.9° of visual angle). Orientation contrasts were created by tilting nodes in clockwise or counter clockwise direction with respect to the base orientation (45° with respect to horizontal direction). To avoid design asymmetries or subjects being biased toward one feature or another, because of large salience differences, we generated perceptually matched color, size, and orientation ranges prior to the experiments. For this, we first determined perceptually matched step sizes for the three features (we will refer to these as delta values Δc , Δs , and Δo , respectively). Using these deltas, for each condition, a range of ten different values was created for each feature (Figure 3).

Fig. 3. Default feature ranges used in the experiments. The perceptual distance (the deltas) between each two consecutive colors, sizes, and orientations was fixed. Also, the perceptual distance between two consecutive colors was matched with respect to the distance between two consecutive sizes and orientation (for an explanation of the low color contrast; see Section 4.1).

This ensured that the perceptual distance (and thus, discriminability) between two consecutive values was the same for all features. Matches were established based on data from previous experiments, [Hannus et al. 2006]. In those experiments, subjects performed a large amount of single feature search trials (for color, orientation, and size) with ten different target–distractor contrasts. From the resulting data, we computed for all three features the mean psychometric curve (sigmoid fits), describing the relationship between feature contrast and search performance.

We then defined color, size, and orientation deltas (Δc , Δs , and Δo) as the difference between the contrasts needed for a performance of 70 and 50%, respectively (note that because of the linearity of most of the psychometric curve, we could just as well have used other performance values, e.g., 30–50% or 40–60%). This approach is comparable to the use of just-noticeable differences (JNDs), but other methods for balancing feature saliency are conceivable as well (e.g., Nothdurft [2000]).

To demonstrate the matching method, we will show how it worked for size; color and orientation contrasts were generated analogously. The mean psychometric curve for size discrimination is shown in Figure 4. It appeared that a $\log_{10}$ difference of 1.24 (17.4%) between target and distractor diameter was needed to obtain a performance of 50% accuracy and a $\log_{10}$ difference of 1.38 (24.0%) was needed for a performance of 70%. The size delta was thus set to 6.6%. Color and orientation deltas were determined in a similar way ($\Delta c = 1.2\%$, $\Delta o = 7^\circ$).

In all experimental conditions, feature dimensions contained ten different values. In conditions where contrast was set to default, a range with ten values was created by modulating the feature’s base value with the delta value. This was computed in the case for size as follows: $size_i = base_size + (i - 5\frac{1}{2}) * \Delta s$, $i = 1, 2, \dots, 10$.

In this range of sizes, the distance between each two consecutive sizes is fixed and it is, therefore, expected that discriminability of sizes 1 and 2 is the same as that of sizes 2 and 3, etc. Moreover, because of the matching, discriminability of two consecutive sizes is expected to be the same as that of two consecutive (default) colors and orientations. As a result, equal search performance is expected in single feature search tasks when using the default ranges.

Fig. 4. Mean psychometric curve for size. Step size Δs was defined as the difference between the contrasts resulting in 70% and 50% performance accuracy.

One of the experimental questions was whether changing contrast in one feature dimension interferes with search performance in other feature dimensions. Therefore, in addition to conditions with default feature ranges, we included conditions in which contrast of one feature was reduced or enhanced while that of the other was kept at default. To achieve this, contrast modification factors C, S, and O were added to the feature range equations. For size we thus get: $size_{s,i} = base_size + (i - 5\frac{1}{2}) * S * \Delta s$, $i = 1, 2, \dots, 10$.

A contrast modification factor set to 1 resulted in stimuli with default contrast, while modification factors smaller than 1 reduced the contrast and modification factors larger than 1 enhanced it; 0 resulted in uniform ranges (base values). Since conditions only differed from each other with respect to search type (single feature, conjunction) and contrast modification factor, in the remainder of this paper we will refer to them by their contrast modifications (e.g., “conjunction search with $C = S = 1$ ” is conjunction search with matched contrasts and “size search with $S = 1$ and $C = 0$ ” is single feature search of size with no variation in the color dimension).

The range of sizes that we could use for the experiment was constrained by some practical aspects. Node sizes too large would result in excessive overlap of nodes, while node sizes too small would make it impossible to generate small gradual increments (node diameters could only be a discrete number of pixels). We chose a size range that avoided both problems and then matched the color and orientation ranges to this.

2.5 Procedure

Participants were instructed to search for the target node in the node-link diagram. They were informed about the identity of the target by means of a cue, as described in Section 2.3. They were asked to keep fixating at the selected node until the end of the trial in case they thought to have found the target. Eye movements were recorded during display of the node-link diagram, which were shown for 4.5 s. Search time was limited for two reasons: (1) to ensure that all subjects would opt for speed in the inevitable speed–accuracy trade-off that has to be made in search tasks like these and (2) to limit total experiment time. After each trial, feedback was given by highlighting the target node and the one selected by the subject (i.e., the one last fixated).

