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Adaptive modulation of color salience contingent upon global form coding and task relevance

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Abstract

Extensive research on local color aftereffects has revealed perceptual consequences of opponent color coding in the retina and the LGN, and of orientation-and/or spatial-frequency-contingent color coding in early cortical visual areas (e.g., V1 and V2). Here, we report a color aftereffect that depends crucially on global-form-contingent color processing. Brief viewing of colored items (passively viewed, ignored, or attended) reduced the salience of the previewed color in a subsequent task of color-based visual search. This color-salience aftereffect was relatively insensitive to variations (between color preview and search) in local image features, but was substantially affected by changes in global configuration (e.g. the presence or absence of perceptual unitization); the global-form dependence of the aftereffect was also modulated by task demands. The overall results suggest that (1) color salience is adaptively modulated (from fixation to fixation), drawing attention to a new color in visual-search contexts, and (2) these modulations seem to be mediated by global-form-and-color-selective neural processing in mid to late stages of the ventral visual pathway (e.g., V4 and IT), in combination with task-dependent feedback from higher cortical areas (e.g., prefrontal cortex).

Keywords: Adaptation; Aftereffect; Attention; Color; Face; Global form; Grouping; Salience; Visual search

1. Introduction

Color processing begins as cone signals are relayed to color opponent cells in the retina and in the LGN (parvo layers), which encode local cone contrasts (e.g., Derrington, Krauskopf, & Lennie, 1984; Rodieck, 1979). Color information is then multiplexed with coding of local geometric features in early cortical visual areas. For example, large proportions of V1, V2, and V4 cells show preferences for both color and local image features such as orientation and spatial frequency—a multiplexing of color and local features (e.g., Desimone & Schein, 1987; Friedman, Zhou, & von der Heydt, 2003; Kiper, Fenstemaker, & Gegenfurtner, 1997; Lennie, Krauskopf, & Sclar, 1990; Leventhal, Thompson, Liu, Zhou, & Ault, 1995; Ts'o & Gilbert, 1988). In late stages of the ventral form-processing pathway (see Mishkin, Ungerleider, & Macko, 1983; Ungerleider & Mishkin, 1982), such as in the inferotemporal cortex (IT), cells have large receptive fields, and are selective for global form as well as being broadly tuned to color—a multiplexing of color and global form (e.g., Komatsu & Ideura, 1993; Komatsu, Ideura, Kaji, & Yamane, 1992; Tanaka, 1996; Tanaka, Saito, Fukuda, & Mariya, 1991).

Behavioral consequences of the opponent characteristics of early local color coding have been investigated extensively using psychophysical techniques, typically measuring how color sensitivity and perceived hue (along various color-contrast axes) are affected by local color adaptation and masking (see Lennie & D'Zmura,

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1988; for a review). Perceptual manifestations of local multiplexing of color and orientation/spatial-frequency in early cortical visual areas have been demonstrated as color-contingent tilt aftereffects (e.g., Flanagan, Cavanagh, & Favreau, 1990; Held & Shattuck, 1971; Held, Shattuck-Hufnagel, & Moskowitz, 1982), orientation-/spatial-frequency-contingent color aftereffects (e.g., Day, Webster, Gillies, & Crassini, 1992; McCollough, 1965; Werner, 2003; see Humphrey & Goodale, 1998; for a review), and orientation/spatial-frequency tuning of chromatic adaptation (threshold elevation) effects (e.g., Bradley, Switkes, & de Valois, 1988; Vimal, 1997).

Here, we report evidence for a rapid, adaptive, and global-form-contingent modulation of color salience. In previous research on color adaptation, investigators primarily used single-item displays to examine the effects of previewing a color on the visibility and appearance of a subsequently presented color. However, in addition to providing information about object qualities (e.g., whether or not a fruit is ripe), color plays a crucial role in guiding attention (e.g., spotting a yellow banana). In particular, an odd-colored object presented among homogeneously colored objects attracts attention so long as the color difference is sufficient—color-singleton pop-out (e.g., Bravo & Nakayama, 1992; Egeth & Yantis, 1997; Nagy & Sanchez, 1990; Treisman & Gelade, 1980). We thus investigated how color preview affected the relative salience of colors in subsequent displays containing multiple colored items. Color-based visual search was used to assess color salience (a faster search time indicating greater salience of the target color relative to the distractor color).

Our prior results indicated that the salience of a briefly previewed color was subsequently reduced (Goolsby, Grabowecky, & Suzuki, 2003; Goolsby & Suzuki, 2001a). For example, a preview of a display containing red items facilitated the subsequent search for a green target presented among red distractors, presumably due to the reduced salience of the red distractors. We first replicated this basic phenomenon of the *color-salience aftereffect* (Experiment 1.1), and showed that the fast-adapting aftereffect (produced by a color preview as brief as 27 ms; Experiment 1.3) was broadly tuned to color (ruling out primary contributions from cognitive categorization of color; Experiment 1.2), and position tolerant (ruling out primary contributions from retinal and early cortical adaptation). We then conducted a series of experiments to elucidate the mechanisms underlying the color-salience aftereffect.

Feature specificity of visual aftereffects generally provides insights into the relevant neural substrates. For example, if the color-salience aftereffect is primarily due to general satiation by the previewed color, the aftereffect should increase with greater color energy in the preview display and be unaffected by variations in non-color image features. Alternatively, if the color-salience aftereffect is primarily mediated by low-level cortical cells with small receptive fields (e.g., cells in V1 and V2), the aftereffect should be sensitive to changes (between color preview and search) in local and spatial features such as position, size, and contour orientation of the display items. In contrast, if the color-salience aftereffect is primarily mediated late in the ventral visual pathway (perhaps in IT), where color-tuned cells show selectivity for global form but tolerance for variations in local and spatial features, the aftereffect should be tolerant of changes in local and spatial features but sensitive to changes in global configurations (see Suzuki, 2001, in press, for reviews on low-level and high-level pattern aftereffects).

The standard preview display had uniform-colored items that were essentially identical in shape and configuration to the items in the subsequent search display; the geometric features of the standard preview display were thus matched to those of the search display. Pattern specificity of the color-salience aftereffect was assessed by geometrically altering the standard preview display and measuring how the aftereffect was reduced. *If the color-salience aftereffect was substantially reduced when a certain geometric feature was changed between preview and search, the underlying neural substrate should be selective for that feature*. In a preliminary study, a large colored patch (much larger in area than all of the items in the standard preview display combined) produced no aftereffect (also see Experiment 2.1). This striking pattern sensitivity of the color-salience aftereffect motivated the current series of experiments in which the geometry of the color preview display was systematically varied to determine the critical pattern features to which the aftereffect is sensitive.

Sensitivity to local and spatial features, a signature of low-level processing, was tested by varying the eccentricity (Experiment 2.3), size (Experiment 2.4), local shape (Experiment 2.5), and number (Experiment 2.6 and 2.7) of the items in the preview display. Sensitivity to global configuration, a signature of high-level processing, was tested by manipulating perceptual grouping of the preview items. Strong grouping was induced, with minimal local changes, by connecting the items with lines to form a triangle (Experiment 2.1) and by inducing a face organization with added peripheral items (Experiment 2.2). Overall, the color-salience aftereffect was relatively tolerant of changes in local and spatial features of the preview items (Experiment 2.3–2.6). In contrast, the aftereffect disappeared when the preview items were perceptually unitized into a single object centered at the fixation point (Experiments 2.1–2.2, 2.8). Interestingly, this sensitivity to perceptual unitization was adaptively modified according to the demands of the task (Experiments 2.9 and 2.10). The overall geometric selectivity of the color-salience aftereffect suggested that this color aftereffect depended on the global stimulus geometry and the specific task demands that made preview displays search relevant.

A series of control experiments were conducted to verify that the color-salience aftereffect was due to an automatic reduction in salience of the previewed color, indicative of neural adaptation, and it was not due to observers' strategic responses. We confirmed that the aftereffect was relatively independent of the degree to which the preview color predicted the target color in the subsequent search (Experiment 3.1), and also of whether or not the observer ignored (Experiment 3.2), actively attended to, or responded to (Experiment 3.3A and B) the preview displays. The color-salience aftereffect also dissociated from the apparently related phenomenon of priming effects on color-singleton search (e.g., Goolsby & Suzuki, 2001b; Maljkovic & Nakayama, 1994, 2000; Suzuki & Goolsby, 2003); whereas the previously attended color became *more* salient in the priming effect (Experiment 3.4), the previewed color (whether or not it was attended) became *less* salient in the color-salience aftereffect.

In summary, we demonstrated that brief exposure to uniform-colored items substantially reduced the salience of the items of the previewed color in subsequent color-based visual search. Unlike classic aftereffects on color visibility and appearance, the color-salience aftereffect was relatively insensitive to variations in local and spatial features, but it was acutely sensitive to changes in global configuration and task relevance. The overall results suggest that (1) color salience is constantly adjusted (from fixation to fixation), drawing attention to a new color, and (2) the underlying mechanisms appear to involve global-form-and-color-selective neural processing in mid to late stages of the ventral visual pathway (e.g., V4 and IT), in combination with task-dependent feedback from higher cortical areas (e.g., the prefrontal cortex). We will describe a specific form of interaction among V4, IT, and the prefrontal cortex that can account for our behavioral results.

2. General methods

All experiments followed the same basic format. *Color-singleton-search displays* (an odd-colored target presented among homogeneously colored distractors) were randomly or pseudo-randomly intermixed with *color-preview displays* consisting of uniform-colored items. When a display contained a color singleton, observers responded to the shape of the singleton target. When a display contained uniform-colored items (no singleton), observers passively viewed the display (except when attention during preview was manipulated in Experiments 3.2–3.4) while maintaining central fixation. *Standard* preview displays were identical to the singleton-search displays in geometric properties except for minor changes in item shape in some cases (consisting of circles or unchipped diamonds instead of chipped diamonds). Standard preview displays provided a baseline against which the effects of geometrically modified preview displays were evaluated.

2.1. Observers

All observers were undergraduate students at Northwestern University who were naïve to the purpose of the experiments and who gave informed consent to participate and received course credit. All had normal or corrected-to-normal visual acuity. Self-identified color-anomalous observers were excluded. The number of observers tested in the individual experiments were 11 (Experiment 1.1), 21 (Experiment 1.2), 22 (Experiment 1.3), 23 (Experiment 2.1), 20 (Experiment 2.2), 31 (Experiment 2.3), 20 (Experiment 2.4), 20 (Experiment 2.5), 20 (Experiment 2.6), 17 (Experiment 2.7), 23 (Experiment 2.8), 18 (Experiment 2.9), 18 (Experiment 2.10), 28 (Experiment 3.1), 15 (Experiment 3.2), 29 (Experiment 3.3A), 23 (Experiment 3.3B) and 15 (Experiment 3.4). [1]

2.2. Apparatus

Stimuli were displayed on a 17″ or 21″ color monitor (75 Hz) and all experiments were controlled with a Macintosh PowerPC 8600 (300 MHz) using Vision Shell software (micro ML, Inc.). Luminance (cd/m^2) and color (CIE) were measured with a Minolta Chroma Meter CS-100.

2.3. Stimuli

The singleton-search displays and the standard preview displays consisted of three diamond shapes (some standard preview displays had circles or unchipped diamonds) arranged on an invisible approximate iso-acuity ellipse (Kröse & Julesz, 1989; Rovamo & Virsu, 1979) centered around the fixation marker (Fig. 1A). The horizontal axis of the ellipse subtended 10.1° of visual angle and the vertical axis subtended 8.2°. The diamond shapes were presented at any of the twelve possible locations (at 0°, 30°, 60°, 90°, 120°,..., 330° positions relative to the vertical meridian) with the constraint that the three diamonds were approximately equidistant from each other (i.e., separated from each other by 120° rotation or four location steps). Each diamond subtended 1.3° by 1.3° visual angle and had its left or right

[1] Due to variations in the size of the participant pool across academic terms, the number of participating observers varied across experiments.

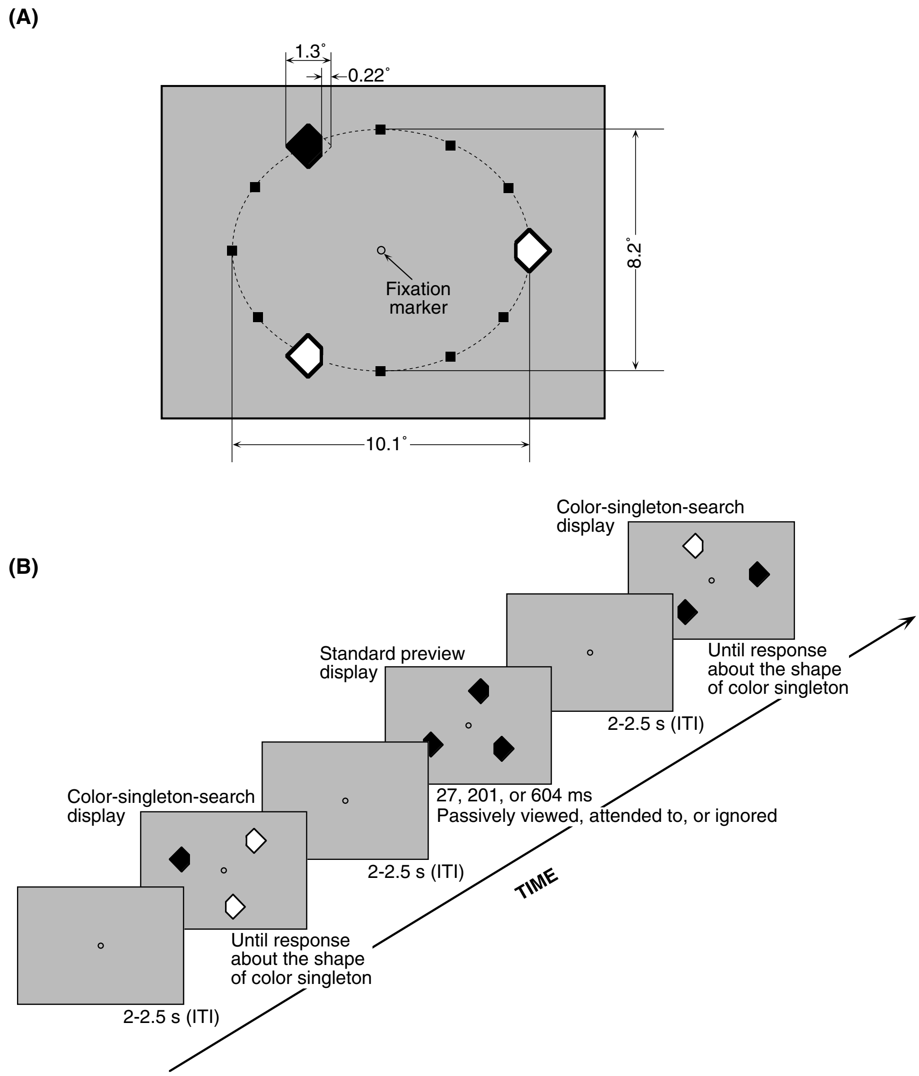

Fig. 1. The stimuli and procedure. (A) The 12 possible item locations are shown with an example of a color-singleton target (black item) and two distractors (white items). Item locations were randomized, but the three items (for the color-singleton-search displays and standard preview displays) were always approximately equidistant from one another (four location steps or 120° rotation apart). The dashed iso-acuity ellipse and the placeholder squares were not presented in the actual displays. (B) A trial sequence is shown for a color-singleton-search display followed by a uniform-colored standard preview display followed by another color-singleton-search display. The interval between successive displays (inter-trial interval, or ITI) was randomly varied between 2 and 2.5 s. The colored stimuli were actually presented against a black background; in the figure, black and white indicate different colors.

side "chipped" (i.e., either the left or right corner of each diamond was missing) with the depth of chip subtending 0.22°. The side of the chip for each diamond was randomly determined for each display.

We used three-item search displays to maximize sensitivity for measuring the color-salience aftereffect. When the observer has to focus attention on the singleton target (to respond about its shape) and the color of the target is unpredictable from trial to trial as in the current study, color-singleton search becomes easier as the number of distractors is increased. This set-size effect occurs presumably because the higher density of distractors causes stronger distractor grouping and an increased local color gradient around the singleton target (e.g., Bravo & Nakayama, 1992), and/or because the larger number of distractors (independently of density) generates a stronger total long-distance color contrast between the singleton target and the distractors (e.g., Santhi & Reeves, 2004). Regardless of the exact mechanism of the set-size effect, because color-singleton search is most difficult with the minimal display size (one target and two distractors), we reasoned that search performance on three-item displays would be most sensitive to subtle changes in color salience from aftereffects. A result consistent with this reasoning was obtained in Experiment 2.9.

The color-singleton target was either green (presented among red distractors) or red (presented among green distractors). The location and color of the color-singleton diamond were determined randomly for each display. The red (CIE[0.629, 0.346]) and the green (CIE[0.299, 0.598]) used were set to be equiluminant for each observer, as determined by heterochromatic flicker photometry (e.g., Kaiser, 1988) at a frequency of 20 Hz. The red had a mean fixed luminance of 3.4 cd/m^2 (with minor variations due to normal monitor fluctuations over time) and the green had an adjusted luminance ranging from 1.9 to 4.4 cd/m^2 for individual observers. The same green and red colors were used in the preview displays except in Experiments 1.1 (where some of the preview displays were achromatic) and 1.2 (where the colors of the preview displays were systematically varied). The stimuli were presented against a dark background (all color guns on the monitor turned off, 0.01 cd/m^2) in a dimly lit room.

The fixation marker was presented at the center of the screen; it was a small achromatic open circle (18.3 cd/m^2, CIE[0.262, 0.282], diameter = 0.26°) drawn with a one-pixel-wide line (each pixel subtending 0.043°). The fixation marker remained on throughout each trial. Observers were seated in a hard-backed chair at 50 cm from the screen. The experimenter remained with the observer throughout each experiment to monitor eye blinks and head movements; no excessive blinking or head movements were detected. The observer's head was not fixed using a chin rest, but the experimenter measured and adjusted (if necessary) the observer's viewing distance at the start of each block of 150 trials.

2.4. Procedure

Each stimulus display (i.e., a color-singleton-search display or color-preview display) was immediately preceded by a blank fixation screen that lasted for a variable interval of 2–2.5 s (randomly selected from a uniform distribution to reduce any effects of temporal expectation) (Fig. 1B). Observers were instructed to fixate the central marker prior to the presentation of each stimulus display.

When a display contained a color-singleton item, observers responded to the side of chip of the target diamond with a key press (a paradigm initially developed by Bravo & Nakayama, 1992). Observers pressed the 'z' key with the left index finger to report a left-side chip and pressed the '/' key with the right index finger to report a right-side chip. The location of the response keys relative to the observer was thus compatible with the side of chip reported. As the side-of-chip discrimination required a high acuity judgment, eye movements to the target were allowed (though not encouraged) as in our prior studies (Goolsby & Suzuki, 2001b; Suzuki & Goolsby, 2003). The search display remained on until the observer made a response. Observers were instructed to respond as quickly as possible while preserving accuracy at or above 95%. The response time and accuracy were recorded from each color-singleton search trial. No feedback was given on responses because it might potentially interfere with sequential effects and/or with cueing manipulations.

When a display contained uniform-colored items (or contained three items of each color in Experiment 3.4), observers passively viewed (Experiments 1.1–1.3, 2.1–2.10, 3.1–3.2 and 3.3B), ignored, or attended to (Experiments 3.2–3.4) the color preview display while maintaining central fixation. Color-preview displays were presented for 604 ms in most experiments (except when the preview duration was varied in Experiment 1.3, and when observers performed attention-related secondary tasks on preview displays in Experiments 3.2–3.4). The standard preview duration of 604 ms was chosen to be comparable to the mean RTs for the color-singleton search (based on pilot data).

Color preview displays were randomly or pseudo-randomly intermixed among the color-singleton-search displays. In Experiment 3.3B, the cued and uncued standard preview displays and search displays were randomly intermixed with equal probability. In Experiments 2.3 and 2.5, where two types of preview displays were intermixed (e.g., the standard and a geometrically altered version), the proportion of the RT-generating search displays was 50% with each of the two types of preview displays occurring with 25% probability. Because the preview displays were randomly intermixed among the search displays, in some cases, two or more preview displays occurred in a sequence. To avoid potential confounds from repeated preview displays, a search RT was entered in the analysis only when a search display was immediately preceded by a preview display, which was in turn immediately preceded by a search display.

In the remaining experiments where two or more types of preview displays were intermixed, the sequence was made more efficient by avoiding repetitions of preview displays (ensuring a sufficient number of search RTs for each type of preview display). Following each search display, the probability of another search display was reduced to 30% while the probability of a preview display was increased to 70%. Following a preview display, the probability of a search display was increased to 80% (20% for a preview display). When two preview displays occurred in a row, the following display was forced to be a search display. This way, unproductive repetitions of preview displays were reduced while keeping the overall probabilities (when summed over the 2^3 possible histories of three consecutive displays) approximately equal for search (50.3%) and preview (49.7%) displays.

All observers were given one block of 15 practice trials (counting both search and preview displays as trials) after the instructions, followed by the experimental trials that typically consisted of three blocks of 150 trials. Short breaks were given between blocks. Observers were tested individually.

2.5. Data analyses

We classified each color-singleton-search RT on the basis of the immediately preceding preview display. For example, suppose the current search trial had a red target among green distractors. If the immediately preceding preview display had all red (target-colored) items, the search RT would be classified as a target-color-preview RT. Alternatively, if the preview display had all green (distractor-colored) items, the search RT would be classified as a distractor-color-preview RT. In a color-salience aftereffect, the salience of the previewed color was reduced in the subsequent color-singleton search, making it more difficult to find the target when the target color was previewed, and making it easier to find the target when the distractor color was previewed (see Experiment 1.1). *The color-salience aftereffect was thus generally measured in terms of the degree to which the distractor-color-preview RT was faster than the target-color-preview RT*. Outlier-resistant median RTs were used to obtain the central tendencies of RTs under different preview conditions within each observer. Means of these median RTs from individual observers were then used for statistical analyses.

Note that we examined first-order color-salience aftereffects from immediately preceding color-preview displays. Because the preview color was randomly determined in each preview display, potential higher-order aftereffects from specific prior sequences of preview colors were averaged out and treated as random variability in the statistical analyses. We did not investigate higher-order sequential effects because we wished to keep each experiment relatively short to avoid training-dependent effects. We limited each experiment to an hour, restricting the total number of preview displays to about 225 (intermixed with 225 search displays). Consequently, we did not have enough repetitions of each specific sequence of preview displays to analyze higher-order sequential effects.

RTs were analyzed for correct trials only (in which the observer correctly indicated the side of chip of the color-singleton diamond). Across the 18 experiments reported here, a total of 374 observers were tested. The distribution of their overall percent correct on color-singleton search is shown in Fig. 2. Two observers (indicated by x's) had unusually low accuracy, and were excluded from the analyses (one from Experiment 2.4 and the other from Experiment 3.3B). The overall accuracy was high ($M = 97.74\%$, SD = 1.86% without the two outliers). Except in Experiment 1.2, the magnitude of the color-salience aftereffect was measured as:

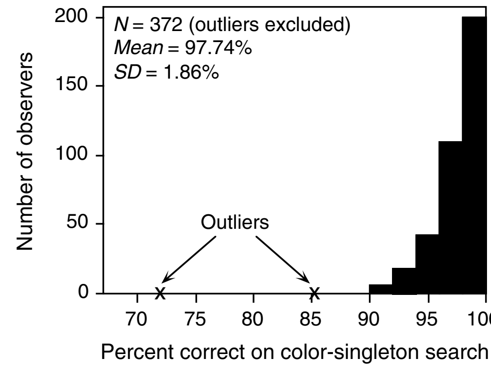

Fig. 2. Distribution of percent correct on color-singleton search for the 374 observers tested across 18 experiments. The x's indicate the two outlier observers who were excluded from the analyses due to their poor performance.

$$\text{Color-salience aftereffect} = [\text{Target-color-preview RT}] - [\text{Distractor-color-preview RT}].$$

Of the 49 measurements of color-salience aftereffects for manipulations of the preview displays, there were only four cases in which the accuracy was statistically different between the target-color-preview and distractor-color-preview conditions. In one of the four cases (for the standard preview in Experiment 1.3), the accuracy and RT varied in the same direction (a potential speed–accuracy trade-off). However, in the remaining three cases (standard preview in Experiment 2.2, standard preview in Experiment 2.8, and size-change preview in Experiment 3.4), the accuracy and RT varied in opposite directions. We thus found little evidence that the RT-based measures of color-salience aftereffects were confounded by speed–accuracy trade-offs. This allowed us to focus on RT analyses, revealing how the speed of selecting the color-singleton target was influenced by modulations of color salience from the preceding color-preview displays.

3. Experiments 1.1–1.3

3.1. Basic properties of the color-salience aftereffect

We first demonstrated a standard color-salience aftereffect (Experiment 1.1), and then examined its chromatic tuning (Experiment 1.2) and its dependence on preview duration and position (Experiment 1.3).

3.2. Experiment 1.1. Standard color-salience aftereffect

In demonstrating the *standard* color-salience aftereffect, the geometric properties of the preview and search displays were matched; both contained three chipped diamonds in the same general configuration (Fig. 1B), though the exact locations of the diamonds were randomized. If previewing colored items temporarily reduced the salience of that color, previewing the target color should slow target selection in the subsequent color-singleton search by making the target less salient, whereas previewing the distractor color should speed target selection by reducing salience of the distractors and thereby making the target more salient. This slowing (from target-color preview) and speeding (from distractor-color preview) was measured relative to search RTs following achromatic preview displays.

3.2.1. Stimuli

The color of the preview diamonds was either uniformly red, green, or achromatic (CIE[0.262, 0.282] and approximately equiluminant with the red and green as measured by the photometer).

3.2.2. Results and discussion

The RT for color-singleton search was systematically affected by the color of the immediately preceding preview display. The mean RT was significantly slowed (by 66 ms) when target-colored diamonds were previewed ($t(10) = 4.938$, $p < 0.001$), and significantly speeded (by 44 ms) when distractor-colored diamonds were previewed ($t(10) = 3.308$, $p < 0.01$), compared to when achromatic diamonds were previewed (see Fig. 3). These results suggest that passive viewing of uniform-colored items reduced the salience of the previewed color when it appeared in the subsequent color-based search. As indicated in Fig. 3, we will use the difference between the slowed RT following target-color preview and the speeded RT following distractor-color preview as the overall measure of this color-salience aftereffect (except in Experiment 1.2). In the following two experiments, we examined chromatic, temporal, and spatial properties of the color-salience aftereffect.

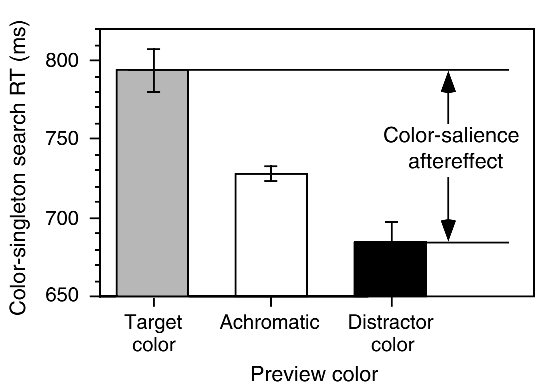

Fig. 3. *Experiment 1.1*: Color-singleton-search RT following target-colored, achromatic, or distractor-colored preview displays (standard preview displays with chipped diamonds). The difference between the slower RT following the target-color preview and the faster RT following the distractor-color preview was used as the general measure of the color-salience aftereffect (except in Experiment 1.2). The error bars represent ±1SE. In this and in Figs. 7–21, the variance due to differences in the overall RT among the observers was removed before computing SE.

3.3. Experiment 1.2. Chromatic tuning

To gain insights into the color processing involved in the color-salience aftereffect, we examined its chromatic tuning. We systematically varied the color of the preview display along the green-red axis. If the color-salience aftereffect was due to cognitive categorization of the previewed color (as green or red), the aftereffect might change stepwise as the appearance of the preview color shifted from greenish to reddish, or might disappear as soon as the preview color was categorized as distinct from green and red (e.g., yellow, orange). Alternatively, color-selective cortical cells tend to be broadly tuned to color with no evidence of stepwise categorical responses or preferential responses to "primary" colors such as green and red (e.g., Friedman et al., 2003; Komatsu et al., 1992; Yoshioka, Dow, & Vautin, 1996). Thus, if the color-salience aftereffect was mediated by adaptation of cortical color-processing mechanisms,[2] the aftereffect should be broadly tuned to color and should gradually change as the preview color was gradually varied from green to red.

3.3.1. Stimuli

All preview displays were standard as in Experiment 1.1, consisting of three chipped diamonds just like the search displays. The color of the preview diamonds was varied between green and red by adjusting the relative strength of the red and green phosphors (in terms of their luminance proportions). The preview color was varied across "green" (R = 0%, G = 100%; CIE[0.299, 0.598]), "lime" (R = 20%, G = 80%; CIE[0.397, 0.521]), "yellow" (R = 40%, G = 60%; CIE[0.469, 0.465]), "light orange" (R = 60%, G = 40%; CIE[0.529, 0.424]), "orange" (R = 80%, G = 20%; CIE[0.578, 0.384], and "red" (R = 100%, G = 0%; CIE[0.629, 0.346]). These color coordinates are plotted in the lower panel of Fig. 4. The luminances of these preview colors were approximately equated based on photometer readings. The green and red were the same as those used in the search displays. Each preview color appeared with equal probability.

[2] Because the color-salience aftereffect is relatively insensitive to changes in position and local-features between the preview and search displays (Experiments 1.3, 2.1–2.4), adaptation of cells in the retina and LGN are unlikely to contribute substantially.

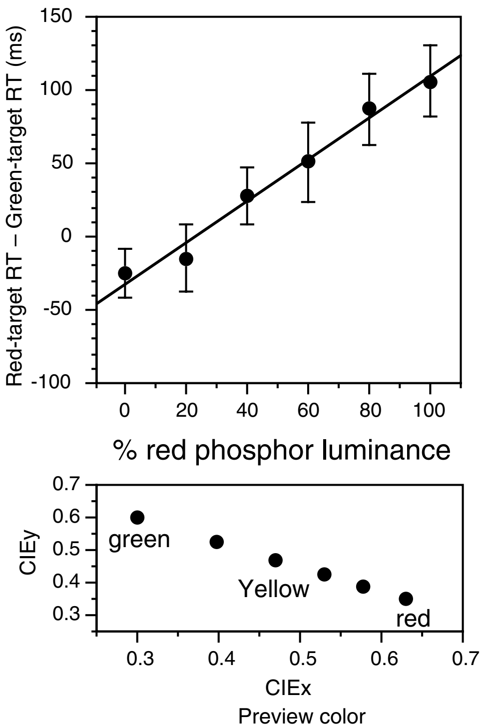

Fig. 4. *Experiment 1.2*: The color tuning of the color-salience aftereffect (produced by the standard preview displays with chipped diamonds). The upper panel shows the color-salience aftereffect (here measured as the red-target RT minus the green-target RT) produced by preview colors that were various mixtures of the red and green phosphors, ranging from 0% red (100% green) to 100% red (0% green) based on the luminance ratio. The line is the linear fit. The fact that the function is shifted up overall (in the positive direction) indicates that the green-target RT was on average faster than the red-target RT. The lower panel shows the CIE coordinates of the corresponding colors. The error bars represent ±1SE.

3.3.2. Results and discussion

The color-salience aftereffect was broadly tuned to color. The red-target RT minus the green-target RT is plotted in Fig. 4 (top panel) as a function of the percentage of the red phosphor luminance in the preceding preview display. As the red component was increased and the apparent color changed from green, through lime, yellow, light orange, and orange, to red in the preview display, the red target RT slowed linearly relative to the green target RT. This indicates that the relative salience of red in the search display gradually reduced as the red component was increased in the preview color. The good linear fit ($F(1, 100) = 52.418$, $p < 0.001$) with the absence of significant quadratic and higher-order trends (Fs < 0.5) indicated that the color-salience aftereffect was broadly tuned to color (a sigmoidal or a step function would have suggested that the relevant color representation was categorical).

When observers were asked to recall the number of intermediate colors they saw during the experiment, they reported one (5 of 21 observers), two (14 of 21), or four (2 of 21) colors in addition to the standard red and green. Common color names given for these intermediate colors were "orange" (19 of 21), "yellow" (9 of 21), and "yellow–green" (7 of 21). A separate group of observers ($N = 17$) assigned color names to the intermediate colors after viewing them one at a time outside the context of the experiment. These observers identified the 80% red color as either "orange" (12 of 17), "orange–red" (4 of 17), or "reddish" (1 of 17), and they identified the 80% green color as either "green" (16 of 17) or "lime green" (1 of 17). Importantly, neither of the 60%/40% colors were labeled red or green by any observer. Observers labeled the 60% red color as either "orange" (16 of 17) or "maize" (1 of 17), and they labeled the 60% green color as "yellow" (10 of 17), "orange" (4 of 17), "tan" (1 of 17), "golden" (1 of 17), or "yellowish-green" (1 of 17). Two conclusions are warranted from the color naming data: (1) observers had difficulty in discriminating the intermediate colors, and (2) with the exception of the 80% green condition, observers tended to categorize the intermediate colors as being distinct from red and green. The fact that the color-salience aftereffect was broadly tuned to these intermediate colors is inconsistent with its mediation by cognitive categorization of the preview color as red or green, and is consistent with its mediation by adaptation of broadly color-tuned cortical mechanisms.

The result is also consistent with a previous study suggesting that color-singleton search (with homogeneously colored distractors) operates on a color representation in which basic colors (determined by color naming data) do not receive any special status (Smallman & Boynton, 1990); they found that the ease of color-singleton search depended on the separation of the target and distractor colors in color space regardless of whether or not those colors were categorized as basic colors.

3.4. Experiment 1.3. Dependence on preview duration and position

Research on pattern aftereffects suggests that brief stimuli (less than about 150 ms) selectively adapt high-level global-form processing (perhaps mediated by IT) with little influence on low-level processing of local orientation (perhaps mediated by V1 and V2) (see Suzuki, 2001, in press, for reviews). A reliable color-salience aftereffect from a preview of less than 150 ms would thus be consistent with high-level mediation of the aftereffect. We included preview durations of 27 ms and 201 ms as well as the standard 604 ms to assess the shape of the function relating the color-salience aftereffect to preview duration.

If a 27 ms preview turned out to be sufficient to reliably produce the color-salience aftereffect, we could also examine the position dependence of the aftereffect.

Because a saccadic eye movement cannot be initiated within 27 ms (e.g., Fischer & Breitmeyer, 1987), the preview items would be projected only to their specific retinal positions. Note that the standard preview displays and the search displays both consisted of an array of three evenly spaced items with the array being randomly rotated across the 12 positions around the iso-acuity ellipse (Fig. 1A). The preview and search items were therefore either overlapping, separated by one position step = 2.4° (with SD = 0.16° due to the elliptical arrangement), or separated by two position steps = 4.6° (with SD = 0.17°).

Receptive field sizes of cells selective for form and color in the ventral visual pathway increase in higher visual areas, from averaging only 0.05° (central radius of the parvocellularly-projecting ganglion cells) in the retina, 0.3°–1° in V1, ~3° in V2, 1.5°–4° in V4 (parafovea at retinal eccentricities of 2°–5° from the fovea), to encompassing large portions of the visual field (a mean of 30° but up to 100°) in IT (e.g., Croner & Kaplan, 1995; Desimone & Gross, 1979; Desimone & Schein, 1987; Dow, Snyder, Vautin, & Bauer, 1981; Foster, Gaska, Nagler, & Polen, 1985; Gattass, Sousa, & Gross, 1988; Gross, Rocha-Miranda, & Bender, 1972; Ito, Tamura, Fujita, & Tanaka, 1995). Thus, if the color-salience aftereffect was mediated by adaptation in the retina or V1, the aftereffect should be highly position specific on the order of a fraction of a degree to a degree. In other words, if the retina or V1 was the primary site of the color-salience aftereffect, the aftereffect should be absent when the preview and search items were separated by substantially greater than a degree.

3.4.1. Stimuli

All preview displays were standard (with chipped diamonds). The preview color was either green or red as in all of the following experiments. The preview duration was varied randomly among 27 ms, 201 ms, and 604 ms.

3.4.2. Results and discussion

To examine how the color-salience aftereffect depended on preview duration, the magnitude of the color-salience aftereffect (target-color-preview RT—distractor-color-preview RT) was plotted as a function of the preview duration in Fig. 5. Although the aftereffect diminished with decreasing preview duration ($F(1,42) = 4.964$, $p < 0.05$ for the linear component), the aftereffect was robust following only 27 ms of color preview ($t(21) = 6.127$, $p < 0.0001$).

To examine the position specificity of the color-salience aftereffect, the magnitude of the aftereffect was examined as a function of the distance between the preview and search items (see Fig. 6). To increase the statistical power to detect any position dependence, we first pooled the results from six of the reported experiments

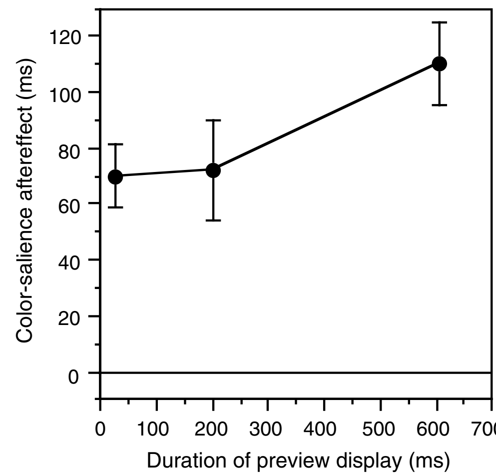

Fig. 5. *Experiment 1.3*: The color-salience aftereffect as a function of the duration of the standard preview displays (with chipped diamonds). The aftereffect is shown as RT differences (target-color-preview RT—distractor-color-preview RT) to clearly show its dependence on duration. The error bars represent ±1SE.

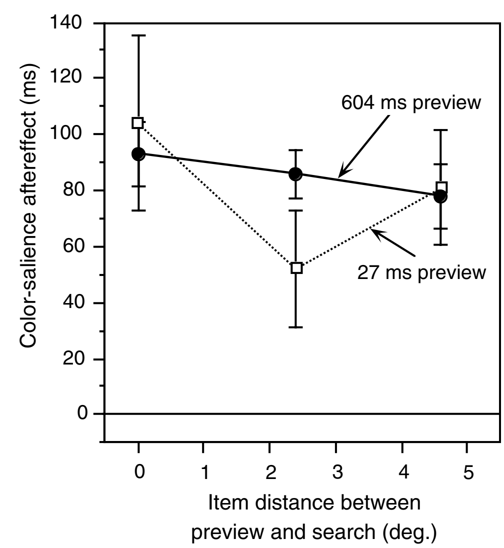

Fig. 6. *Experiment 1.3*: The color-salience aftereffect as a function of the distance between the preview and search items (0°—overlapping, 2.4°—one location-step apart, or 4.6°—two location-steps apart). The aftereffect is shown as RT differences (as in Fig. 5) to clearly show its dependence on distance. Solid circles: data pooled from six experiments (125 observers) in which the standard preview displays (with chipped or unchipped diamonds) were presented for 604 ms. Open squares: data from Experiment 1.3 in which the standard preview displays (with chipped diamonds) were presented for 27 ms. The error bars represent ±1SE.

(Experiments 2.3–2.8, totaling 125 observers [3]) in which the preview displays were standard (lasting 604 ms and consisting of three chipped diamonds or three

[3] Four observers from Experiment 2.5 were excluded because of empty cells for the two-position step condition.

unchipped diamonds, which were all green or all red). The magnitude of the aftereffect appears to have diminished with increasing distance between preview and search items (the solid curve in Fig. 6) though this trend was not significant ($F(1,248) = 1.090$, n.s. for the linear component). Notably, the aftereffect was reliable ($t(124) = 6.700$, $p < 0.0001$) even when the preview and search items were 4.6° apart.

This position tolerance, however, might be an overestimate because it is possible that the observer might have made a couple of saccades during the 604 ms preview period, resulting in adaptation of additional retinal positions. We thus also examined the effect of distance for 27 ms preview during which a saccade could not have occurred. The magnitude of the aftereffect again appears to have diminished with increasing distance (the dashed curve in Fig. 6) though this trend was not significant ($F(1,42) = 0.364$, n.s. for the linear component). Importantly, the color-salience aftereffect following 27 ms preview was reliable ($t(21) = 3.995$, $p < 0.001$) even when the preview and search items were separated by 4.6°.

The fact that the color-salience aftereffect was produced by a brief (27 ms) color preview and that it was preserved across substantial position shifts (4.6°) suggested that the color-salience aftereffect was unlikely to be explained solely in terms of retinal, subcortical, or early cortical adaptation (in V1 and V2). In the next series of experiments (Experiments 2.1–2.10), we further investigated the mechanisms mediating the color-salience aftereffect by examining (1) its specificity for local and spatial features—a signature of low-level visual processing (Experiments 2.3–2.6), (2) its specificity for global configurations—a signature of high-level visual processing (Experiments 2.1–2.2, 2.8), and (3) its dependence on task contexts—a potential signature of prefrontal or other higher-level feedback (Experiments 2.9 and 2.10).

4. Experiments 2.1–2.10

4.1. How does the color-salience aftereffect depend on local and spatial features, global configuration, and task context?

In high-level visual areas along the ventral form-processing pathway (such as IT), neurons with large receptive fields respond with broad color tuning and concurrent selectivity for specific form "trigger" features (e.g., Fujita, Tanaka, Ito, & Cheng, 1992; Komatsu & Ideura, 1993; Tanaka, 1996; Tsunoda, Yamane, Nishizaki, & Tanifuji, 2001). Though a variety of trigger features have been discovered for different IT cells, a systematic understanding of the overall organization of shape coding in IT has yet to emerge (see Brincat & Connor, 2004; Kayaert, Op de Beeck, Biederman, & Vogels, 2004; Kayaert, Biederman, & Vogels, 2003 and Tsunoda et al., 2001 for potential coding principles, and Suzuki, in press for a review of relevant behavioral and physiological results). Nevertheless, if the color-salience aftereffect involved adaptation of this type of color-tuned and global-form selective cells, the aftereffect might be reduced or eliminated by geometrically altering the color preview displays. Specifically, if the color-salience aftereffect was eliminated by *adding* colored regions to the standard preview displays, such a result would support the involvement of global-form-selective color coding. If the color-salience aftereffect was mediated by low-level cells with small receptive fields that locally responded to color contrasts, the aftereffect should either increase or remain unchanged when colored regions (and contours) were added to the preview displays.

In hypothesizing global-form selectivity of the color-salience aftereffect, we reasoned that the mechanisms underlying the color-salience aftereffect might be closely associated with the mechanisms of visual search. Reducing the salience of already encountered colors would boost the relative salience of new colors to be examined. Such an adaptive modulation of color salience, of which the color-salience aftereffect is an example, should increase the efficiency of color-based visual search by adaptively reducing the relative salience of the prevalent distractors. A typical geometric context in which people engage in visual search is *the presence of multiple discrete objects*. For example, one might search for a key on a cluttered desk, but search would be unnecessary if the key was the only object on the desk. We hypothesized that removal of this search-relevant geometric configuration (the presence of multiple discrete objects) from the preview displays might disrupt the color-salience aftereffect. In the following two experiments (Experiment 2.1–2.2), we formed each preview display into a single global object. The global-form selectivity of the color-salience aftereffect was then assessed by measuring decrements in the magnitude of the aftereffect from the geometrically altered color preview displays relative to the baseline aftereffect from the intermixed standard preview displays.

4.2. Experiment 2.1. A large patch and a global triangle as preview configurations

The preview displays contained either a large colored patch (11 times as large in area as the sum of the three diamonds in the standard preview display) or an outlined triangle formed by connecting the three items with thick lines. If the color-salience aftereffect was a general color habituation phenomenon, the large colored patch should have produced a strong aftereffect. Furthermore, because the outline triangle was generated by adding colored regions and contours to the standard preview displays, if the color-salience aftereffect was due to the sum of local color adaptation, it should have increased.

4.2.1. Stimuli

The standard preview displays were intermixed with the patch preview displays (consisting of a 6.3° by 5.3° flat ellipse centered at the fixation point) and the triangle preview displays (the three items in the standard preview displays connected by 0.73° thick lines to form a global triangle). The shape of the three items in the standard preview displays was changed from chipped diamonds to circles (equated in area) to make the standard items more similar in shape to the elliptical patch and to make the outline triangle appear smooth.

4.2.2. Results and discussion

Contrary to the predictions from color habituation and local color adaptation, and consistent with mediation by global-form-selective color coding, the color-salience aftereffect disappeared for the patch preview and triangle preview displays despite the fact that both had larger colored areas than the standard preview displays (Fig. 7); the magnitudes of the aftereffect were 46 ms ($t(22) = 2.678$, $p < 0.02$) for the standard preview, −21 ms ($t(22) = -1.298$, n.s.) for the patch preview, and 12 ms ($t(22) = 1.030$, n.s.) for the triangle preview. The striking absence of the color-salience aftereffect from the patch and the triangle preview displays was replicated with additional observers ($N = 26$ and $N = 23$, respectively). In particular, the triangle preview displays did not produce a reliable color-salience aftereffect even when the items were connected with a thin (1-pixel wide) line, leaving the individual circles clearly visible. We also note that the result for the standard preview condition in this experiment (and in Experiments 2.5, 2.7–2.8, and 2.10) demonstrated that the color-salience aftereffect was reliable when the individual items in the standard preview displays were locally altered (e.g., from chipped diamonds to circles).

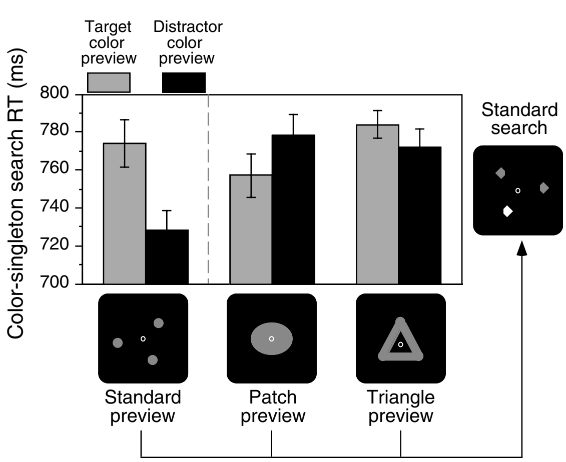

Fig. 7. *Experiment 2.1*: The color-salience aftereffect produced by the standard (with circles), patch, and triangle preview displays. For each preview type, the target-color-preview RT is shown on the left (gray bar) and the distractor-color-preview RT is shown on the right (black bar); the RT data in all subsequent figures are presented using the same convention (except Fig. 21). The error bars represent ±1SE. Examples of the preview displays are illustrated on the bottom, and an example of the singleton-search display is illustrated on the right; the stimulus illustrations are not to scale in this and all subsequent figures. The standard and triangle preview displays, and the search displays were randomly rotated for each presentation.

4.3. Experiment 2.2. Adding a face configuration to preview displays

Because a face configuration is a strong grouping factor (e.g., Mermelstein, Banks, & Prinzmetal, 1979; Suzuki & Cavanagh, 1995), it provides a way to perceptually unitize the three standard preview items while keeping the individual items discrete and intact. By adding three peripheral arcs as eyebrows and a mouth, we transformed the three standard-preview circles into a smiling face. In this experiment (and in Experiment 2.9), the preview and search items were always presented in upright or inverted triangular arrays (appearing as inverted or upright faces when the face organization was imposed).

4.3.1. Stimuli

The face preview displays (upright face or inverted face) were intermixed with the standard preview displays (inverted-triangle array or upright-triangle array). In the face preview displays, the added arcs were drawn with 0.13° thick curves; each "eyebrow" arc was 4.6° wide and 1.8° tall, presented 3.2° (center-to-center) eccentric to each "eye," and the "mouth" arc was 15.3° wide and 4.5° tall, presented 4.8° (center-to-center) eccentric to the "nose" (see Fig. 8 for illustrations). The items in the standard preview displays were circles (rather than diamonds) as in Experiment 2.1.

4.3.2. Results and discussion

The color-salience aftereffect disappeared when the face configuration was imposed on the preview displays (Fig. 8); the magnitudes of the aftereffect were 75 ms ($t(19) = 4.418$, $p < 0.0005$) and 42 ms ($t(19) = 2.283$, $p < 0.04$) for the inverted and upright triangular arrays of the standard preview, and 5 ms ($t(19) = 0.314$, n.s.) and 3 ms ($t(19) = 0.173$, n.s.) for the upright and inverted face preview. Note that the face configuration eliminated the color-salience aftereffect despite the fact that the preview and search items were presented at the same positions with 50% probability (due to the use of only upright and inverted configurations). This provides further evidence against potential contribution from local color adaptation.

In Fig. 8 (left panel), it appears that the color-salience aftereffect from the standard preview was reduced for

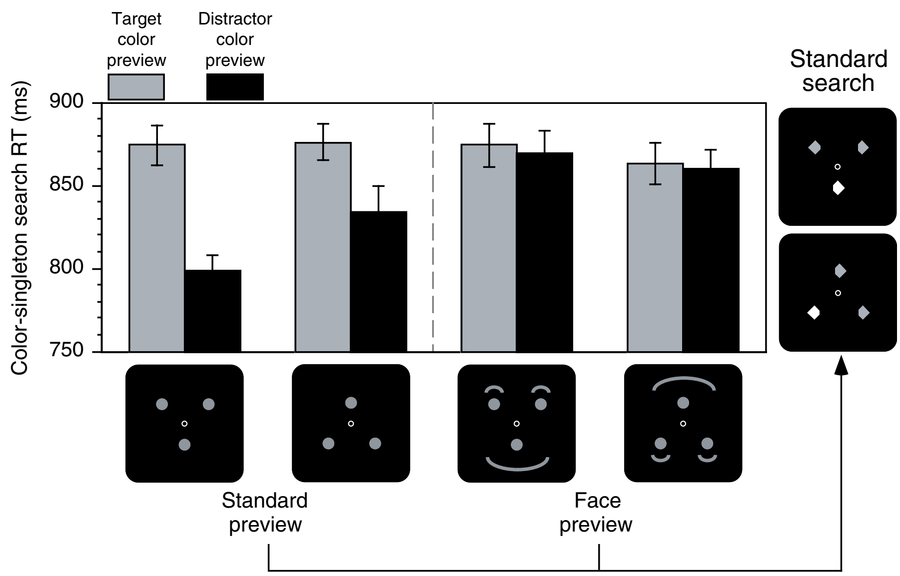

Fig. 8. *Experiment 2.2*: The color-salience aftereffect produced by the standard (with circles) and face preview displays. For each preview type, the data are plotted separately for the upright and inverted display orientations (no other orientations were used in this experiment; see illustrations on the bottom). The singleton-search displays were also presented only in the upright and inverted orientations (see illustrations on the right). The error bars represent ±1SE.

the upright-triangle configuration (42 ms effect) relative to the inverted-triangle configuration (76 ms effect), though this reduction was not significant ($t(19) = 1.473$, n.s.). It is possible that the three items perceptually grouped more readily when they were arranged as the vertices of an upright triangle than when they were arranged as an inverted triangle. If so, the reduced aftereffect from the upright-triangle configuration would be consistent with our hypothesis that perceptual grouping reduces the color-salience aftereffect. This putative triangular grouping, however, was apparently not strong enough to substantially reduce the aftereffect.

We also note that the face configuration eliminated the color-salience aftereffect whether the face orientation was upright or inverted. Although there are many reports of superior processing of upright faces (see Valentine, 1988 for a review), at least some global processing of faces occurs for both upright and inverted faces. For example, a good proportion of face selective cells in the temporal cortex respond well to inverted faces (e.g., Perrett, Rolls, & Caan, 1982; Perrett et al., 1988; Tanaka et al., 1991). The fusiform face area (thought to contain face selective cells in humans; Kanwisher, McDermott, & Chun, 1997) was also activated by both upright and inverted faces (Kanwisher, Tong, & Nakayama, 1998). Furthermore, face-specific aftereffects, indicative of global processing of faces, occur for both upright and inverted faces (e.g., Leopold, O'Toole, Vetter, & Blanz, 2001; Watson & Clifford, 2003; Webster & MacLin, 1999; Zhao & Chubb, 2001).

The elimination of the color-salience aftereffect by the addition of colored regions and contours to the preview displays clearly disconfirmed the mediation of the aftereffect by color habituation or local color adaptation, and supported mediation of the aftereffect by global-form-selective color coding. In support of our hypothesis that the color-salience aftereffect might depend on search-relevant configurations (i.e., presence of multiple discrete objects), perceptual unitization of the preview items (into a patch, an outline triangle, or a face) eliminated the aftereffect. To confirm this sensitivity to perceptual unitization, we verified in the next set of experiments that the color-salience aftereffect was relatively unaffected by substantial geometric alterations to the preview displays so long as the alterations did not induce strong grouping and perceptual unitization. In particular, if the color-salience aftereffect was mediated by high-level processing of global form and color, the aftereffect should tolerate spatial and local changes to the preview items. We thus examined the effects of changing the item eccentricity (Experiment 2.3), item size (Experiment 2.4), item shape (Experiment 2.5), and the number of items (Experiment 2.6).

4.4. Experiment 2.3. Changing the item eccentricity

4.4.1. Stimuli

In the low-eccentricity preview displays, the retinal eccentricity of the three items was reduced such that they were presented along an invisible ellipse that had identical dimensions to the patch used in Experiment 2.1. The standard preview displays (with chipped diamonds) were intermixed with the low-eccentricity preview displays (also with chipped diamonds).

4.4.2. Results and discussion

In contrast to the absence of the color-salience aftereffect from the patch preview displays, the low-eccentricity preview displays produced a reliable aftereffect (Fig. 9); the magnitudes of the aftereffect were 69 ms ($t(30) = 6.406$, $p < 0.0001$) for the standard preview and 48 ms ($t(30) = 3.563$, $p < 0.005$) for the low-eccentricity preview. Though the aftereffect from the low-eccentricity preview appears to have been reduced relative to that from the standard preview, this difference was not significant ($t(30) = 1.139$, n.s.).

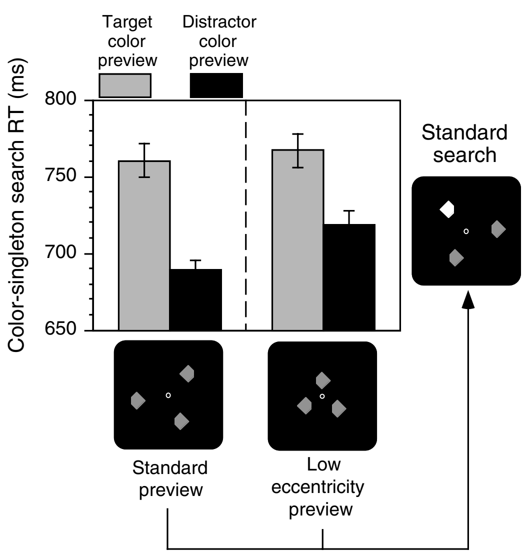

Fig. 9. *Experiment 2.3*: The color-salience aftereffect produced by the standard (with chipped diamonds) and low-eccentricity preview displays (see illustrations on the bottom). The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

4.5. Experiment 2.4. Changing the item size

4.5.1. Stimuli

The size of the preview diamonds was reduced to 44% (area-wise) of the standard size (0.86° by 0.86°) in the medium preview displays, and to 11% of the standard size (0.43° by 0.43°) in the small preview displays. The standard preview displays (with chipped diamonds) were intermixed with the medium and small preview displays (also with chipped diamonds).

4.5.2. Results and discussion

All preview sizes produced reliable color-salience aftereffects (Fig. 10); the magnitudes of the aftereffect were 97 ms ($t(17) = 8.887$, $p < 0.0001$) for the standard preview, 58 ms ($t(17) = 3.051$, $p < 0.01$) for the medium preview, and 50 ms ($t(17) = 6.453$, $p < 0.0001$) for the small preview. Though the aftereffect diminished with decreasing item size ($F(1,34) = 7.170$, $p < 0.02$, for the linear trend), it was quite remarkable that a reliable color-salience aftereffect was still obtained from the small diamonds which appeared more like tiny dots.

4.6. Experiment 2.5. Changing the item shape

4.6.1. Stimuli

In the different-shape preview display, the three diamonds were changed to a circle (1.1° diameter), a square (0.95° by 0.95°), and a plus symbol (consisting of two orthogonal 1.21° by 0.43° bars), that were matched in

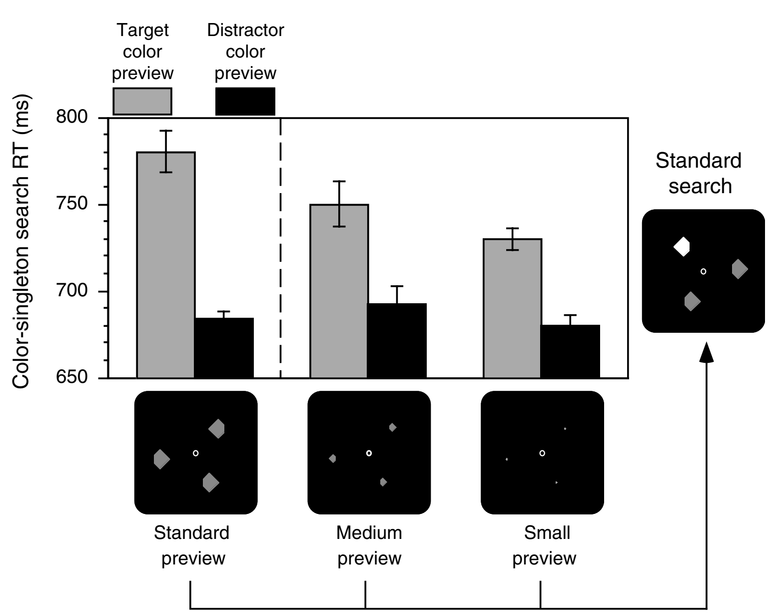

Fig. 10. *Experiment 2.4*: The color-salience aftereffect produced by the standard (with chipped diamonds), medium, and small preview displays (see illustrations on the bottom). The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

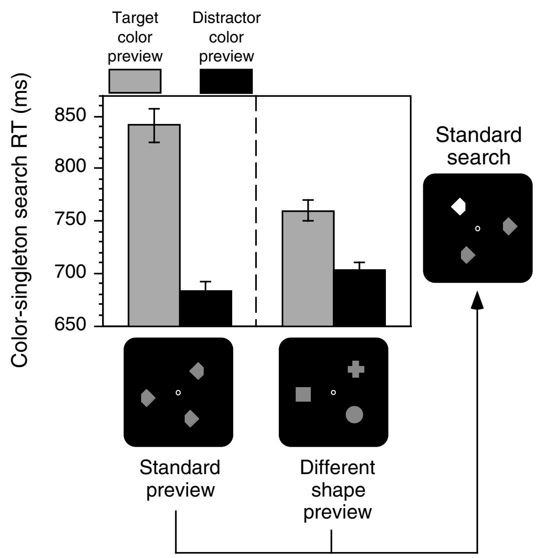

Fig. 11. *Experiment 2.5*: The color-salience aftereffect produced by the standard (with chipped diamonds) and different-shape preview displays (see illustrations on the bottom). The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

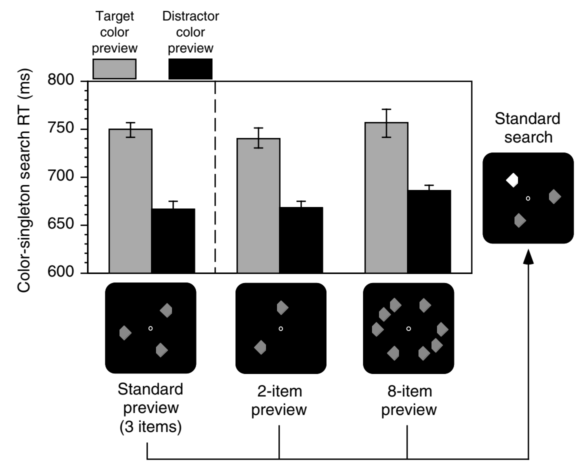

Fig. 12. *Experiment 2.6*: The color-salience aftereffect produced by the standard (with three chipped diamonds), 2-item, and 8-item preview displays (see illustrations on the bottom). The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

area to the diamonds (see Fig. 11 for illustration). Though these shapes differed from the diamonds and from one another with respect to various local features, the different-shape preview display still contained three discrete objects. The standard preview displays (with chipped diamonds) were intermixed with the different-shape preview displays.

4.6.2. Results and discussion

The different-shape preview displays produced a reliable color-salience aftereffect (Fig. 11); the magnitudes of the aftereffect were 159 ms ($t(19) = 7.522$, $p < 0.0001$) for the standard preview and 58 ms ($t(19) = 3.816$, $p < 0.005$) for the different-shape preview. The aftereffect from the different-shape preview was reduced relative to that from the standard preview ($t(19) = 4.864$, $p < 0.0005$); a potential reason for this reduction will be discussed in the general discussion section.

4.7. Experiment 2.6. Changing the number of items

4.7.1. Stimuli

The number of preview diamonds was varied across 2, 3 (the standard), and 8. The diamonds (all chipped) were always placed on the invisible iso-acuity ellipse shown in Fig. 1A. In the 2-item preview displays, the two diamonds were separated by four location steps (120° rotation); this separation was the same as the inter-item separation in the standard (3-item) displays. In the 8-item preview displays, the four empty locations were distributed such that the whole display appeared to be broken into two groups of three items and two lone items to prevent perceptual grouping of items into a global ellipse (see Fig. 12 for illustration, but note that the items were more sparsely distributed in the actual displays than as depicted in Fig. 12; see Fig. 1A). The 2-, 3 (standard)-, and 8-item preview displays were intermixed.

4.7.2. Results and discussion

The color-salience aftereffect was reliable regardless of the number of items in the preview displays (Fig. 12); the magnitudes of the aftereffect were 83 ms ($t(19) = 6.308$, $p < 0.0001$) for the standard (3-item) preview, 74 ms ($t(19) = 5.551$, $p < 0.0001$) for the 2-item preview, and 71 ms ($t(19) = 4.120$, $p < 0.001$) for the 8-item preview. The aftereffect was not different for the 2-, 3-, and 8-item preview displays ($F(2,38) = 0.249$, n.s.).

Because the positional overlap between the preview and search items was considerably greater for the 8-item preview than for the 2-item preview, this insensitivity to the number of preview items provided further evidence against contributions from local color adaptation. Furthermore, the undiminished aftereffect obtained from the 8-item preview displays suggested that the absence of the color-salience aftereffect from the face preview displays (Experiment 2.2) was not due to addition of extra items.

The results from Experiments 2.3–2.6 demonstrated that the color coding mediating the color-salience aftereffect tolerated a variety of geometric alterations so long as the preview display appeared to consist of multiple discrete objects. In striking contrast, the results from Experiments 2.1 and 2.2 demonstrated that the aftereffect was eliminated when the items appeared as a single unitized object. These results supported our search-relevance hypothesis that activation of the color processing mechanisms underlying the color-salience aftereffect was selective for a typical search context in which *multiple* discrete objects were present. However, in addition to containing a single unitized object, the preview displays that did not produce a color-salience aftereffect (the large patch, outline triangle, and the face displays) differed from the standard preview displays in other geometric aspects. To further elucidate the geometric selectivity of the color-salience aftereffect, we examined single-item preview displays that were identical to the standard preview displays except in number.

4.8. Experiment 2.7. Single-item preview matched to the standard preview

4.8.1. Stimuli

In the single-item preview display, the single item was either a diamond (unchipped to prevent inadvertent response), or a circle (matched in area to the diamond). The single item was presented at any of the 12 positions along the invisible iso-acuity ellipse (Fig. 1A). The standard preview displays (with unchipped diamonds) were intermixed with the single-diamond and single-circle preview displays.

4.8.2. Results and discussion

Both the single-diamond and single-circle preview displays produced reliable color-salience aftereffects (Fig. 13); the magnitudes of the aftereffect were 61 ms ($t(16) = 2.835$, $p < 0.02$) for the standard preview, 37 ms ($t(16) = 2.448$, $p < 0.03$) for the single-diamond preview, and 37 ms ($t(16) = 3.017$, $p < 0.01$) for the single-circle preview. The aftereffects from the single-diamond preview and the single-circle preview appear to have been reduced relative to that from the standard preview, but these differences were not significant ($t(16) = 1.203$, n.s., for the standard vs. single-diamond preview, and $t(16) = 1.394$, n.s., for the standard vs. single-circle preview). In a replication study, however, the color-salience aftereffect from the single-diamond preview was only marginally significant and was significantly reduced relative to the aftereffect from the standard preview (see Experiment 2.8).

These results suggest that previewing multiple objects makes the color-salience aftereffect more reliable, though it is not an absolute requirement. Because the color-salience aftereffect is only partially selective for the presence of multiple objects, some additional selectivity must account for the absence of the aftereffect from the patch, triangle, and face preview displays.

In real life situations, visual search is performed when there are multiple distractor objects, but only when the target has not already been found. In other words, a search is typically performed only when the target has not already been directly fixated. The color-salience aftereffect might thus be selective for the presence of peripheral objects in addition to the presence of multiple objects. This selectivity for *multiple peripheral objects* could account for the results.

The color-salience aftereffect was reliable when the item eccentricity, size, shape, and number were substantially altered so long as the preview displays still

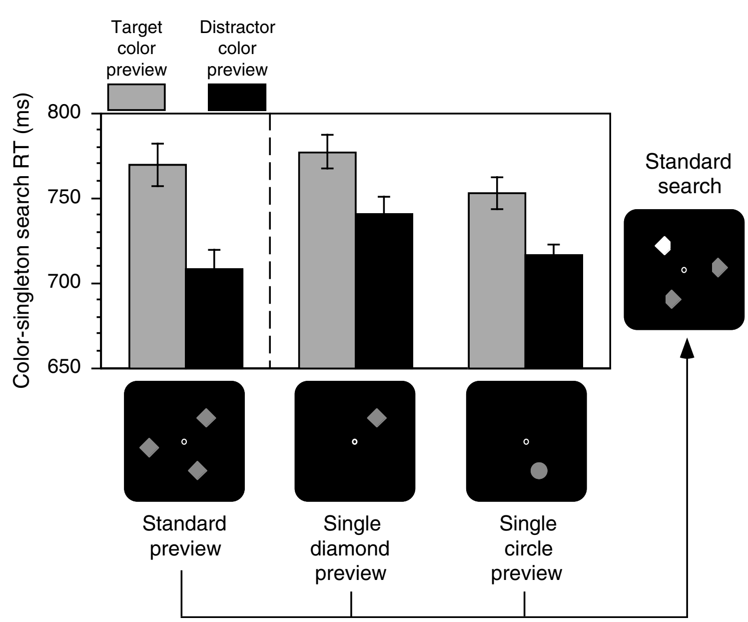

Fig. 13. *Experiment 2.7*: The color-salience aftereffect produced by the standard (with unchipped diamonds), single-diamond, and single-circle preview displays (see illustrations on the bottom). The standard preview and search displays were randomly rotated for each presentation. The location of the single item in the single-diamond and single-circle preview displays was random along the invisible ellipse (see Fig. 1A) for each presentation. The error bars represent ±1SE.

contained multiple peripheral objects (Experiments 2.3–2.6). The aftereffect was absent from the patch, triangle, and face preview displays, all of which contained only one salient perceptual object which was centered at the fixation point, deviating from both the multiplicity and periphery requirements for the color-salience aftereffect (Experiments 2.1 and 2.2). The single peripheral item (a diamond or a circle) produced a less reliable aftereffect presumably because the multiplicity requirement was violated but the periphery requirement was not (Experiments 2.7 and 2.8). This line of reasoning led to a prediction that the single diamond (which produced a reduced aftereffect when presented peripherally) should produce no aftereffect when it was presented at fixation.

4.9. Experiment 2.8. Single-item preview: peripheral versus central

4.9.1. Stimuli

The single-peripheral preview display was the same as the single-diamond preview display in Experiment 2.7. In the single-central preview display, the diamond was presented centrally behind the fixation point. The standard preview displays (with unchipped diamonds) were intermixed with the single-peripheral and single-central preview displays.

4.9.2. Results and discussion

As expected, the single-peripheral preview displays produced only a weak color-salience aftereffect, and the single-central preview displays produced no aftereffect (Fig. 14); the magnitudes of the aftereffect were 74 ms ($t(22) = 7.198$, $p < 0.0001$) for the standard preview, 30 ms ($t(22) = 1.974$, $p < 0.062$) for the single-peripheral preview, and 8 ms ($t(22) = 0.598$, n.s.) for the single-central preview. The aftereffect from the single-peripheral preview was reduced relative to that from the standard preview ($t(22) = 2.331$, $p < 0.03$).

The results so far are all consistent with the hypothesis that the color-salience aftereffect is selective for a typical search context in which multiple peripheral objects are present. In the next two experiments (Experiments 2.9 and 2.10), we examined whether this selectivity was fixed or adjustable to task demands.

4.10. Experiment 2.9. Face preview revisited: making face configuration search relevant with task demands

The face preview display used in Experiment 2.2 produced no color-salience aftereffect (Fig. 8) presumably because a single, centrally presented face (which is typically processed as a unitized whole) deviated substantially from a typical search context. If the geometric selectivity of the color-salience aftereffect was fixed, the face preview display should not produce the aftereffect under any circumstance. However, if the color-salience aftereffect generally facilitated visual search by reducing the salience of the prevalent distractor color, its selectivity might adjust to the task environment as visual search can be performed under different conditions. We thus hypothesized that the geometric selectivity of

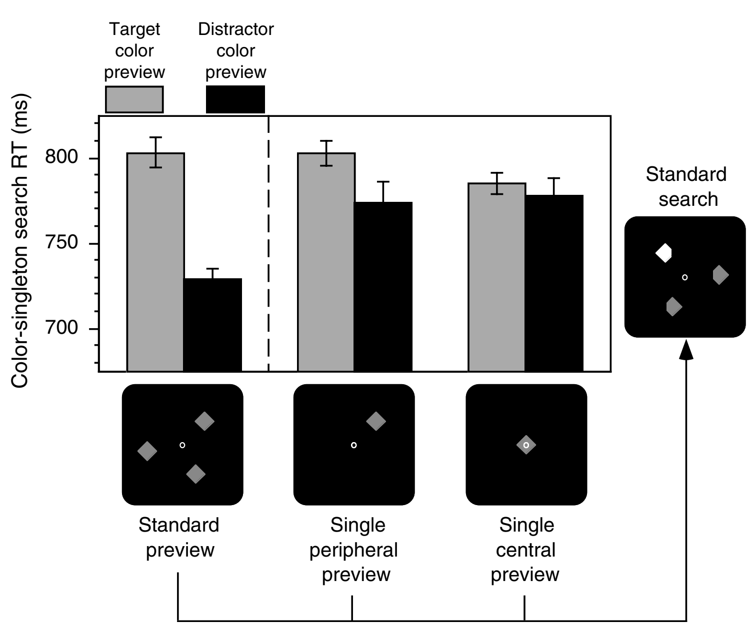

Fig. 14. *Experiment 2.8*: The color-salience aftereffect produced by the standard (with unchipped diamonds), single-peripheral, and single-central preview displays (see illustrations on the bottom). The standard preview and search displays were randomly rotated for each presentation. The location of the single item in the single-peripheral preview display was random along the invisible ellipse (see Fig. 1A) for each presentation. The error bars represent ±1SE.

the color-salience aftereffect might extend to include geometric configurations which would not normally fit into the "default" search context (e.g., presence of multiple peripheral objects), when those configurations became search relevant. Specifically, we hypothesized that if we intermixed displays in which a color singleton search was required within a face configuration, the face preview display might produce a color-salience aftereffect because the face configuration should no longer be an irrelevant geometric context for performing color-singleton search.

4.10.1. Stimuli

As in Experiment 2.2, the three preview items were arranged in either the upright or inverted triangular array, and the face configuration (arcs surrounding the three standard items) was imposed on half of the preview displays. Unlike in Experiment 2.2, the preview items were chipped diamonds rather than circles. The face configuration was also imposed on half of the search displays with the added arcs having the same color as the distractors—face search displays. The standard and face preview displays, and the standard and face search displays were intermixed (see Fig. 15 for illustrations).

4.10.2. Results and discussion

The color-salience aftereffect from the face preview to the standard search, which was absent in Experiment 2.1, now became as strong as the standard aftereffect (from the standard preview to the standard search) (Fig. 15, left panel). Reliable aftereffects also occurred on the face search trials whether the preview was the face display or the standard display (Fig. 15, right panel). The magnitude of the aftereffect was 73 ms ($t(17) = 6.775$, $p < 0.0001$) from the standard preview to the standard search, 79 ms ($t(17) = 3.879$, $p < 0.005$) from the face preview to the standard search, 24 ms ($t(17) = 2.174$, $p < 0.05$) from the standard preview to the face search, and 37 ms ($t(17) = 3.822$, $p < 0.005$) from the face preview to the face search.

The overall magnitude of the color-salience aftereffect (averaged across the standard and face preview) was smaller for the face search than for the standard search (31 ms vs. 76 ms, $t(17) = 2.935$, $p < 0.01$). This reduced aftereffect was likely due to the fact that the increased number of distractor-colored items in the face search displays made the color-singleton search easier (e.g., Bravo & Nakayama, 1992), and thereby reduced the impact of color-salience modulation from the aftereffect; indeed, the overall RT was significantly faster for the face search than for the standard search (523 ms vs. 564 ms, $t(17) = 5.451$, $p < 0.0001$).

We demonstrated that the geometric selectivity of the color-salience aftereffect flexibly adjusted to the task environment; the selectivity excluded face configurations by default (Experiment 2.1) presumably because a face is typically processed as a unitized whole and is thus search irrelevant, but the selectivity expanded to include face configurations when the task required that searches also be performed within a face. We replicated this adaptive flexibility of the color-salience aftereffect using an additional stimulus configuration.

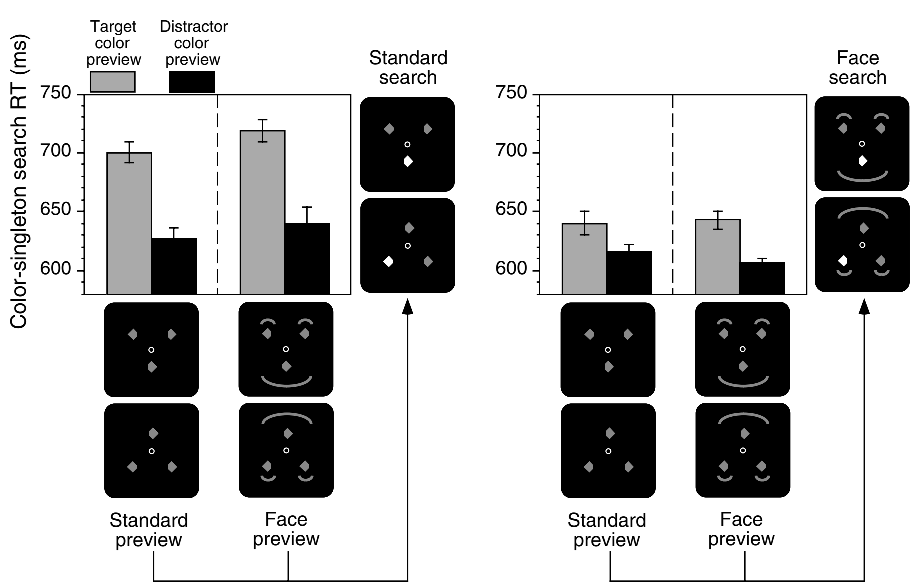

Fig. 15. *Experiment 2.9*: The color-salience aftereffect produced by the standard (with chipped diamonds) and face preview displays. The color-singleton search was performed either in the standard context (left panel) or in the face context (right panel); these search contexts were randomly intermixed. The standard and face preview displays (see illustrations on the bottom) as well as the standard and face search displays (see illustrations on the right) were presented in two orientations (upright or inverted, as in Experiment 2.2; see Fig. 8). The error bars represent ±1SE.

4.11. Experiment 2.10. Single-item preview revisited: making central single item search relevant by task demands

A single diamond presented behind the central fixation point produced no aftereffect (Experiment 2.8; see Fig. 14) presumably because it violated both the multiplicity and periphery requirements of the color-salience aftereffect. According to our search-relevance hypothesis, the periphery requirement comes from the fact that a directly fixated object is typically not the target of search (because it has usually been found). We thus created a somewhat unusual search display where a central item could be as likely a target as the peripheral items. If the geometric selectivity of the color-salience aftereffect adjusted to the modified task demand (as in Experiment 2.9), the selectivity of the aftereffect should now include a single-central item because the search display often contained a central target.

4.11.1. Stimuli

The preview display contained either four diamonds—the standard preview (with a central diamond), or a single diamond presented behind the fixation point—the single-central preview. The standard and single-central preview displays were intermixed. The search display was the same as the standard search display, except that it also contained a central diamond behind the fixation point; any of the four items could be the odd-colored target with equal probability (see Fig. 16 for illustration).

4.11.2. Results and discussion

To confirm task-dependent flexibility, the color-salience aftereffect from the single-central preview, which was absent in Experiment 2.8, now became reliable (Fig. 16); the magnitude of the aftereffect was 62 ms ($t(17) = 5.098$, $p < 0.0001$) for the standard preview and 35 ms ($t(17) = 3.625$, $p < 0.005$) for the single-central preview. