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Salience from feature contrast: additivity across dimensions

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Abstract

Test targets ('singletons') that displayed orientation, motion, luminance, or color contrast, or pairwise combinations of these, were presented in line texture arrays, and their saliences were quantified in comparison to reference targets at defined luminance levels. In general, saliency effects in different stimulus dimensions did add, but did not add linearly. That is, targets with feature contrast in two dimensions were generally more salient than targets with only one of these properties, but often less salient than predicted from the sum of the individual saliency components. Salience variations within a dimension were compared with and without a second saliency effect added. The resulting gain reduction in the combined stimulus conditions was interpreted to reflect the amount of overlap between the respective saliency mechanisms. Combinations of orientation and color contrast produced the strongest gain reduction (about 90% for color in orientation) thus indicating the strongest overlap of underlying saliency mechanisms. Combinations of orientation and motion contrast revealed about 50% overlap, slightly smaller rates were found for combinations of color and motion. All combinations with luminance contrast (orientation and luminance, motion and luminance) produced only little gain reduction ($< 30\%$) thus indicating a higher degree of independence between the underlying saliency mechanisms than for other stimulus dimensions.

Keywords: Popout; Conspicuousness; Contextual modulation; Orientation contrast; Motion contrast; Luminance contrast; Color contrast; Summation; Psychophysics

1. Introduction

1.1. Background: salience and search

Searching for an object can be an easy or a difficult task. Some objects pop out and are immediately detected, others are less conspicuous and search may take considerable time. The basis of this difference is not yet completely understood. Several studies seemed to suggest that the conspicuousness, or salience, of an object is related to the presence of certain features (like vertical edges, green or red color, closure, or gaps); if such features occur only with targets, these are quickly found (Treisman & Gormican, 1988; Foster & Ward, 1991; Wolfe, Friedman-Hill, Stewart & O'Connell, 1992). Other experiments have shown that salience, and hence the speed of search are strongly influenced by visual context; the same target may be salient or not, dependent on how it is embedded in the scene (Moraglia, 1989; Nothdurft, 1992).

Given the crucial role of saliency effects not only for the detection of targets but also for the control of eye movements (Deubel, Findlay, Jacobs & Brogan, 1988; Deubel & Frank, 1991; Nothdurft & Parlitz, 1993) and focal attention (Julesz & Bergen, 1983; Julesz, 1984; Wolfe, Cave & Franzel, 1989; Joseph & Optican, 1996; Nothdurft, 1999), the underlying mechanisms have received considerable interest in vision research (cf. Engel, 1971, 1977). Studying popout and saliency effects in regular line patterns we noticed that the salience of a particular line element is related to the local differences in certain stimulus dimensions (Nothdurft, 1991, 1992, 1993b; see also Beck, 1982). For example, a vertical line among horizontal lines is salient and easily found, while a vertical line between nearly vertical lines is not particularly salient and may require scrutinized search in order to be detected. Thus, in these patterns salience is not related to the vertical orientation of the target per se, but to the orientation difference between the target

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and surrounding lines. We proposed the concept of orientation contrast to describe this phenomenon (Nothdurft, 1991, 1992). The larger the orientation difference between the target and its surround, the more salient it is. The relationship between salience and local orientation contrast is nonlinear (Nothdurft, 1993c).

Not only local, but also the global properties of a scene affect the salience of an object. A line with high orientation contrast on a homogeneous background is salient and easily found, the same line on a non-uniform background is not (cf. Nothdurft, 1991, 1992). Thus, the overall orientation contrast in the pattern reduces the relative salience of the target; to make it pop out orientation contrast must be locally increased.

Salience is not only generated from orientation contrast but also from differences in other stimulus dimensions like motion, color, luminance, or depth (Nakayama & Silverman, 1986; Dick, Ullman, & Sagi, 1987; Nagy & Sanchez, 1990; D'Zmura, 1991; Nothdurft, 1993b, 1995). A target that moves in a direction different from that of its neighbors is salient, as is a line that is brighter than surrounding lines or has a different color. All these saliency effects seem to display qualitatively similar properties. They increase with the local feature contrast of the target to neighboring objects, and decrease with the overall feature contrast elsewhere in the pattern (Nothdurft, 1993b,c, 1994, 1995). Thus, an object that moves in a direction different to that of its neighbors would be salient, unless the neighbors themselves moved in directions different to those of their neighbors.

The notion that search time is related to the relative salience of the target, rather than to the occurrence of specific features, was supported by the following experiment (Nothdurft, 1993a). Targets (vertical lines) that were detected fast when presented at high orientation contrast (90°) were detected more slowly, with increasing reaction time for an increasing number of items, when local orientation contrast was reduced to that of the other items in the pattern (10°). Only the context, not the target itself was changed for this new condition. If the salience of the target was then increased by feature contrast in another dimension, e.g. by increasing local motion or color contrast, it was again detected fast. This manipulation did not change the stimulus properties in the search-relevant dimension (subjects continued to search for a vertical line, irrespective of its color or movement). But in terms of salience, given by the increased feature contrast in another dimension, the target was now more attractive than before and was immediately found, independently of set size.

This experiment illustrates that salience is a property on its own and not necessarily associated with certain features. Salience per se is not feature specific. A red line among green lines can be as salient as a vertical line among horizontal ones or a line moving to the left among lines moving to the right. This allows comparison of different saliency effects and their quantification with respect to each other (Nothdurft 1993c; Nothdurft & Parlitz, 1993). I have made use of this in this present study to measure the saliences of different targets. With respect to functional aspects, this non-specificity of saliency effects seems reasonable: If the visual system could distinguish between different saliency effects, one of the presumed functions of salience — to attract gaze and attention for the investigation of an object — would become superfluous. However, if many salient objects must be distinguished, saliency effects from different dimensions can apparently be sorted out fast (Nothdurft, 1997; cf. Pashler, 1988).

1.1.1. Neural correlates of salience

It is not yet certain which neural mechanisms produce the percept of salience. The strong influence of the surround on a target's salience suggests that contextual modulation effects may be particularly important. Such effects were demonstrated in a series of studies on single cells in area V1 (e.g. Allman, Miezin & McGuinness, 1985, 1990; Knierim & Van Essen, 1992; Lamme, 1995; Sillito, Grieve, Jones, Cudeiro & Davis, 1995; Zipser, Lamme, & Schiller, 1996; Kastner, Nothdurft & Pigarev, 1997, 1999; Lee, Mumford, Romero & Lamme, 1998; Nothdurft, Gallant & Van Essen, 1999). While the responses to a stimulus in the receptive field (RF) are frequently suppressed when similar stimuli are simultaneously presented in the unresponsive regions outside the RF, the suppression is often weaker or even absent when the surrounding stimuli are different to that in the RF. Thus, in the mean response of the cell population, responses to contrasting stimuli are relatively enhanced over those to uniform texture fields. These response differences correlate well with the salience of popout targets, i.e. of targets with increased orientation or motion contrast (cf. Nothdurft, 1991, 1994; Knierim & Van Essen, 1992; Kastner et al., 1997, 1999; Nothdurft et al., 1999).

Contextual modulation in area V1 shows a variety of properties that have not yet been studied psychophysically; their investigation was the major aim of the present work. Saliency effects were measured in psychophysical experiments and the results were compared with the properties of contextual response modulation in single cells. Three different aspects were studied: (i) the additivity of saliency effects in different dimensions, (ii) the time course and temporal properties of salience, and (iii) the spatial structure and the contextual properties of saliency effects. The present paper addresses the first issue and presents data from experiments which compared the salience of targets ('singletons') that were defined by feature contrast in single dimensions or pairwise combinations of these. The two other aspects will be addressed in forthcoming papers.

1.2. Additivity of saliency effects

Targets can be salient from orientation or motion contrast, from differences in relative disparity, and from luminance or color contrast. Are these different saliency effects based on the same neural mechanisms or are they encoded independently of each other in the brain? One way to study the interference of neural mechanisms is to study the additivity of the effects they produce. Do saliency effects from different stimulus dimensions add (cf. Fig. 1), and if so, is the addition linear?

Before attempting to answer these questions, we might propose some expectations. Many cells in V1 are tuned for several stimulus properties, e.g. for both the orientation and the movement direction of a line. If all cells that encode the orientation of a target were already maximally activated by the target's orientation contrast, one should expect no or only little increase in the responses when the target also displays motion contrast. In this case, when different feature properties are multiplexed in the neural response, one might expect that saliency effects do not add linearly. Other feature properties are represented in a more exclusive way. For example, color sensitive cells in area V1 do not seem to encode the direction of motion; vice versa, motion sensitive cells are usually poor in distinguishing color (Livingstone & Hubel, 1988; cf. DeYoe & Van Essen, 1988). For combinations of these properties, which seem to be represented in different sets of neurons, one might expect linear summation of saliency effects.

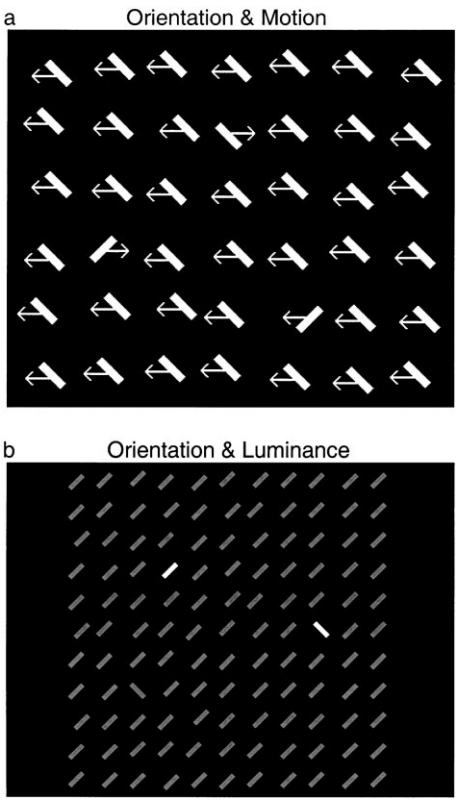

Fig. 1. Topics of this paper: Do saliency effects from different dimensions add? (a) Are targets defined by orientation and motion contrast more salient than targets defined by either contrast alone? (b) How independent are saliency effects that might be encoded in different processing stages of the visual system, for example, luminance and orientation? Is a bright orthogonal line more salient than a bright parallel line or an orthogonal line that has the same luminance as the background lines? (Yes, it is. If you are not convinced, move your eyes away from the targets and find out at which eccentricities they lose their salience.) The study reports three series of experiments. Experiments in series A measured salience of orientation and/or motion contrast, experiments in series B that of orientation or motion and/or luminance contrast. Experiments in series C measured combinations of color and orientation or motion.

Unfortunately, physiology itself does not fully support this model. Not all orientation-tuned cells in area V1 are modulated by orientation contrast; on the other hand, orientation non-selective cells can be notably modulated (Knierim & Van Essen, 1992; Kastner et al., 1999; Nothdurft et al., 1999). But if the tuning properties of a cell do not predict its sensitivity in contextual modulation, then additivity effects or the failure of linear additivity are not necessarily related to the multiple encoding of stimulus properties in single cells. Instead, we would need to know which cells are modulated by feature contrast in different dimensions. In measurements of the sensitivity of single cells for orientation and motion contrast in cats (Kastner et al., 1999) we found 22% of the neurons showing increased responses to orientation contrast, and 36% showing increased responses to motion contrast. But only 11% of the cells preferred feature contrast in both dimensions, that is half of the cells that responded to orientation contrast. Only these cells may fail to show additivity when orientation contrast and motion contrast are combined. Based on these data, we would predict that saliences from motion and orientation contrast should add, but probably not linearly because some cells are activated in each single contrast case. Contrary to these expectations are observations by Zipser et al. (1996) who did not find increased responses in the population of 64 cells in the monkey when different segmentation keys (orientation differences, color differences, etc.) were combined. Other studies (Schmitt and Bach, 1997) did observe additivity effects between different segmentation keys in human evoked potentials.

Since psychophysics deals with the complete visual system, it is not obvious that we will be able to identify the level at which saliency mechanisms interact. For example, saliency effects from orientation contrast and saliency effects from motion contrast could be encoded independently of each other and interfere at another place where saliency effects are integrated. If the salience transfer function would show saturation, com-

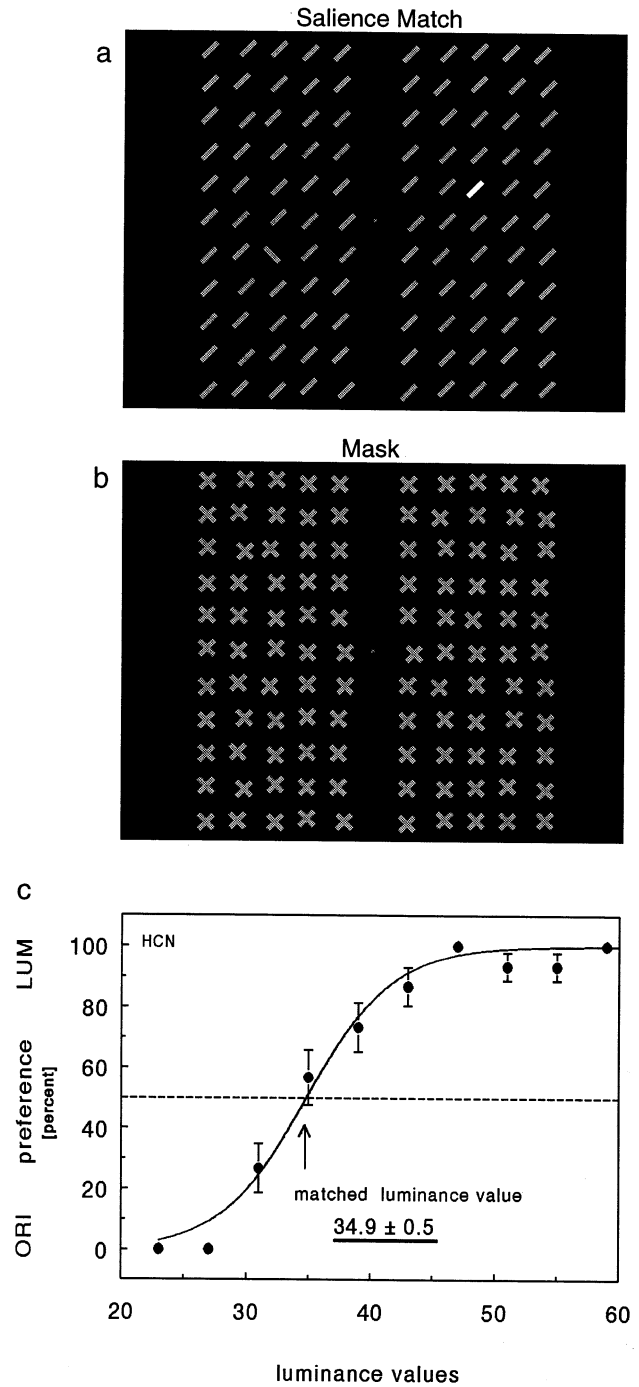

Fig. 2. The salience matching task. (a) Example of a stimulus pattern, (b) Mask. (c) Data and analysis. Subjects saw texture patterns with two salient lines (a), one on each side of the fixation spot, and were asked to indicate which target was more salient. Test targets, randomly assigned to one side of the screen, were lines orthogonal to the surround (as shown here) or moving in a different direction, brighter lines or lines of a different color. Reference targets, presented on the other side of the screen, were lines brighter than background elements but otherwise identical to them. Eleven different reference target luminances were used to estimate the relative salience of the test target. Data were summed over 25–50 presentations of each individual target pair (c). Finally, sigmoidal curves were fitted to the data to estimate the 50% value which then was taken as the salience-matched luminance value of the test target (arrow).

binations of saliency effects might seem to interfere even if their first-order neural mechanisms do not. We will discuss this possibility below. However, the data did not suggest such a common saturation effect in the investigated range; thus data presentation in the paper is made along the above model of direct interaction of saliency effects — without specifying the exact underlying mechanisms.

Of particular interest is the distinction of saliency effects that are possibly generated in different processing stages of the visual system. While orientation and motion contrast are clearly encoded in area V1 (Allman et al., 1990; Bach & Meigen, 1992; Knierim & Van Essen, 1992; Lamme, van Dijk, & Spekreijse, 1992; Lamme, van Dijk & Spekreijse, 1993a,b; Lamme, 1995; Sillito et al., 1995; Zipser et al., 1996; Kastner et al., 1997, 1999; Lee et al., 1998; Nothdurft et al., 1999) luminance contrast, and to some extent perhaps color contrast too, already activate cells in the retina and the lateral geniculate nucleus.

Three series of experiments were performed in this study. In series A, test targets were defined by orientation contrast, motion contrast, or a combination of both (cf. Fig. 1a). In series B, test targets were defined by orientation or motion contrast presented alone or in combination with luminance contrast (cf. Fig. 1b). In series C, orientation or motion contrast was combined with color contrast. In each of these series, saliences were measured for targets defined by feature contrast in the single dimensions and for targets with combined contrast effects.

2. Methods

2.1. Overview

The experiments were designed as matching experiments in which the salience of a test target presented in one half of the visual field was compared with the salience of a reference target presented in the other half (Nothdurft, 1993c).

Stimuli were line arrays (Fig. 2a) with two salient elements which both were made to pop out from the surrounding 'background' elements. Test targets were the elements whose saliences were to be measured; they were orthogonal lines, lines that moved in a direction opposite to that of background lines, lines that were brighter than the surrounding lines, or lines that had a different color. Reference targets had the same form and orientation as the surrounding background lines and, in motion tests, moved in the same direction, but were brighter than these. Reference lines and surrounding background lines were always white. In the course of an experiment, a given test line condition was combined with reference targets at different luminance lev-

els and subjects were asked to indicate which of the two targets was more salient. Repeated presentations, in which test lines and reference lines were randomly exchanged, gave ratings of relative salience (Fig. 2c). The exact luminance value at which the reference target matched a given test target in salience was obtained from nonlinear fits of sigmoidal curves to these data points (arrow).

2.2. Stimuli and stimulus presentation

Texture patterns (cf. Fig. 2a) were made of oblique lines ($\pm 45°$); all lines of a pattern had the same orientation except orientation-defined test targets which were always orthogonal. Between the two possible values, line orientation was randomly selected from trial to trial. Stimuli displayed two texture fields made from a 9×9 rectangular line raster with a grid spacing of 1.9 deg; line size was 1×0.25 deg. The middle column of the texture field was left blank to avoid interference with the fixation point. Test and reference targets were randomly presented in these texture fields, one on each side, at eccentricities of 3.8–5.7 deg.

Texture patterns were masked (Fig. 2b), that is lines were replaced by crosses made of two orthogonal lines at the positions of the previously displayed lines. Neither test nor reference targets could be detected once the mask was switched on. Masks were stationary and were presented until the subject responded, maximally for half a second.

Stimuli were generated by DOS-based programs on a PC and were displayed on a 17'' monitor, using standard VGA graphics modes. Resolution was 640×480 pixels at 60 Hz refreshing rate (non-interlaced).

The monitor was placed 67 cm in front of the subjects, which gave a pixel size of about 2 min of arc (0.036 deg). The texture patterns were quadratic and covered a visual field of 16.5×16.5 deg. Stimuli were generally white on a dark background; only in series C were red and green lines on a dark background used as well. Luminance settings were controlled by 6-bit computer values (0, …, 63, corresponding to 0.44, …, 50 cd/m^2) which in the upper range were linearly related to the logarithm of measured luminance. For simplicity, these computer values are used throughout the study to quantify the relative saliences of test targets. Background texture lines had a luminance value of 23 (6.9 cd/m^2) on 1.7 cd/m^2 screen luminance. Reference lines were shown at different luminances above this level. Test targets displayed the same luminance as background lines, except when they were made to display luminance contrast. Masking elements were brighter than the background lines (value 43; 23.3 cd/m^2).

Presentation time was 150 ms. For subjects NQ and HCN who both revealed particularly high sensitivity to orientation contrast, shorter presentation times (100 ms) were used in some tests.

2.3. Test conditions

Experiments were split into three series. In series A, test targets were orthogonal and/or moved in the opposite direction to the background lines. In series B and C, test targets were either orthogonal or moved in the opposite direction, and/or were brighter than surrounding lines (series B) or had a different color (series C). The different conditions of a test series were interleaved.

While *orientation* contrast was restricted to 0° (no contrast) and 90° (maximal contrast), two graduations of feature contrast were used for the other dimensions to obtain saliency effects of different strength. *Motion* contrast was obtained from single displacements in the horizontal direction, 50 ms after stimulus onset. With a total presentation time of 100–150 ms this produced the percept of smooth line movement. Two displacement amplitudes (2 and 4 minarc) were regularly tested; a larger third amplitude (6.5 minarc) was only tested with subject FS, who did not find movement contrast very compelling. Because motion-defined targets and background elements moved into opposite directions, relative motion had double amplitude (4, 8.5, 13 minarc).

While only white lines were used in series A and B, the lines of the test target field in series C were all in *color*. All color settings were combinations of the red and green phosphors of the monitor; there was no blue component in these tests. For each subject, two color pairs were selected, which produced distinct saliency effects in the middle of the salience scale. In patterns with color contrast, test targets were set to one color and the background elements (in the test target field) to the other. The two combinations of each color pair were randomly intermixed. In patterns with exclusive orientation or motion contrast in series C, test targets and background elements were shown in the same color; the four colors selected for each subject were randomly intermixed in these conditions. Reference targets and the surrounding background lines were always white, as in test series A and B. All colors were pairwise matched in luminance by minimizing heterochromatic flicker at 25 Hz; they were also matched to the luminance of the white background lines in the reference target field. This ensured that (a) saliency effects from color contrast were (as closely as possible) free from luminance artifacts, and (b) matches were not disturbed by luminance differences between the left and the right texture fields of the stimulus.

2.4. Subjects

Experiments were carried out by five subjects including the author. Four of them (three female, one male) were in the age of 17–19 years and were paid for their

participation in these experiments; one (male) was 50 years and worked for free. All subjects had normal or corrected-to-normal visual acuity, and all but one had normal color vision (Farnsworth–Munsell 100 hue test). SW was a deuteranomolous subject (male) with clear deficiencies in the blue-green range (midpoint of error score: 55).

The experiments described here were carried out over 4 months in sessions of 1–2 h each. Intermixed were experiments on other tasks that are not reported here. Before the series were started it was confirmed that subjects could easily detect orientation-defined targets in stimulus presentations of 150 ms or less and reliably performed the matching task. Three subjects who had not performed such tasks before went through an initial training period of two to four sessions to become familiar with the tasks and to improve the detection of orthogonal targets in brief presentations. The two other subjects did not require special training as to this point.

All five subjects participated in the experiments of series A and B and four of them also in series C. Subject SW failed to detect color defined targets at 150 ms presentation time, and could not be tested in series C.

2.5. Test procedures

All experiments were performed under fixation of a green spot in the center of the screen, which was visible throughout the run. In the first sessions fixation was controlled by means of a video camera focused on the subjects' eyes; even small deviations from fixation were easily detected with this system. However, all subjects accurately followed the instructions to fixate, and controls were only occasionally made in later sessions. In addition, the short stimulus presentation times used (≤ 150 ms) excluded any advantages from gaze shifts towards the targets.

Subjects indicated the side with the more salient target by pressing specific keys on either side of the keyboard. They could take as much time as they wanted for reply. The new stimulus presentation started 1–1.5 s after the response.

All subjects quickly learned to compare targets for their relative salience. In the first matching tests, subjects were regularly instructed to select the more salient target irrespective of why it appeared to be salient. These instructions were given to avoid subjects biasing themselves to a certain type of target, for example to orthogonal lines, thus converting the matching task into a target detection task. The short stimulus presentation times and the random assignment of test and references targets to the left or right side of the screen clearly helped to avoid such a bias. When explicitly asked, subjects were often not aware which of the two targets was orthogonal and which one was brighter than the background. They sometimes did not even notice that one target was orthogonal, although they had clearly seen two salient items. Because of the short presentation time, subjects sometimes linked the observed salience to the (in fact uniform) crosses of the mask reporting that single crosses popped out, one on the left and one on the right side.

Every test target condition was compared with 11 reference targets (which all displayed the same form but different levels of luminance contrast), in random sequence, to obtain salience ratings as in Fig. 2c. The 50% values of these curves were taken as the matching points at which a particular test target was as salient as the reference target with this luminance value. Each specific target combination (individual data points in Fig. 2c) was presented 30–50 times; the number of repetitions (N) depended on the rating values obtained (adaptive N) and was adjusted during the run so that the standard errors of the mean did not exceed a given threshold. The number of individual repetitions was set to $N = 15$ or $N = p(1-p)/\sigma^2$ whichever was larger, with p giving the actual preference rate for one or the other target. This 'adaptive N' method automatically increased the number of presentations near the matching point (50%). In the measurements presented here, σ was set to 10% and data curves as in Fig. 2c were typically obtained from two repeated runs. A single matched luminance value (arrow in Fig. 2c) was then based on two series of comparisons with 11 reference targets, each repeated over 15–25 individual presentations. This gave a total of 370–500 stimulus presentations for every salience match. There are theoretically more efficient procedures to obtain the matched luminance value for a given test target, like PEST (Taylor & Creelman, 1967) or other staircase methods (cf. Nothdurft, 1993c). However, one problem with staircase approaches is that salience differences between the targets become smaller when measurements approach the point of convergence (which often does not represent the 50% level of matched salience); hence subjects must improve concentration in the course of the run. I myself as a subject found it helpful to see from time to time patterns in which one of the two targets was clearly more salient than the other. It helped to keep decision criteria constant and free of biases to one or the other target type.

Salience matches were performed in multiple test runs in which various test conditions were randomly interleaved and several matching curves as in Fig. 2c were achieved simultaneously. These runs which could last up to 2 h or more, were split into sections of 15–30 min each. In addition, subjects could pause whenever they wished.

2.6. Analysis

Salience ratings for individual conditions (as in Fig. 2c) were fitted by sigmoidal curves of the form $y = 100/(1 + e^{(-(x-a0)/a1)})$ using the Levenberg–Marquardt algorithm. The two independent parameters define the matched luminance value ($a0$) and the slope of the curve ($a1$). Fits were usually obtained with $r^2 > 0.8$ (frequently $r^2 > 0.9$); only in a few cases were fits slightly poorer ($r^2 > 0.7$). Saliency matched luminance values of a given test target were taken from the fitted $a0$ values and usually plotted with the standard error of this fit.

3. Results and discussion

3.1. Series A: the combination of orientation and motion contrast

The first series of experiments investigated the interference of saliency effects in the orientation and motion domains. We asked two sorts of questions: (1) Is a target that is orthogonal to its neighbors *and* moves in a different direction more salient than a target that has only one of these properties (additivity)? Is the saliency gain in one dimension, e.g. motion, changed when another saliency effect, e.g. orientation, is added (gain reduction)?

Fig. 3 shows salience matches of subject NQ for three different test targets, an orthogonal line ('ORI'), a line that moves in the opposite direction to surrounding

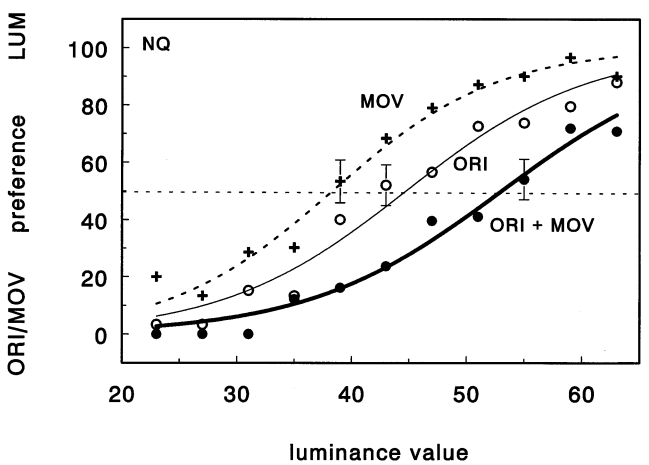

Fig. 3. Salience matches for three different target conditions. In comparison to a fixed set of luminance-defined reference targets, the three test targets produced different salience ratings. Targets that were orthogonal to surrounding lines (ORI) were more salient than targets that moved in the opposite direction (MOV). But both targets were less salient than targets that combined these properties (ORI + MOV). Data from one subject. Error bars indicate the confidence range of the measured rating, equivalent to the standard error of the mean; only the largest SEM is plotted for each curve.

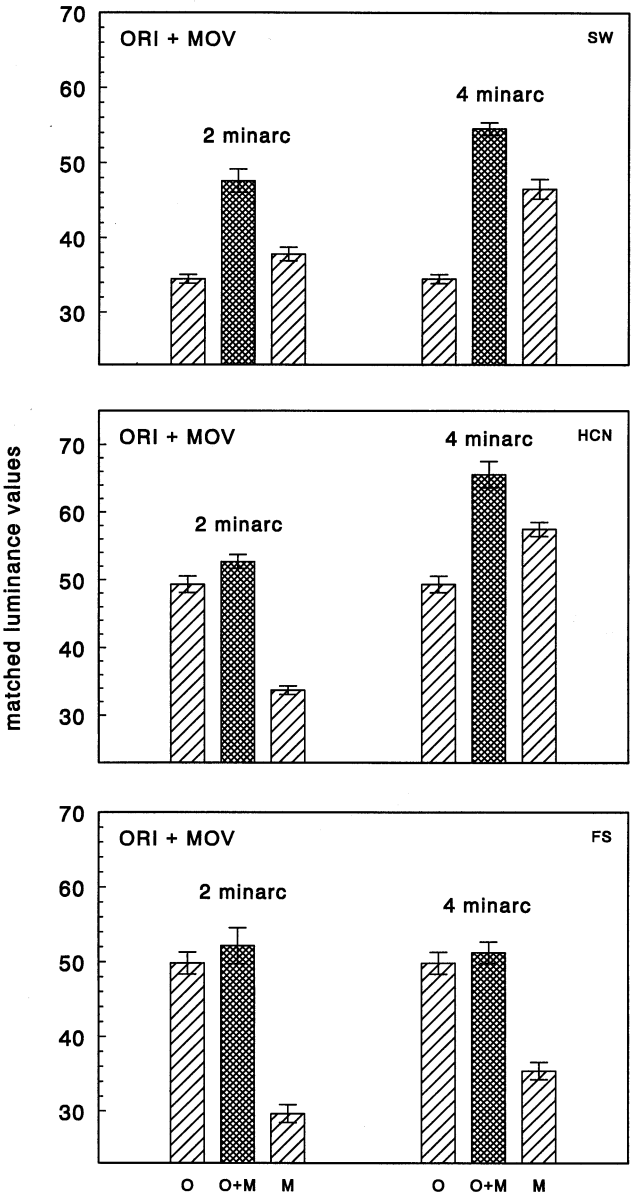

Fig. 4. Salience matches of three subjects in series A. Histograms plot the matched luminance values for different test conditions: O, targets defined by orientation contrast; M, targets defined by motion contrast; O + M, targets defined by a combination of both. Two amplitudes of motion were tested (left- and right-hand histograms). Subject SW (top) was less sensitive to orientation than to motion contrast, subject FS (bottom) showed reverse sensitivities.

lines ('MOV'), and a line with both these properties ('ORI + MOV'). The curves are shifted against each other; reference targets with luminance values near 45, for example, were more salient than the purely motion-defined test target but less salient than the orientation- and motion-defined target.

3.1.1. Summation of saliency effects

The matched saliences (50% values) of these conditions are plotted in Figs. 4 and 5. Fig. 4 shows data of

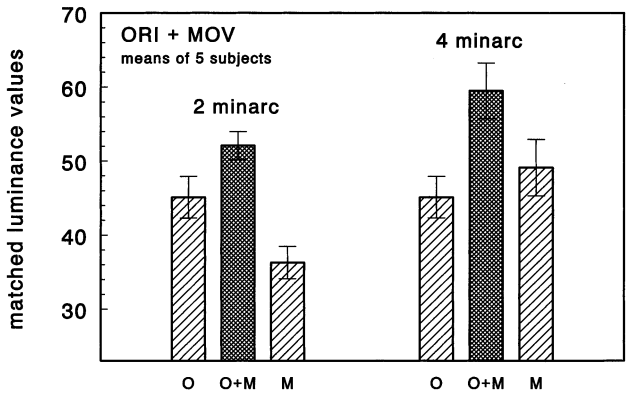

Fig. 5. Salience matches for orientation and/or motion contrast (series A); mean data and SEM of all five subjects. Presentation as in Fig. 4.

three selected subjects to illustrate the variation that was observed. The salience levels evoked by orientation (O) or motion defined (M) test targets varied considerably among these subjects. Motion contrast produced very small saliency effects in subject FS, which only marginally increased the salience of the orthogonal target. Subjects SW and HCN demonstrated stronger saliency effects from motion contrast but differed in their sensitivity to orientation contrast. Despite these individual variations, all subjects found the target with combined feature contrast (center bars of the histograms) more salient than targets with only one such property (adjacent bars). In the mean data of all five subjects (Fig. 5) the orientation target was more salient than the motion target at the small movement amplitude (left-hand histogram), but slightly less salient than the motion target at double amplitude (right-hand histogram). In both cases, combinations of the two saliency mechanisms together produced the most salient targets; the salience differences between combined and single feature contrasts were all significant (paired t-test: O vs O + M, $t > 3.68$, $P < 0.025$; M vs O + M, $t > 4.9$, $P < 0.01$). However, while these data clearly demonstrate additivity of saliency effects in orientation and motion, the addition is obviously nonlinear. In both histograms of Fig. 5, the center bar is smaller than the sum of the outer bars (paired t-test: $t > 4.1$, $P < 0.02$). The measured saliences represent 83 and 76% of the linear sums; the deviations from linear addition (100%) were highly significant (one-sided t-test: $t > 7.8$, $P < 0.001$).

3.1.2. Gain reduction of motion-defined saliency effects by added orientation contrast

The variations in salience with the different motion amplitudes provide another measure of the linearity of saliency effects. Increasing the amplitude also increased the salience of the target. We may thus compare the increase of salience for motion targets alone with the increase of salience for the combined test conditions (i.e. we take the difference between the 'M' bars in Fig. 5 and compare it with the difference between the 'O + M' bars).

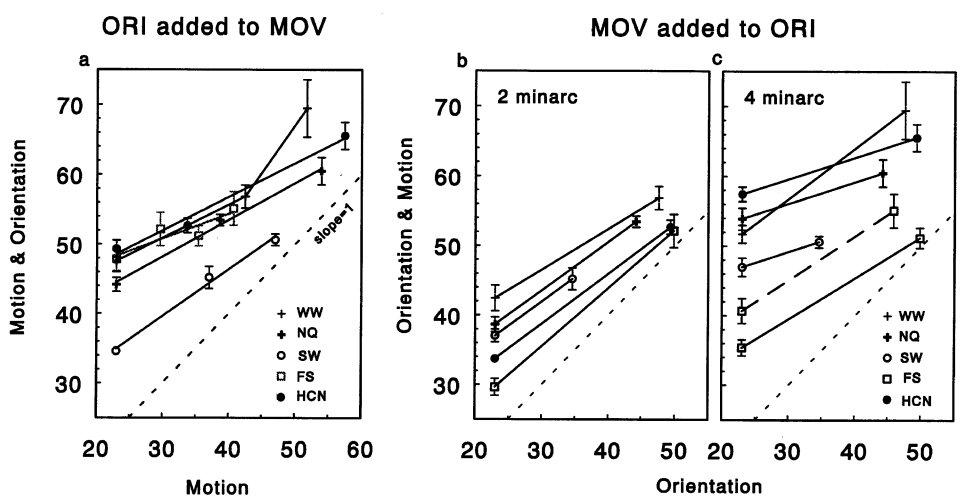

Fig. 6. Gain reduction effects for orientation and motion. (a) Salience variations from pure motion contrast (abscissa) plotted against salience variations with the same targets when maximal orientation contrast was added (ordinate). Single data of all five subjects; error bars give the SEM of the fitted salience matches (cf. Fig. 2c). Slopes of regression lines resemble the gain reduction factor; slopes of 1 (dashed line) indicate no attenuation by the added saliency effect. All subjects produced regression lines with slopes below 1, indicating considerable gain reduction from added orientation contrast. Thus saliency mechanisms for motion and orientation contrast are partly shared (for details, see Appendix). Except for subject WW, data points fitted well to straight lines, that is gain reduction was proportional to the salience from motion contrast. (b, c) Salience variations in orientation with (ordinate) or without (abscissa) added motion contrast, for two different levels of motion salience (amplitudes of the motion component). For most subjects, gain reduction increased (slopes decreased) when motion salience was increased (c vs b). For subject FS, the motion salience was further increased (6.5 minarc amplitude; dashed curve in b) but slopes did not continue to decrease in this case.

This relationship is shown in Fig. 6a; each line represents the data from one subject. Salience variations from different motion amplitudes (including zero, i.e. no motion) are plotted against salience variations from the same targets when maximal orientation contrast was added. The data illustrate two interesting observations. First, for most subjects the data points lie on a straight line; that is the salience variations in the combined test condition were linearly related to the salience variations in the motion-alone case. Second, the lines are not parallel to the dashed line but have slopes significantly smaller than 1 (mean: 0.51 ± 0.05; one-sided t-test: $t > 9.5$; $P < 0.001$), indicating that the deviations from linearity increased proportionally to the salience of the pure motion target. (For subject WW, only the flatter part of the curve was taken for the mean; see Appendix).

3.1.3. Gain reduction of orientation-defined salience by added motion contrast

Fig. 6b,c show the corresponding analysis for saliency variations in orientation (0 and 90°), presented alone or with additional motion contrast. The slopes for the smaller motion amplitude (Fig. 6b) were steeper (mean: 0.71 ± 0.04) than those for the larger amplitude (Fig. 6c; mean: 0.45 ± 0.09); both means differed significantly from 1 (one-sided t-test: $t > 6.1$, $P < 0.005$). Motion contrast at a larger third amplitude (6.5 minarc) was only tested with subject FS and produced a similar slope to the 4 minarc movement (Fig. 6c; open squares, dashed connection line).

3.1.4. Discussion

It is interesting to consider how these observations may be related to underlying neural mechanisms (cf. Appendix). If the saliency effects from orientation and motion contrast were produced by completely independent mechanisms, the salience variations from motion contrast (Fig. 6a) should not be affected by the added orientation contrast; slopes should be 1 in this case. On the other hand, if motion and orientation saliency effects were produced by the same mechanism, no salience variations should be seen once the mechanism was fully activated by maximal orientation contrast, and slopes should be zero. From the cat data reported above (Kastner et al., 1999) we would expect an intermediate level of interaction. Orientation and motion contrast should have activated both shared and independent saliency mechanisms. Thus salience in the combined test conditions should increase but the increase should be smaller than that for motion alone; slopes should be positive but smaller than 1, as was found. The observed gain reduction of about 50% in Fig. 6a suggests that about half of the cells that encode salience from motion contrast also encode salience from orientation contrast. The fact that most of the data points in Fig. 6a lie on straight lines, indicates that the proportion of shared mechanisms was constant over the investigated salience range.

Different to Fig. 6a where feature contrast in the added dimension was maximal (orthogonal orientation), the added motion contrast in Fig. 6b was not at its maximum. A small saliency effect from motion might have produced incomplete activation of the underlying neural mechanisms, and thus might have indicated a smaller proportion of shared processes than a strong motion saliency effect. This is apparent from Fig. 6b,c. The small motion amplitude produced only 29% gain reduction for orientation-defined salience variations (Fig. 6b); the large motion amplitude produced 55% reduction (Fig. 6c). We do not know whether larger amplitudes would have increased gain reduction any further, but this was not clearly the case for subject FS. Thus about 50%, at least, of the orientation-sensitive mechanisms should be shared with those sensitive for motion contrast. If this were related to the number of activated cells, about half of the cells responding to orientation contrast should also respond to motion contrast — a number closely met by the cat data mentioned above (a more detailed analysis of gain reduction effects is given in the Appendix). From the strong but not complete interference of saliency effects from orientation and motion contrast we conclude that the underlying neural mechanisms are partly shared and partly independent of each other.

3.2. Series B: combinations of orientation or motion and luminance contrast

The orientation and the movement direction of a stimulus are generally not encoded in neurons at processing stages earlier than area V1; hence saliency effects based on differences in these dimensions must be of cortical origin. This is in agreement with numerous studies that have demonstrated responses to orientation and motion contrast in area V1 (Allman et al., 1990; Bach & Meigen, 1992; Knierim & Van Essen, 1992; Lamme et al., 1992, 1993a, 1993b; Lamme, 1995; Sillito et al., 1995; Kastner et al., 1997, 1999; Lee et al., 1998; Zipser et al., 1998; Nothdurft et al., 1999) but not before. However, other stimulus properties are distinguished at earlier processing stages, and saliency effects from these dimensions might indeed be evaluated subcortically. In particular, the luminance and color of a stimulus are already distinguished by neurons in the retina and the lateral geniculate nucleus. In the following two test series I measured the additivity of saliency effects combining a clearly cortical mechanism (orientation or motion contrast) with a potentially subcortical one (luminance or color contrast).

Fig. 7 shows original matching data of subject WW for a test target that was brighter than the background

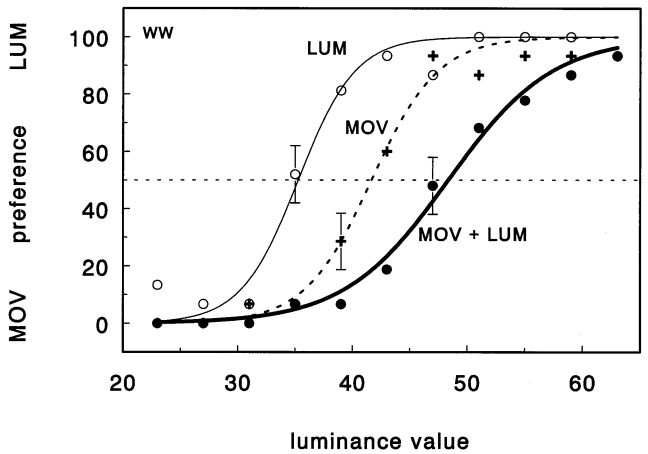

Fig. 7. Salience ratings for motion and luminance; subject WW. A line that moved in the opposite direction to neighboring lines (MOV; amplitude 4 minarc) produced different saliency ratings than a brighter line (LUM; luminance value 35). A line with both motion and luminance contrast (MOV + LUM) was the most salient one. Error bars give the largest SEM on each curve.

lines ('LUM'; target luminance value: 35), a test target that jumped horizontally in the opposite direction ('MOV'), and a test target that combined both these properties ('MOV + LUM'). Reference targets were always lines brighter than background lines, so that in the LUM condition both targets were bright lines that had to be compared in salience. The matched luminance value obtained was very close to 35, illustrating the accuracy of the method. The motion-defined target was clearly more salient (matched luminance value: 41.7 ± 0.5), and the target that was brighter and moved in opposite direction to the surroundings, was the most salient target of this sample (matched luminance value: 48.4 ± 0.4).

In Fig. 8 the mean salience-matched luminance values of all subjects for orientation, motion, and luminance targets are shown. In all tests, the targets with the combined feature contrast were more salient than the targets with one contrast only (paired t-test: $t > 3.62$; $P < 0.025$). The measured saliences for the combined test conditions were, in fact, close to the linear predictions. They represented 90% (orientation and luminance), 93% (motion and luminance, 2 minarc amplitude), and 87% (motion and luminance, 4 minarc amplitude) of the sum of individual saliences; the deviations from 100% were not significant (one-sided t-test: $t < 1.5$; $P > 0.05$) except for the combination with the large motion amplitude ($t > 2.5$; $P < 0.05$).

Fig. 9 shows the salience variations in single or combined contrast conditions for some of these combinations. Slopes were often close to 1, but there was considerable variation among the subjects. The mean slopes for the different combinations varied between 0.88 and 0.71, for the 2 and 4 minarc movement amplitudes, respectively, added to luminance contrast; the grand mean for all slopes with luminance contrast was 0.80. Mean slopes were generally not significantly different from 1 (one-sided t-test; $P > 0.05$) except for the combination of the largest movement and largest luminance saliences (Fig. 9e) for which the deviation from 1 was just significant ($t > 2.4$; $P < 0.05$). Subject WW produced the flattest slopes in all graphs of Fig. 9. The other four subjects revealed almost identical slopes at low luminance (Fig. 9b) or motion contrast (Fig. 9d),

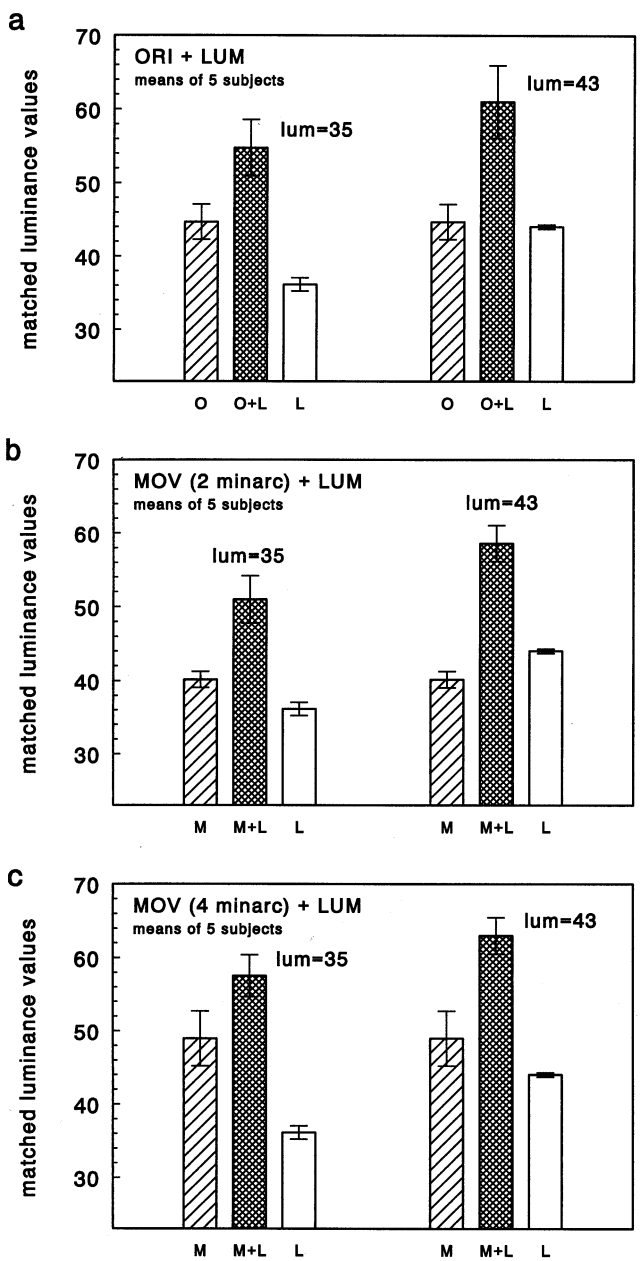

Fig. 8. Salience matches for luminance and orientation (a) or motion (b, c), series B. Two luminance settings (left-hand histograms: 35; right-hand histograms: 43) and two motion amplitudes were used. All combinations produced strong additivity effects that were larger than those for orientation and motion (Fig. 5). Mean data and SEM of all five subjects.

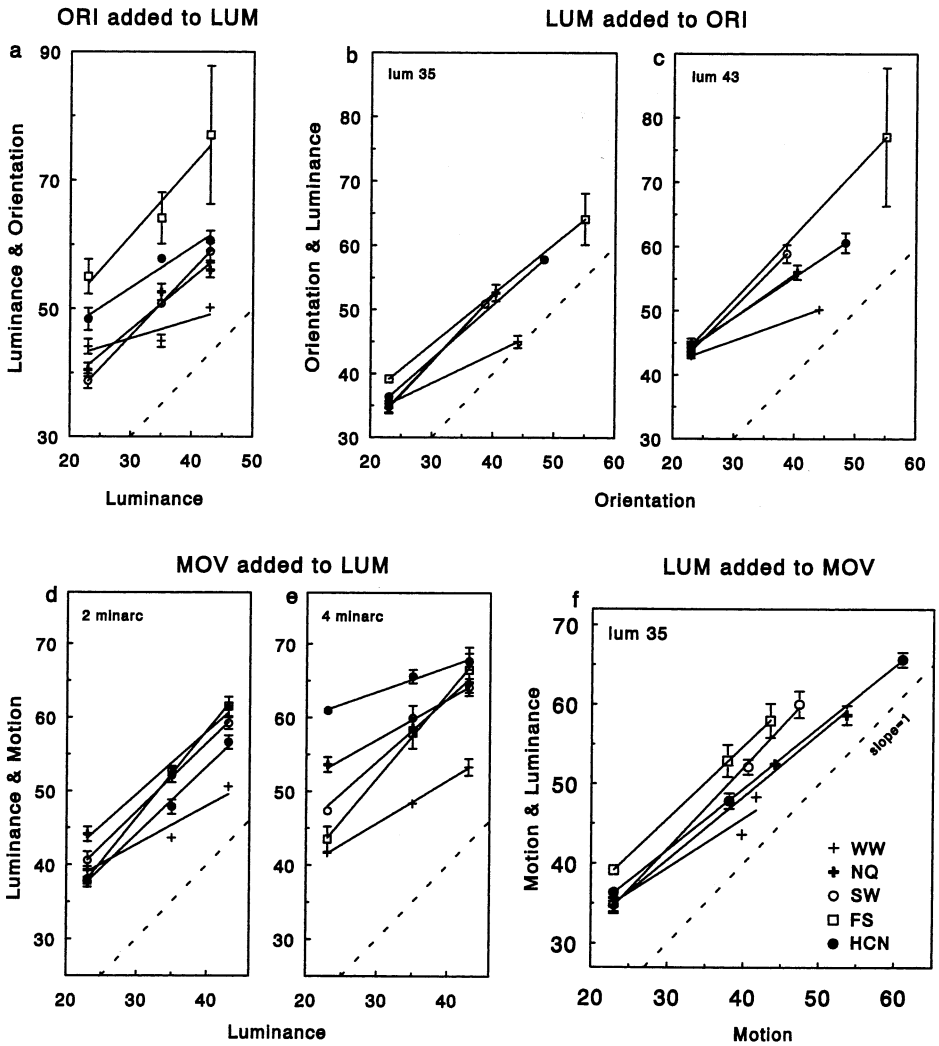

Fig. 9. (a–f). Gain reduction effects for various combinations with luminance. Salience variations from luminance contrast were relatively little affected by added orientation or motion contrast. Regression lines were generally steeper, than in Fig. 6 and often close to 1, except for subject WW. Plot conventions as in Fig. 6.

although the perceived saliences varied in strength (cf. Fig. 9a). Some subjects produced flatter slopes when luminance or motion contrast was increased (Fig. 9c,e) but others still had slopes near 1. Interestingly, the individual data points in Fig. 9a,d,e,f were generally well fitted by the regression lines, with only few exceptions (e.g. subject WW in Fig. 9a,d,f).

3.2.1. Discussion

The nearly linear summation of saliency effects from orientation or motion contrast and saliency effects from luminance contrast indicates that the underlying neural processes are far more independent of each other than was the case for the combinations of orientation and motion (cf. Fig. 6). However, a closer look at Fig. 9 revealed considerable variation among subjects, the reason for which is not yet clear.

3.3. Series C: combinations of orientation or motion and color contrast

Quite a different observation was made for combinations of color with orientation or motion contrast (Fig. 10). The combined feature targets were again more salient than the single component targets. But contrary to the combinations with luminance contrast, deviations from linearity were pronounced in some conditions. The additivity effect for orientation and color (Fig. 10a) was very small and, in fact, not significant for the lower color contrast ($t < 2.07$; $P > 0.1$). For all other combinations in Fig. 10, the combined stimuli were notably more salient than their single components, but variations and the smaller number of subjects ($n = 4$; cf. Section 2) did not establish all these differences as significant. The saliences of the combined test conditions were reduced to, on average, 69% of the linear

sum of individual saliences for color and orientation, and to 79% for color and motion. These reductions were significant for all combinations (one-sided t-test: $t > 3.9$, $P < 0.025$). This indicates that the saliency mechanisms for orientation and motion contrast were not independent of those encoding differences in color.

The interdependence of orientation and color is also seen in Fig. 11a. All subjects revealed flat curves for low and medium color contrast and a one-to-one relationship (slopes near 1) for higher color contrast. (This second stage was not reached by subject HCN.) Combinations of color and motion (Fig. 11b) did not reveal such a distinction but data points fell close to the fitted regression lines. Three subjects produced fairly flat curves in this condition (slopes near 0.5), for one (FS) the curve was much steeper (slope near 0.9). The reverse analyses are shown in Fig. 11c,d, for medium color contrast. When salience variations from orientation contrast are plotted against such variations with additional color contrast (Fig. 11c) data points fell close to the dashed line that indicates equal salience for the single and the combined conditions (this is equivalent to the flat slopes seen in Fig. 11a). Salience variations from motion and (medium) color contrast (Fig. 11d) produced steep slopes; for higher color contrast slopes were flatter (not shown).

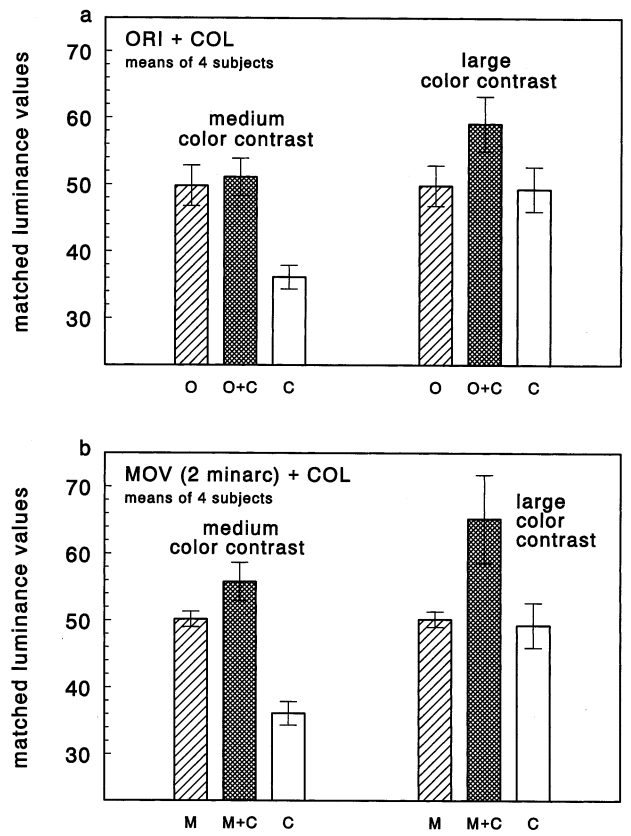

Fig. 10. Salience matches for color and orientation (a) or motion contrast (b), series C. Two isoluminant color contrasts were used that produced medium (left-hand histograms) or strong (right-hand histograms) salience. Additivity effects were particularly small for combinations of color and orientation. Mean data and SEM of four subjects.

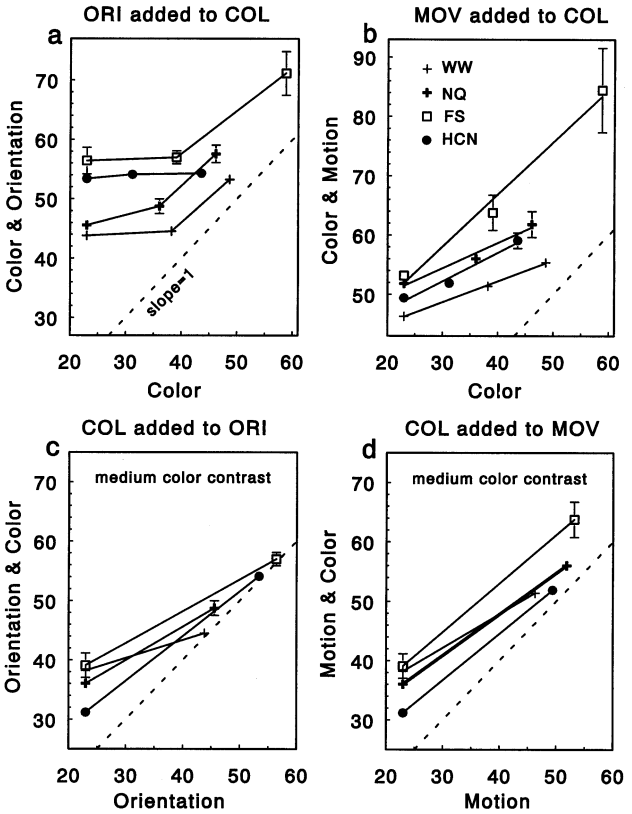

Fig. 11. Gain reduction effects in combinations with color. Individual data of 4 subjects. (a, b). Salience variations from color contrast, with and without added orientation (a) or motion contrast (b; 2 minarc amplitude). While motion contrast often produced gain reduction similar to that in the previous tests, the combination of color with orientation saliency effects revealed two distinct stages of gain control. Gain reduction was almost complete for low to medium color contrast (zero slopes) and almost absent for higher color contrast (slopes near 1). (c, d). Salience variations in the orientation (c) or motion domain (d) when medium color saliency effects are added. Combinations with orientation contrast fall close to the dashed line (small additivity effects); regression lines for combinations with motion contrast have slopes of 0.6–0.8.

3.3.1. Discussion

Orientation and medium color contrast were the only combination for which additivity effects were small. The flat curves in Fig. 11a suggest that the saliency mechanisms activated by medium color contrast were completely embedded in the saliency mechanisms activated by (maximal) orientation contrast. When color contrast was further increased, the pool of shared mechanisms eventually became saturated and the salience variations in color were completely transferred into the salience variations seen with the combined stimuli (slopes near 1; see Appendix A for an analysis of this phenomenon.) For combinations of color and

motion, additivity effects were more pronounced but clearly different from linear summation. For these conditions, the interaction of saliency effects was comparable to that found for combinations of orientation and motion (Fig. 6) but distinct from that seen in the combinations with luminance (Fig. 8).

3.4. Overview of the observed gain reduction effects

Figs. 12 and 13 summarize the results from the analyses above. Fig. 12 gives an overview of gain reduction in the primary dimension when a saliency effect in the second dimension was added. Instead of slopes, their mean deviation from 1 is plotted here, so that the data directly indicate the presumed overlap of saliency mechanisms. If measurements were made with different salience levels of the added component (as in Fig. 6b,c), the data from the larger saliency effect were taken (Fig, 6c, in this case). Even these might have underestimated the degree of interaction between components if saliency effects were not yet maximal (cf. Appendix). For curves with two distinct slopes (Fig, 11a) gain reduction was calculated from the flatter part. Gain reduction effects varied between 91% for (medium) color contrast in orientation and 23% for orientation in luminance. Thus the saliency effects from medium color contrast were almost anulled (91% reduction) when orientation contrast was added. Saliency

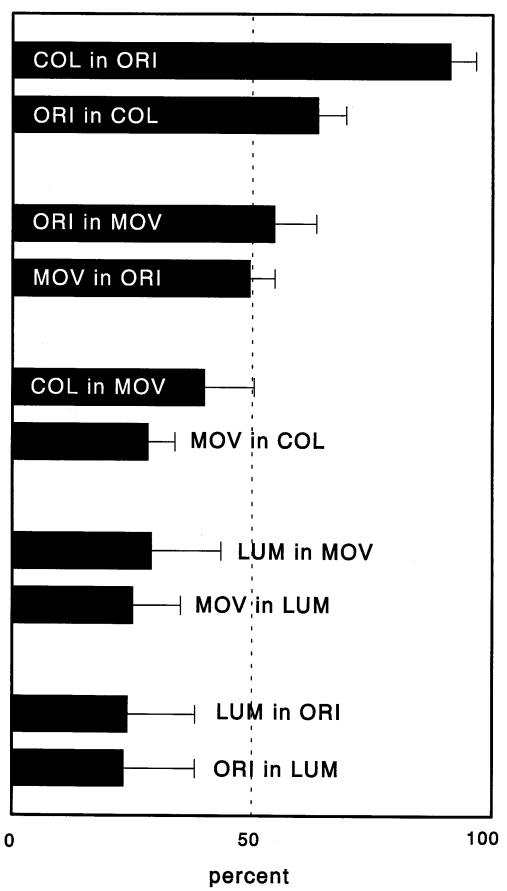

Fig. 12. Shared saliency processes as estimated from the measured gain reduction effects. Mean data of all five subjects (four subjects for combinations with color). Values were estimated from regression lines as plotted in Figs. 6, 9 and 11. If measurements were made with saliency effects of different strength, the data from the more salient test were used. Some of these may still have underestimated the amount of interaction between saliency effects. For bi-sected curves (e.g. Fig. 11a), slopes of the flatter part were taken. Combinations of color- and orientation-defined saliences revealed the strongest overlap of underlying mechanisms, all combinations with luminance the smallest overlap.

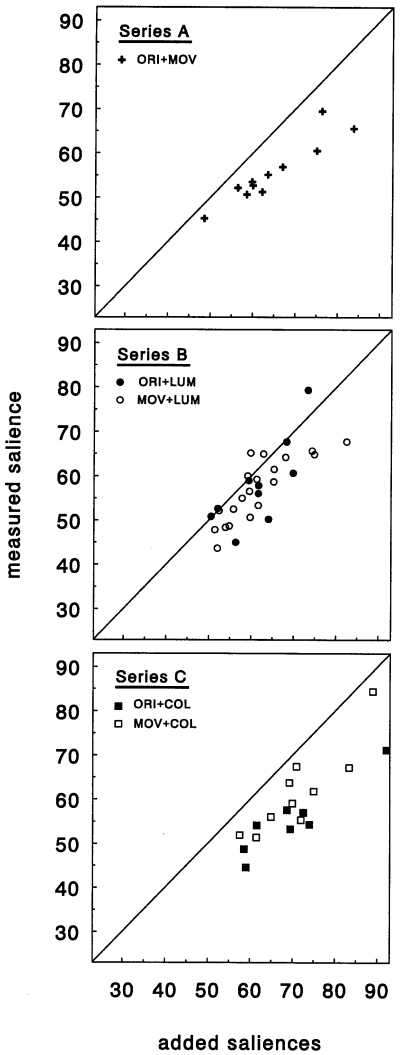

Fig. 13. Overview of combined saliency effects. For all tested combinations, the measured salience levels (ordinates) are plotted against the linear sum of component salience levels (abscissa). Each point represents data of one subject. (a, b, c) Data from the different test series of this study. All distributions are shifted away from the dashed line indicating linear summation, which is only reached by data from combinations with luminance contrast. Deviations from midline, i.e. from linearity, are most pronounced for combinations of color and orientation. The graphs do not indicate that nonlinearities increased with salience and hence do not suggest a common saturation effect of salience.

effects from maximal color contrast were reduced by, on average, 71%. The gain reduction effects were pairwise similar for each stimulus combination, except for color and orientation. The measured effects of color contrast upon saliency effects in orientation were reliably different from the effects of orientation contrast upon saliency effects in color (paired t-test; $t > 7.38$, $P < 0.005$); all other pairs were not significantly different ($P > 0.1$).

Fig. 13 summarizes the degree of additivity effects for all stimulus combinations tested. The measured combination saliences (ordinate) are plotted against the sums of component saliences (abscissa); each point corresponds to the data of one subject. Despite the considerable scatter of data points, the different combinations produced distinct distributions. Only for combinations with luminance contrast did the distributions reach the midline that marks linear additivity (Fig. 13b); for all other combinations, data points fell further away from that line. Even for luminance contrast however, many data points were displaced from this line, indicating that saliences did not always add linearly. Deviations from the midline, i.e. from linearity, were most pronounced for combinations with color. With respect to the deviation from linearity (distance from midline), the distributions for combinations with luminance contrast were significantly different from those with color (Fig. 13c; independent t-test; $t > 4.72$, $P < 0.0001$) and reliably different from that for the combination of orientation and motion (Fig. 13a; $t > 2.61$; $P < 0.02$) which itself was not significantly different from the distribution for combinations with color ($P > 0.16$). Among the different color combinations, the deviations from linearity produced by orientation and color were stronger than those produced by motion and color ($t > 2.18$, $P < 0.05$), in agreement with Fig. 11.

The graphs in Fig. 13 also show that deviations from the midline (i.e. the degree of interaction) occurred at all salience levels and were not restricted to cases in which the added saliency effects were particularly high. This indicates that the observed nonlinearities do not reflect common saturation.

3.4.1. Discussion

Fig. 12 shows an interesting ranking of overlapping saliency mechanisms, from strong interactions between color and orientation, to small interactions between orientation and luminance. In the means, saliency effects were never added in an exactly linear manner (0% overlap); that is, no two saliency effects were found to be strictly independent in all subjects. The combinations with luminance contrast revealed the smallest overlap; some subjects did indeed show linear additivity in some of these conditions. This suggests that saliences from luminance contrast were mediated by processes independent of those encoding other saliency effects. Other combinations, like orientation and motion, produced stronger gain reduction effects, reflecting stronger interactions of the underlying neural processes. However, the large variation that was observed between subjects calls for a careful interpretation of these effects. While some differences between combinations of saliency effects were significant, the continuous variation in gain reduction effects in Fig. 12 does not indicate strictly distinct levels of interaction between different pairs.

The fact that deviations from linear summation were seen at all salience levels (Fig. 13) excludes a simple explanation of the observed gain reduction effects. As mentioned in Section 1, saturation in the salience transfer function would also produce nonlinear summation effects, independently of whether or not the underlying mechanisms interact at an early level. However, if this had been the case, deviations from linearity (from the midline in Fig. 13) should be particularly pronounced on the right-hand side of the graphs, which clearly was not the case. Thus, the measured gain reduction was not due to common salience saturation, at least not in in the investigated salience range. Similar conclusions can be drawn from a number of observations in this study. In Figs. 6, 9 and 11, for example, lines starting at a higher salience level on the ordinate could display steeper slopes than others starting at a lower level. This is contrary to the assumption that deviations from linearity should increase with the level of salience. Second, different subjects often reported different saliency effects for the same stimulus but, nevertheless, revealed similar slopes for the gain reduction effects. Third, data points in the scatter plots often fell upon straight lines; this should not have happened if deviations from linearity increased with salience, as is the case for saturation. All these observations suggest that the different gain reduction effects observed in this study did not depend on the (accidental) salience levels evoked by the stimulus components, but were indeed related to the specific stimulus combination tested.

4. General discussion

The above findings can be summarized in two statements: (1) Targets that were salient from discontinuities in one visual dimension generally became more salient if another discontinuity was added. This indicates that saliency effects were achieved from different and, at least partly independent mechanisms. (2) Addition was often nonlinear, suggesting that the underlying mechanisms were not completely independent but interfered to some extent. Salience variations in one dimension were commonly attenuated by saliency effects in another dimension; the degree of attenuation was used to estimate the relative proportion of independent and interdependent saliency processes.

4.1. Additivity of saliency effects

The salience of a target is controlled by several stimulus properties; in this study saliency effects from feature contrast in four dimensions were investigated. The common observation was that the various saliency effects added and all contributed to the resulting salience of the target.

Summation effects have also been reported for texture segmentation tasks, which in many aspects display characteristics similar to popout (cf. Nothdurft, 1991, 1992). Abele and Fahle (1995) saw additivity effects for several cues and also measured subthreshold summation between color and orientation, the combination which produced the smallest additivity effects in the present study. Callaghan, Lasaga, and Garner (1986) also observed additivity effects for orientation and color; segments defined by both these properties were detected at shorter reaction times than segments defined by either property alone. For combinations of orientation and luminance, Gray and Regan (1997) measured summation of an orientation-defined and a luminance-defined texture edge in the context of Vernier step threshold and found summation consistent with probability summation, i.e. independent mechanisms at threshold. While all these studies investigated summation effects at or below detection threshold, the present study quantified saliency effects well above threshold. All studies agree on the presence of additivity effects, which indicate contributions from different and, at least partly independent mechanisms.

This work was triggered by physiological observations that indicated some degree of independence of the cortical mechanisms encoding orientation or motion contrast (Kastner et al., 1999). The fact that additivity of salience was now found for nearly all tested combinations of saliency effects buttresses the idea that different saliency components are generally encoded by separate (but perhaps partially overlapping) mechanisms. This is in agreement with the sometimes pronounced differences between sensitivities to feature contrast in different dimensions. Some subjects revealed high sensitivity to motion contrast and lower sensitivity to orientation contrast; other subjects showed opposite preferences. Subject FS, for example, revealed rather low sensitivity to motion contrast, in spite of her earlier training with orientation contrast. It is hard to imagine how these different performance levels could be achieved by one single mechanism.

While the observed additivity of saliency effects is in agreement with our data from cats (Kastner et al., 1999) and with summation effects in visually evoked potentials measured in humans (Schmitt and Bach, 1997), they differ from direct measurements of additivity in alert monkeys. Zipser et al. (1996) recorded responses to texture patches (figures) that segregated from the surround by a variety of properties, like orientation contrast, motion contrast, color or luminance contrast, disparity. While figures defined by feature contrast in a single dimension produced reliably increased responses in a population of 64 cells, the combinations of all distinguishing stimulus properties together did not further increase this response. It is not clear why additivity effects were not seen in these data but were regularly observed in the present psychophysical study (and can be seen in Fig. 1). One explanation might be that the 'figure effects' studied by Zipser et al. are qualitatively different from the saliency effects measured here. Whereas saliences may be graded (one object can be more salient than another one), figures as such are not, once they are clearly detected. One might also consider saturation effects in salience to account for the discrepant findings between the two studies. But it is not obvious that the stimuli used by Zipser et al. were more saturated, in terms of salience, than the line stimuli of the present study. It is impossible to increase the salience from orientation contrast above that of an orthogonal line, therefore if saturation were to play a role it should do so particularly with these stimuli. We have no evidence of strong saturation effects (Fig. 13) but instead found pronounced additivity effects even with orthogonal lines.

4.2. Deviations from linearity

Although saliency effects from different dimensions usually were additive, they did not sum up linearly. Before discussing the consequences of this observation in more detail, it seems appropriate to evaluate the linearity of the applied method to quantify saliences. Salience estimates were made by comparing the test targets with reference targets at different luminance levels. In order to analyze linearity of summation it is essential that the applied scale itself is linearly related to the perceived salience of the luminance targets. I am not aware of such direct measurements with single lines. However, there is good evidence that the scale of luminance values used throughout this study was linearly, or nearly linearly related to salience. Within the used range, the scale was linear with the logarithm of measured luminance so that luminance variations (supposed to reflect salience variations) at one level should directly transfer into similar variations at another level. In agreement with this postulate, the different salience matching curves of a subject were usually displaced but did not vary in their slope (see also Nothdurft, 1993c). Between subjects however, or for different test targets, these slopes could vary considerably. This suggests that the salience scale was linear and that the observed deviations from linear summation of component saliences are not explained by a possible scaling problem. Note that these deviations are also not explained

by the use of power functions instead of the logarithm of luminance (Stevens, 1975). The differences between these two functions are relatively small in the luminance range used here, and could not compensate for the gain attenuation effects seen in combined stimulus presentations.

However, even if the scale for measuring salience were not exactly linear, this would not have affected the ranking in Fig. 12 and the main conclusions based upon it. Combinations of orientation and motion contrast clearly reflected a larger degree of interaction between the underlying mechanisms than combinations of either orientation or motion with luminance. This would be consistent with the fact that contextual modulation from orientation and motion contrast is only seen in cortical cells whereas luminance may directly activate cells at earlier processing stages.

The combinations with color were particularly interesting. Color contrast, too, is encoded early in the visual system (Wiesel & Hubel, 1966). But many color-sensitive cells in the retina or the lateral geniculate nucleus give primarily sustained responses to the color mixture presented in the RF and do not demonstrate strong modulation by simultaneous color contrast in space. Stronger such responses were reported for cortical cells (Livingstone & Hubel, 1984; Ts'o & Gilbert, 1988). Thus it seems possible that color information is represented at different levels. While some information is encoded early in the visual system, the saliency effects associated with color contrast might be primarily cortical. It is not yet clear why the combination of orientation and color contrast revealed a particularly high degree of interaction, and why this was not the case for combinations of color and motion. Physiology has reported many color-selective, non-oriented cells in area V1 (Livingstone & Hubel, 1988; cf. also DeYoe & Van Essen, 1988). Unless the color-contrast sensitive cells are also sensitive for orientation contrast, an almost complete overlap of color saliency mechanisms in orientation salience is not to be expected. Also, the information on the color and the motion of a stimulus seems to be represented in separate pathways (Livingstone & Hubel, 1988) and it is not immediately evident how and where these pathways would interact to produce the considerable amount of interaction found in the present study. The analysis of additivity effects in salience suggests that saliency effects from color contrast are completely embedded in the mechanisms encoding orientation contrast, and to about 40% in the mechanisms encoding motion contrast. Any attempt to relate this observation to neurophysiology seems to be merely speculative at the moment. As discussed above, the tuning properties themselves do not predict the sensitivity of a cell to feature contrast, and more specific data on contextual modulation in all these stimulus dimensions are needed to compare the psychophysically predicted amount of overlap between different saliency effects with that of neural processes. It would be particularly interesting to see whether preferences for feature contrast in certain dimensions are also seen in cells that do not distinguish between these properties in their response.

In summary, the study has shown that there exist different saliency mechanisms for different stimulus properties. Although these mechanisms are similar with respect to certain properties (Nothdurft 1993b, 1994, 1995; Bach & Meigen, 1997), for example, they all depend in a similar way on the local feature contrast relative to the overall feature variation in the pattern, most of them appear to work independently of each other, with only partial overlap. It thus seems feasible that one mechanism or another may be affected exclusively in certain diseases (Regan, Giaschi, Sharpe & Hong, 1992; Regan & Simpson, 1995).

Acknowledgements

I am grateful to all subjects for patient collaboration in the experiments and to two anonymous reviewers for valuable comments.

Appendix A. Estimates of shared saliency mechanisms

In the accompanying paper, salience variations in one dimension were compared with those obtained when a constant saliency effect in a second dimension was added. The combined stimuli often revealed a gain reduction for salience variations in the primary dimension. In order to estimate the amount of overlap of the underlying neural mechanisms, a simple, semi-quantitative analysis is given here. The analysis is described for combinations of orientation and motion contrast (indices o and m) but is similarly applied to any tested stimulus combination.In an approximation, the salience of the target with combined orientation and motion contrast is given by the addition of the individual salience components minus the proportion of overlapping effects in both dimensions,

$$s_{om} = s_o + s_m - s^*_{om}. \quad (1)$$

The overlap depends both on the saliency effects evoked in either dimension alone (s_o and s_m) and on the proportion of saliency mechanisms that are shared between these dimensions,

$$s^*_{om} = \min\,(c_{om} \cdot s_o,\ c_{mo} \cdot s_m). \quad (2)$$

The factors c_{om} and c_{mo} represent the cross-dimensional activation rates; for example, $c_{om} = 0.2$ would indicate that the saliency effects in orientation overlap the saliency effects in motion by 20% (it should be

stressed that these factors resemble the functional cross-dimensional activation rates, with no specification at which processing level the overlap occurs).

Note that the cross-dimensional activation rates of saliency processes in the two dimensions are considered to be different. In principle, the saliency processes in one dimension could completely overlap those in another dimension but activate only a limited number of saliency processes there (this would then imply that maximal saliences in the two dimensions were represented by different amounts of cells).

Obviously, shared saliency mechanisms can produce deviations from the linear sum only to the degree to which saliency effects are activated in both dimensions; the deviation of saliency effects obtained with the combined stimulus would thus depend on the smaller of both components. This gives two solutions for the cross-dimensional activation rates:

for $c_{mo} \cdot s_m \leq c_{om} \cdot s_o$ follows

$$c_{mo} = (s_o + s_m - s_{mo})/s_m = 1 - (s_{om} - s_o)/s_m; \quad (3a)$$

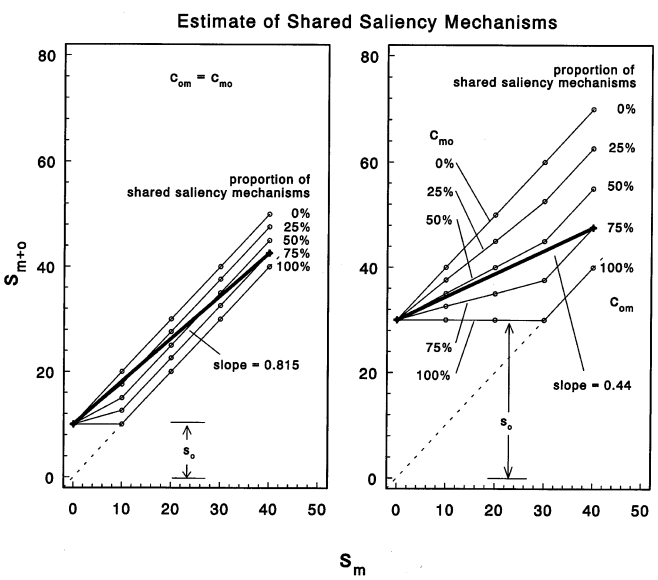

Fig. 14. Analysis of cross-dimensional activation rates from saliency variations in pure and combined stimulus conditions. For explanation, see Appendix. The salience of a target with combined saliency effects (s_{om}) is plotted against the salience of a target with only one such property (s_m). Saliency effects in the primary dimension (s_m) were varied systematically; saliency effects in the second dimension were constant (s_o) at two different levels (a, b). Curves plot different model conditions with similar cross-activation rates ($c_{om} = c_{mo}$). With increasing salience in the primary dimension, the amount of shared saliency mechanisms continuously increases until it is exhausted. Further increases will transfer with no reduction into the combined stimulus condition. Cross-dimension activation rates are represented in the initial slope of these curves, and in the distance of the second angle from equal salience (dashed line). Measurements with distant data points (thick line) may be highly erroneous ('slopes') unless high salience components are used for the added saliency effect in the second dimension.

for $c_{mo} \cdot s_m > c_{om} \cdot s_o$ follows

$$c_{om} = (s_o + s_m - s_{om})/s_o = 1 - (s_{om} - s_m)/s_o. \quad (3b)$$

How do these solutions relate to the scatter plots in Figs. 6, 9 and 11? In Fig. 6, for example, salience variations in motion plus constant orientation contrast were plotted against the salience variations in motion alone. That is, the graphs plot s_{om} as a function of s_m. As long as the constant saliency effect in the second dimension (orientation) is large and the cross-dimensional activation from orientation upon motion saliency mechanisms is not too small (that is, as long the condition in Eq. (3a) is valid), $1 - c_{mo}$ is given by the slopes of regression lines (differences in s_{om} divided by differences in s_m), so c_{mo} is their deviation from slope 1 (dashed line; cf. Fig. 14). For low s_m values, therefore, regression lines through the data points provide a direct estimate of the percentage of saliency mechanisms in orientation that are co-activated by saliency mechanisms in motion. When motion saliency effects increase, the condition of Eq. (3a) may not remain valid and Eq. (3b) could instead be used. In this case, c_{om} is given by the deviation of the salience of the combined stimulus from the sum of component saliences, normalized to the salience of the constant orientation contrast alone (s_o). That is, c_{om} is the amount of s_o by which data points are shifted toward the dashed line. With increasing salience in the motion domain, the two conditions in (3a) and (3b) are easily distinguished (see Fig. 14). For conditions described by Eq. (3a) data curves have the slope c_{mo}. When the pool of shared saliency processes is entirely activated (its size may vary with s_o; cf. Eq. (2)), all further increases in motion salience should also be visible in the combined stimulus. Thus, for conditions described by Eq. (3b) slopes are 1 and data points lie on curves parallel to $s_{om} = s_m$ (dashed line) but shifted in y by $(1 - c_{om})/s_o$. This bisected characteristic of data curves is visible in Fig. 11a.

Fig. 14 illustrates the properties of Eq. (1) for different parameter values. The magnitude of the added saliency component, s_o, has an important effect on the analysis of c_{mo}. If s_o is too small, the amount of shared processes s^*_{om} would quickly be exhausted and not be affected by further increases of salience in the variable dimension. Above $c_{mo} \cdot s_m = c_{om} \cdot s_o$ all curves have slopes of 1, independent of the amount of shared processes. Their displacement from the curve $s_{om} = s_m$ (dashed line) in relation to the added saliency effect s_o, i.e. the quotient s_{om}/s_o, gives the relative proportion of independent saliency mechanisms.

At first glance, this simple and mechanistic model is fairly well reflected in the data of Figs. 6, 9 and 11. Fig. 11a gives a nice illustration of the bisected curves expected from Eq. (2). The different cross-dimensional activation rates were not identical in this combination. The curves have flat slopes for low color contrast,

indicating almost 100% overlap, but are considerably displaced from the dashed line, for higher color contrast. For most other combinations, data points fitted well to a straight line indicating that the condition of ú was not yet reached.

The thick lines in Fig. 14 illustrate a problem associated with the limited availability of feature contrast variations in the experiments. Some data points in Figs. 6, 9 and 11 represent rather distinct measurements along the dimension in which saliency effects were varied, and it is not obvious to which of the two sections of the curves in Fig. 14 they belong. If three or more data points were taken (including the zero point) and these fitted well to a straight line, they probably belong to the section defined by condition (3a). In these cases, the obtained slopes reflect the relative amount of independent saliency processes in the varied dimension ($1 - c_{mo}$). If only two data points were obtained (as was generally the case for salience variations in orientation), they may belong to different sections of the curves and slopes might give incorrect estimates of c_{om}. Slopes should decrease in this case, when the added saliency effect (s_o) is increased (cf. Fig. 14a,b), as was for example observed in Fig. 6b,c. The error would be negligible for small cross-activation rates (all curve sections have slopes near 1); hence subjects with steep curves in Fig. 9 produced similarly steep curves when the added salience was increased. For medium to large cross-dimensional activation rates however, slope estimates should be made from the largest possible saliency effect; data then may still underestimate the true amount of shared saliency mechanisms.

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