The task was performed under eight different conditions with color/size stimuli and under nine different conditions with color/orientation stimuli. As mentioned earlier, conditions only differed from each other with respect to search type (single feature, conjunction) and contrast modification factors C, S, and O. There were four color/size conjunction search conditions: one with matched contrasts ($C = S = 1$), one with reduced color contrast ($C = 0.5$), and two with enhanced size contrast ($S = 1.5$, $S = 2$). There were also four color/size single-feature search conditions: color search with ($S = 1$) and without ($S = 0$) task-irrelevant size contrast and size search with ($C = 1$) and without ($C = 0$) task-irrelevant color contrast. When there was no contrast in a feature dimension, a random value from the default feature range was chosen and assigned to all nodes.

The experiment contained five color/orientation conjunction search conditions: one with matched contrasts ($C = O = 1$), three with modified color contrast ($C = 0.5, 2, 4$), and one with doubled orientation contrast ($O = 2$). The four single-feature search conditions were analogous to those with color/size stimuli.

Some asymmetries can be observed across the conditions. The reasons are as follows. Earlier we observed that color tends to dominate in conjunction search when having matched salience for single-feature search. Our intention to assess whether this color dominance effect can be undone by either decreasing color contrast or increasing size contrast explains the asymmetry in the design of the first experiment. Orientation contrast is limited to a step size that does not result in a feature range exceeding 180° and could, therefore, not be increased much further (with $\Delta o = 7$, this range would already be exceeded when using $O = 3$). We used $C = 0.5, 1, 2, 4$ with the intention to get a more accurate picture of the relationship between (color) contrast and feature salience; $C = 4$ is the maximum, because higher contrasts would exceed the DAC range of our monitor.

Prior to the experiments, 60 random node-link diagrams were generated (as the one shown in Figure 1). Each of these networks appeared exactly once in each condition, in a fixed order. color/size and color/orientation conditions were measured in two separate sessions. Within these sessions, conditions were presented in separate, randomly ordered blocks of 60 trials. At the start of each block, a calibration procedure was performed.

2.6 Analysis

Relying on the assumption that a fixation was always made to inspect the node nearest to the point of fixation, we transformed the sequences of recorded fixations into sequences of node inspections by looking up for each fixation what node was closest to it. Based on these node-inspection sequences, we computed, for every inspection, the error for each of the relevant features. This error was defined as the difference between the feature value index of the target (a number between 1 and 10; see Section 2.4) and that of the inspected node. All statistical tests were carried out on these errors.

Since it is possible that different strategies are used in the search stage and the making of the final decision at the end of the trial, we distinguish between “search fixations” and “decision fixations” in the analysis. The final decision errors can be seen as a measure of eventual task performance and are, therefore, the most important ones from a visualization standpoint. The search stage errors can provide insight in the search strategies and possibly explain the final decision results. In case the previously found feature judgment interactions are merely low-level effects, we can expect to find them in the search stage, while they do not exist in the final decisions.

Analysis of final decisions includes only participants’ eventual choices at the end of the trials. As it often occurred that a subject was still in the process of searching at the end of a trial, we could not simply use all final fixations for this analysis. As a criterion to filter out trials in which subjects were still searching when the trial ended, we only included those in which the last fixation had a duration that was at least two standard deviations longer than the mean duration of all other fixations in that

Fig. 5. Time courses of errors in (a) color/size and (b) color/orientation search with matched contrasts. Trials were split into 15 intervals of 300 ms and mean error is shown for each interval. Note the high correlations between the signals (R^2 is 0.86 for color/size and 0.85 for color/orientation). Bars represent standard errors.

trial. The second type of analysis assesses the error during search. It is likely that not only the very last fixation of a trial was directly related to a subject's decision, but also a couple of fixations preceding the last one (correction saccades). Since such fixations are not directly related to the search process, we excluded them from the analysis. We chose to be conservative and omitted the last 25% of the fixations of every trial. Analyses of these data were done on the means of the signals.

All statistical analyses consisted of repeated-measures analysis of variances tests (ANOVA), with a significance level of 0.05. We tested whether (1) in single-feature search, variation in a task-irrelevant feature interferes with search performance, (2) in conjunction search, contrast of one feature affects search performance of the other, and (3) there was an interaction effect between search type (single feature, conjunction) and feature (color, orientation/size).

3. RESULTS

In the following section, we subsequently present results regarding the error signals, salience matching, the color/size experiment, and the color/orientation experiment.

3.1 Error Signals

As a first visual assessment of the data, we inspected the error signals before beginning the statistical analysis. Figure 5 shows the mean error signals in color/size conjunction search with $C = S = 1$ (left) and color/orientation search with $C = O = 1$ (right). The other conditions resulted in similar signals. Please note that these time courses are only meant as a first (informal) assessment of the data and that all statistical analyses below have been performed on mean errors, as described in the previous section.

A first observation is that color error is smaller than both the size and orientation error. This might make one wonder whether contrasts were matched correctly. However, these are error signals from conjunction-search conditions, while contrasts were matched for single-feature search. Therefore, the quality of matching will be assessed based on the single-feature search data (see next section). A second observation concerns the overall shape of the signals. We see a relatively large decrease in the first 500–1000 ms in all signals, followed by a slow decrease over the rest of the time course. Regarding the

Table I. Summary of the Statistics Regarding the Studied Effects in the Color/Size Data (p values)

	Conjunction Search				Single-Feature Search		Interaction Effect
	Effect of color contrast on		Effect of size contrast on		Effect of size contrast on color error	Effect of color contrast on size error	Search type $\times$ feature
	Color error	Size error	Color error	Size error			
Decision fixations	0.042	0.22	0.83	0.0013	0.18	0.37	0.33
Search fixations	0.003	0.48	0.57	$< < 0.01$	0.32	0.36	0.07

orientation error, we see that there is again a quick decrease at the end of the trials. A final observation is the high correlation between the error signals, suggesting that errors were minimized for both features in parallel.

3.2 Quality of Contrast Matches

To assess the quality of the contrast matches, we checked whether there were any significant differences between color and size and color and orientation errors in single-feature search conditions with irrelevant contrast in the second feature. The difference between color and size error in these conditions was not significant either for decision fixations [$F(1, 5) = 2.98$, $p = 0.14$], or search fixations [$F(1, 5) = 5.89$, $p = 0.060$], indicating that the task difficulty (and thus feature discriminability) was comparable for these features. The difference between color and orientation error during search was significant for search fixations [$F(1, 3) = 38.4$, $p = 0.009$] but not for decision fixations [$F(1, 3) = .606$, $p = 0.49$]. It thus appears that despite the matching procedure, orientation search was more difficult than color search.

3.3 Color/Size Data

This section gives a detailed description of the statistical analyses for all effects that have been studied in the color/size data. A summary (p values) can be found in Table I.

3.3.1 Decision Fixation Errors (Color/Size). Of all color/size trials, 68% met the criterion that the duration of the last fixation was at least two standard deviations longer than the mean fixation duration (see Section 2.6 for the rationale behind this criterion). Repeated-measures one-way analyses of variance (ANOVA) reveal that in conjunction search (Figure 6, top) there is a significant effect of color contrast on color error [$F(1, 5) = 7.37$, $p = 0.042$], but not on size error [$F(1, 5) = 1.94$, $p = 0.22$]. There is also a significant effect of size contrast on size error [$F(2, 10) = 13.81$, $p = 0.0013$], but not on color error [$F(2, 10) = .19$, $p = 0.83$]. This indicates that in conjunction search, color and size contrasts determine decision performance with respect to the feature itself but not to the other.

In single-feature search (Figure 6, bottom) there is no significant difference between error in color search with and without size contrast [$F(1, 5) = 2.39$, $p = 0.18$]. The same holds for size error in single-feature search with and without (task-irrelevant) color contrast [$F(1, 5) = 0.99$, $p = 0.37$]. Thus it seems that color search is not affected by task-irrelevant variation in the size dimension and vice versa.

No significant interaction effect between factors search type (conjunction, single feature) and feature (color, size) was found [$F(1, 5) = 1.18$, $p = 0.33$] (Figure 7). This was tested by using the data from the conjunction-search conditions with $C = S = 1$ (Figure 6, top), those of the color search condition with irrelevant size contrast ($C = S = 1$; Figure 6c), and those of the size-search condition with irrelevant color

Fig. 6. Mean errors for decision fixations in conjunction-search (top) and single-feature search (bottom) conditions, $N = 6$. Bars represent standard errors; x axis is in log scale.

contrast ($C = S = 1$; Figure 6d). This indicates that the difference between color error in single feature search and conjunction search is similar to that between size error in single-feature and conjunction search.

3.3.2 Error During Search (Color/Size). In conjunction search (Figure 8, top) there is a significant effect of color contrast on color error [$F(1, 5) = 30.0$, $p = 0.003$] but not on size error [$F(1, 5) = .57$, $p = .48$]. There is also a significant effect of size contrast on size error [$F(2, 10) = 29.3$, $p < 0.0001$], but not on color error [$F(2, 10) = .59$, $p = 0.57$]. In single-feature search (Figure 8, bottom) there is no significant difference between error in color search with and without (task-irrelevant) size contrast [$F(1, 5) = 1.20$, $p = 0.32$]. The same holds for size error in single-feature search with and without (task-irrelevant) color contrast [$F(1, 5) = 1.00$, $p = 0.36$]. No significant interaction effect between search type and feature was found [$F(1, 5) = 5.31$, $p = 0.070$] (Figure 9).

In summary, we see exactly the same pattern of results for search-fixation errors as we saw for the decision-fixation errors: (1) in conjunction search, feature performance is determined by its contrast,

Fig. 7. Mean error of decision fixations in single-feature and conjunction search, $N = 6$. All data shown is from search tasks with matched contrasts ($C = S = 1$). Bars represent standard error.

but not by the contrast of the other feature, (2) in single-feature search, task-irrelevant variation in the second-feature dimension does not affect performance, and (3) there is no interaction of factors search type and feature on performance.

3.4 Color/Orientation Data

This section gives a detailed description of the statistical analyses of all effects that have been studied in the color/orientation data. A summary (p values) can be found in Table II.

3.4.1 Decision-Fixation Errors (Color/Orientation). A total of 56% of the trials from the color/orientation experiment met the criterion that the duration of the last fixation was at least two standard deviations longer than the mean fixation duration.

In conjunction search (Figure 10, top), there is a significant effect of color contrast on color error [$F(3, 9) = 4.28, p = 0.039$], but not on orientation error [$F(3, 9) = 2.424, p = 0.13$]. Orientation contrast has no significant effect on orientation error [$F(1, 3) = 8.50, p = 0.062$] or color error [$F(1, 3) = 0.65, p = 0.48$]. Thus, it seems that color contrast determines color, but not orientation error, while orientation contrast affects neither of them.

In single-feature search (Figure 10, bottom), no significant difference between color error in single feature search with and without (task-irrelevant) orientation contrast was found [$F(1, 3) = 0.13, p = 0.74$]. The same is true for orientation error in single-feature search with and without (task-irrelevant) contrast in color [$F(1, 3) = 0.18, p = 0.70$]. We again see that variation in the task-irrelevant second-feature dimension does not affect single-feature search performance.

Again, no interaction effect between search type and feature was found [$F(1, 3) = 0.63, p = 0.49$] (Figure 11).

3.4.2 Error During Search (Color/Orientation). In conjunction search (Figure 12, top), there is a significant effect of color contrast on color error [$F(3, 9) = 32.4, p < 0.0001$] and also on orientation error [$F(3, 9) = 8.82, p = 0.005$]. There is also a significant effect of orientation contrast on color error

Fig. 8. Mean errors during search in conjunction (top) and single-feature search (bottom) conditions, $N = 6$. Bars represent standard errors; x axis is in log scale.

$[F(1, 3) = 16.2, p = 0.03]$ but not on orientation error $[F(1, 3) = 0.004, p = 0.95]$. It appears that color error depends on both color and orientation contrast, whereas orientation error depends on color contrast only.

In single-feature search (Figure 12, bottom), no significant difference between color error in single-feature search with and without (task-irrelevant) orientation contrast was found $[F(1, 3) = 0.036, p = 0.86]$. The difference between orientation error in single-feature search with and without (task-irrelevant) color contrast is also not significant $[F(1, 3) = 6.34, p = 0.09]$.

No interaction effect between search type and feature was found $[F(1, 3) = 0.76, p = 0.45]$ (Figure 13).

4. DISCUSSION

The primary goal of our experiments was to determine whether earlier reported feature judgment interactions have relevance for information visualization. We will first discuss color/size and color/orientation search interactions in the light of our results and then consider some secondary findings. Thereafter,

Fig. 9. Error of search stage fixations in single-feature and conjunction search, $N = 6$. All data shown is from search tasks with matched contrasts ($C = S = 1$). Bars represent standard error.

Table II. Summary of the Statistics Regarding the Studied Effects in the Color/Orientation Data (p values)

	Conjunction Search				Single-Feature Search		Interaction Effect
	Effect of color contrast on		Effect of ort contrast on		Effect of ort contrast on color error	Effect of color contrast on ort error	Search type x feature
	Color error	Ort error	Color error	Ort error			
Decision fixations	0.039	0.13	0.48	0.062	0.74	0.70	0.49
Search fixations	<<0.01	0.005	0.03	0.95	0.86	0.09	0.45

we will discuss some more general considerations. We will start with briefly discussing the saliency matching procedure.

4.1 Saliency Matching

As mentioned previously, in the present experiments, we consider visualizations in which different data dimensions should receive equal weight and attention. To avoid any strong *a priori* bottom-up attentional biases for one or the other feature in the displays in our experiments, we attempted to match feature saliency in our stimuli. We did so by choosing feature contrasts that resulted in equal performance improvement in simple visual search tasks.

A consequence of this requirement (and practical restrictions related to display size and resolution) is that color contrasts became relatively weak. (Another way to look at this is that color, when used at higher contrasts, is an extremely powerful attentional cue). Hence, a first message from this study is that when equal perceptual weighting of data dimensions coded using size and color features is

Fig. 10. Mean errors for decision fixations in conjunction-search (top) and single-feature search (bottom) conditions, $N = 4$. Bars represent standard errors.

required, very low color contrasts have to be used. In Section 4.4, we will further discuss the suitability of orientation for coding continuous data dimensions.

While the use of low color contrast is no issue in an experimental setting as used here, it may be in other situations. Moreover, we suggest to exercise caution when extrapolating our findings to displays that involve high-color contrast features (as are often used when display clarity rather than salience balancing is the first requirement).

4.2 Color/Size Interactions

We did not find any strong evidence for interactions in judgment of color and size. A first indication for the absence of such interactions is that in single-feature search it did not matter whether variation in the (task-irrelevant) second feature was present. Second, in conjunction search, manipulating color contrast did not affect size error or vice versa. Third, no significant interaction effects were observed between factors search type (single-feature, conjunction) and feature (color, size), meaning that the difference between color error in single-feature search and conjunction search is similar to that between

Fig. 11. Mean error of decision fixations in single-feature and conjunction search, $N = 4$. All data shown is from search tasks with matched contrasts ($C = O = 1$). Bars represent standard error.

size error in single feature and conjunction search. All of these findings speak against interaction and hold for the analysis of the search stage fixations as well as the final decision fixations.

We should note, however, that the interaction effect for search stage fixations was marginally significant ($p = 0.07$) and in the same direction (biased toward color), as we found earlier in a basic search task [Hannus et al. 2006]. This could indicate that some form of interaction does actually exist during search, in line with earlier reported studies. Nevertheless, it presumably is too small to consider when designing visualizations. If interference exists, it seems to be very weak and the analysis of decision fixations showed that it does not affect the eventual search decisions. The only situation we can think of in which it potentially plays a role is a color/size search task that requires very quick decisions.

The reader should also keep in mind that in the current study we used a limited range of (isoluminant) colors, for reasons explained earlier. Further research is needed to determine whether our finding of lack of cross-talk applies also for displays that use a larger range of saturations and which are not isoluminant (as in most actual information displays).

4.3 Color/Orientation Interactions

Using the same criteria as above, we found two indications for interactions in judgment of color/orientation combinations: in the search stage, color contrast affects orientation error and orientation contrast affects color error. This could be evidence for a symmetric interaction between color and orientation. However, we observed some irregularities in the color/orientation results that make us hesitate to draw any firm conclusions. We observed that increasing orientation contrast did not diminish orientation error. Also, considering that the expected value of the error was 3.3 for random fixations, we saw that orientation error during the search stage was exceptionally high (approximately 3, Figure 12). Apparently, saliency matching did not work properly for orientation. Further proof that orientation trials were more difficult than size trials is formed by the observations that only 56% of the color/orientation, but 68% of the color/size trials met our "final fixation criterion" (see Section 2.6) and that the average number of fixations was 13.2 in a color/size, but 14.4 in a color/orientation trial. We, therefore, will consider the orientation dimension in more detail below.

Fig. 12. Mean errors during search in conjunction-search (top) and single-feature search (bottom) conditions, $N = 6$. Bars represent standard errors.

4.4 Using Orientation in Visualization

Contrast matching was unsuccessful for orientation. A possible explanation can be found in Nothdurft [1993]. In this study it was shown that the amount of variance in the orientation of background elements strongly affects orientation salience: increased variance in background orientation results in decreased target salience. In our stimuli, the distractor nodes as well as the links can be seen as oriented background elements. Since the stimuli contained a large number of distractors with many different orientations, background orientation variance was very high in our experiments. Contrast matching, however, was based on a search task with very little variation in background orientation (all distractors had the same orientation and there were no links). This clearly illustrates that elementary psychophysical findings cannot always be directly translated to information visualization applications.

One might consider increasing orientation contrast to obtain better salience matches with color and size. However, orientation contrast was already close to maximum in our stimuli (covering 63 of 180 possible angular degrees in conditions with $O = 1$ and 126 in the condition with $O = 2$). It is,

Fig. 13. Mean error of search stage fixations in single-feature and conjunction-search, $N = 4$. All data shown is from search tasks with matched contrasts ($C = O = 1$). Bars represent standard error.

therefore, impossible to further increase salience by enhancing contrast. Besides, this might result in more background variation, decreasing performance even further. While lowering the number of different orientations in the stimuli is a viable option, in practice this would also translate into reducing the amount of information that can be visualized through orientation. We, therefore, conclude that orientation is a less suitable feature for visualizing data dimensions that cover a large variety of different values (an exception is formed by data that contain spatial dependencies, such as magnetic or flow fields; see Ware and Knight [1995] for an example).

Orientation appears to be more strongly affected by such background variation influences than are size and color. Nevertheless, the latter dimensions can also be affected by interactions with their background. Perceived size is affected by the size of background elements, as, for example, demonstrated by the Ebbinghaus illusion. Color induction may change the perceived color of surfaces (e.g., Brenner and Cornelissen [1991]). However, such effects are different from those observed with orientation, as increased background variation tends to reduce rather than enhance such spatial interactions (e.g., Brenner and Cornelissen [2002]). This again shows that it is difficult to generalize findings from one type of display to other types and, hence, that experimentation is an important tool for optimal display design.

4.5 Feature Hierarchy

Some authors have proposed the existence of a “feature hierarchy” [Healey 2001; Ebert 2004], referring to the observation that particular features are more salient than others (or, more precisely, that variations in particular feature dimensions are more salient than variations in others). The exact details of such a hierarchy remain unclear, however. Healey seems not to make a distinction between feature interference (or interaction) and feature hierarchy; Ebert says that some features are more “significant” perceptual cues than others. We propose to make a clear distinction between feature interference/interaction, on the one hand, and feature hierarchy, on the other. In our view, the former refers to appearance and judgment of one feature affecting that of another, whereas feature hierarchy signifies that variations in some feature dimensions are more salient and easier to discriminate than variations in other dimensions.

Whereas Ebert seems to regard this hierarchy as static, we favor a more flexible notion. We believe that the reason why features may seem to be organized in a static hierarchy sometimes is simply that feature contrasts are ignored in such assessments. We noticed that color contrast has to be kept very low in order to match its discriminability with that of a size contrast that is suitable for visualization purposes (the more we increase size contrast, the more display space is occupied and the less information can be presented). As typical visualizations use highly saturated colors, it is not surprising that it is always found to be the most salient feature.

The fact that our matching procedure was effective (at least for color and size) clearly demonstrates that the feature hierarchy is not at all static. Contrast of color and size were successfully matched, resulting in equal performance for single-feature search tasks. Our results also show that manipulation of contrasts makes it possible to match discriminability in conjunction search. This can be demonstrated by considering Figures 6b and 8b: color is more salient when $S < 1.5$; color and size are matched when $S = 1.5$; size is more salient when $S > 1.5$. Altogether, this shows that feature hierarchies are not fixed, but determined by feature contrasts. This means that the term “hierarchy” can even be misleading in this context, as it can easily suggest that there is a fixed ordering of feature discriminability.

4.6 Quantification and Balancing of Feature Contrasts in Visualization

The results of our experiments show that feature contrast and salience are closely related to each other. It appears that color contrast determines search performance on color but leaves size performance unaffected, and vice versa. For information visualization these are important properties, because they allow for independent control of discriminability and salience of information that is coded by color and size. Nonetheless, apart from some exceptions (e.g., Tufte [1986]), feature contrast appears often not to be considered an important issue in visualization design and most of the time designers seem to choose their contrasts by intuition. Discriminability in information dimensions of such visualizations is quite arbitrary and it is very likely that variations in some dimensions are (unpredictably) more salient than others. Nevertheless, it seems reasonable to assume that a visualization in which the discriminability and salience of represented information directly reflects its importance is more effective than a visualization in which there is no correspondence between these two quantities. Therefore, if we strive for visualizations with optimal effectiveness, it is necessary to quantify and carefully balance feature contrasts. Based on the above considerations we could say that existence of a clear relationship between feature contrast and salience serves as a criterion for a feature’s suitability for information visualization purposes.

For features that meet this criterion, control over salience of the information dimensions visualized by them can be obtained by first determining their contrast–salience relationships. Because of individual differences, the best results would be achieved if these relationships are separately determined for each person. A drawback of our matching procedure in this respect is that it is a very time-consuming process. It would, therefore, be interesting to investigate whether there are simpler and more efficient ways to measure and balance an individual’s sensitivity to contrasts in different features, comparable to how the classical flicker fusion test [Ives 1912] can be used to determine psychophysical isoluminance. Such a method could then be implemented in visualization applications and give users the opportunity to adapt such applications to their own perceptual systems. As long as such a method is not available, suboptimal results (but still better than nothing) can be expected using the average contrast sensitivities of a group of individuals.

Although outside the scope of the current experiment, another important aspect relating to quantification of visual features concerns the total number of just-noticeable differences, i.e., the number of discrete values that can accurately be coded by a feature. Some work has been done regarding this

matter (e.g., Weigle et al. [2000] studied “orientation categories”), but there are many unanswered questions and more research is needed on this point.

4.7 The Use of Psychophysics in Visualization

The need of perceptually motivated methods in visualization has been recognized by many of today’s visualization researchers. The simplest approach is to incorporate facts that are already known from perception research literature. Unfortunately, as results in perception research are generally obtained by methods that do not adequately reflect visualization practices, it is often doubtful whether they are also valid in visualization applications. Experiments and user studies are, therefore, needed to verify results from perception research in more visualization-realistic contexts (see also Kosara et al. [2003]). Since this is often a very time-and energy-consuming process, an important question is whether the benefits from such experiments outweigh the costs.

In the work presented here, eye movements were measured during several search tasks in order to find an answer to the question whether earlier reported feature judgment interactions have any significance for information visualization. Here a task was used that is more complex and better reflecting the kind of search tasks found in visualization applications than those on which the previously reported interactions were based. We believe that our results are general enough to be informative for information visualization and, thereby, justify the effort that was put into the experiments. We should note, however, that since in visualization the eventual accuracy and speed with which a task is solved is usually more important than how it is solved, from a purely practical point of view it might have been sufficient to only measure the final node selection decisions and, as such, avoid the need of measuring eye movements.

As a final note, our finding that data from a simple search task could not be used to predict orientation salience in more complex tasks illustrates the risk of straightforwardly generalizing research results from one domain to another and, thereby, shows the usefulness of conducting psychophysical methods in visualization research.

5. CONCLUSION

Visual search experiments were carried out in order to find out whether earlier reported feature judgment interactions are relevant to consider in information visualization. We specifically considered visualizations in which different data dimensions should receive equal weight and attention. Our experiments were performed with combinations of color and size and color and orientation. To avoid design asymmetries as well as subjects’ attention being biased toward a feature with a higher salience than the others, we matched color, orientation, and size discriminability prior to the experiments. Because of human’s outstanding color discrimination abilities, such matching inevitably requires to keep color-contrast low or to make contrast of other features impractically or even impossibly high. We chose to use low-color contrasts, accepting the risk that our results may not necessarily generalize to displays in which high color contrasts are used (but that may violate other assumptions and requirements in data visualizations as well).

The most important findings from this experiment are that color and size are features that can be used independently to represent information (at least as far as the range of colors that were used in our study are concerned) and that salience of features does not have a fixed hierarchical ordering, but depends on the choice of feature contrasts used in a visualization. In addition, orientation appeared to be less suitable for representing information that consists of a large range of values because it does not show a clear relationship between contrast and salience.

REFERENCES

- BERTIN, J. 1983. *Semiology of Graphics*. The University of Wisconsin Press, Madison, WI. [Translated by William J. Berg].
- BRAINARD, D. H. 1997. The psychophysics toolbox. *Spatial Vision* 10, 433–436.
- BRENNER, E. AND CORNELISSEN, F. W. 1991. Spatial interactions in colour vision depend on distances between boundaries. *Naturwissenschaften* 78, 70–73.
- BRENNER, E. AND CORNELISSEN, F. W. 2002. The influence of chromatic and achromatic variability on chromatic induction and perceived colour. *Perception* 31, 225–232.
- CALLAGHAN, T. C. 1989. Interference and dominance in texture segregation: Hue, geometric form, and line orientation. *Perception and Psychophysics* 46, 4, 299–311.
- CORNELISSEN, F. W., PETERS, E. M., AND PALMER, J. 2000. The eyelink toolbox: eye tracking with matlab and the psychophysics toolbox. *Behavior, Research Methods, Instruments & Computers* 34, 4 (Nov.), 613–617.
- DESIMONE, R. AND DUNCAN, J. 1995. Neural mechanisms of selective visual attention. *Annual Review of Neuroscience* 18, 193–222.
- EBERT, D. 2004. *Extending Visualization to Perceptualization: The Importance of Perception in Effective Communication of Information*. Elsevier Academic Press, Burlington, MA. 771–780.
- GEGENFURTNER, K. R. 2003. Cortical mechanisms of colour vision. *Nature Reviews* 4, 563–572.
- HANNUS, A., VAN DEN BERG, R., BEKKERING, H., ROERDINK, J. B. T. M., AND CORNELISSEN, F. W. 2006. Visual search near threshold: Some features are more equal than other features. *Journal of Vision* 6, 4, 523–540.
- HEALEY, C. G. 2001. Formalizing artistic techniques and scientific visualization for painted renditions of complex information spaces. In *Proceedings of the 17th International Joint Conference on Artificial Intelligence*, B. Nebel, Ed. Morgan Kaufmann, San Francisco, CA. 371–376.
- HEALEY, C. G. AND ENNS, J. T. 1998. Building perceptual textures to visualize multidimensional datasets. In *Proceedings of IEEE Visualization*, D. Ebert, H. Hagen, and H. Rushmeier, Eds. IEEE Computer Society. The Institute of Electronics Engineers Inc. ACM Press, New York. 111–118.
- HEALEY, C. G. AND ENNS, J. T. 1999. Large datasets at a glance: Combining textures and colors in scientific visualization. *IEEE Transactions on Visualization and Computer Graphics* 5, 2 (Apr.–Jun.), 145–167.
- HOUSE, D. AND WARE, C. 2002. A method for perceptual optimization of complex visualizations. In *Proceedings of Advanced Visual Interface*, S. Levialdi and E. Pannizzi, Eds. ACM Press, New York. 148–155.
- INTERRANTE, V. 2004. *Art and Science in Visualization*. Elsevier Academic Press, Burlington, MA.
- IVES, H. E. 1912. Studies of the photometry of different colours: I. spectral luminosity curves obtained by equality of brightness photometer and flicker photometer under similar conditions. *Philosophical Magazine* 24, 149–188.
- JOHNSON, C. 2004. Top scientific visualization research problems. *IEEE Computer Graphics and Visualization: Visualization Viewpoints* 24, 4, 13–17.
- KOSARA, R., HEALEY, C. G., INTERRANTE, V., LAIDLAW, D. H., AND WARE, C. 2003. Thoughts on user studies: why, how, and when. *IEEE Computer Graphics & Applications* 23, 4, 20–24.
- LI, Z. 2002. A saliency map in the primary visual cortex. *Trends in Cognitive Sciences* 6, 1 (Jan.), 9–16.
- LIVINGSTONE, M. S. AND HUBEL, D. H. 1988. Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science* 240, 740–749.
- LURIA, S. M. AND STRAUSS, M. S. 1975. Eye movements during search for coded and uncoded targets. *Perception and Psychophysics* 17, 303–308.
- NOTHDURFT, H. C. 1993. The conspicuousness of orientation and motion contrast. *Spatial Vision* 7, 341–363.
- NOTHDURFT, H. C. 2000. Saliency from feature contrast: additivity across dimensions. *Vision Research* 40, 1183–1201.
- PELLI, D. G. 1997. The VideoToolbox software for visual psychophysics. *Spatial Vision* 10, 437–442.
- ROE, A. W. AND TS’O, D. Y. 1999. Specificity of color connectivity between primate V1 and V2. *Journal of Neurophysiology* 82, 5, 2719–2730.
- SHANNON, P., MARKIEL, A., OZIER, O., BALIGA, N. S., WANG, J. T., RAMAGE, D., AMIN, N., SCHWIKOWSKI, B., AND IDEKER, T. 2003. Cytoscape: A software environment for integrated models of biomolecular interaction networks. *Genome Research* 13, 2498–2504.
- SNOWDEN, R. J. 1998. Texture segregation and visual search: A comparison of the effects of random variations along irrelevant dimensions. *Journal of Experimental Psychology: Human Perception and Performance* 24, 5, 1354–1367.
- TORY, M. AND MÜLLER, T. 2004. Human factors in visualization research. *IEEE Transactions on Visualization and Computer Graphics* 10, 1, 72–84.
- TREISMAN, A. M. AND GELADE, G. 1980. A feature-integration theory of attention. *Cognitive Psychology* 12, 1 (Jan.), 97–136.

- TUFTE, E. R. 1986. *The Visual Display of Quantitative Information*. Graphics Press, Cheshire, CT.
- VON DER HEYDT, R., FRIEDMAN, H. S., AND ZHOU, H. 2003. *Searching for the Neural Mechanism for Color Filling-In*. Oxford University Press, London, 106–127.
- WARE, C. 2000. *Information Visualization: Perception for Design*. Morgan Kaufmann, San Francisco, CA.
- WARE, C. AND KNIGHT, W. 1995. Using visual texture for information display. *ACM Transactions on Graphics* 14, 1, 3–20.
- WEIGLE, C., EMIGH, W. G., LIU, G., TAYLOR, R. M., ENNS, J. T., AND HEALEY, C. G. 2000. Oriented sliver textures: A technique for local value estimation of multiple scalar fields. In *Graphics Interface*. 163–170.
- WILLIAMS, D. AND REINGOLD, E. 2001. Preattentive guidance of eye movements during triple conjunction search tasks: The effects of feature discriminability and saccadic amplitude. *Psychonomic Bulletin & Review* 8, 476–488.
- YOSHIOKA, T. AND DOW, B. M. 1996. Color, orientation and cytochrome oxidase reactivity in areas V1, V2 and V4 of macaque monkey visual cortex. *Behavioural Brain Research* 76, 1–2, 71–88.
- ZEKI, S. AND SHIPP, S. 1988. The functional logic of cortical connections. *Nature*, London 335, 6188, 311–317.

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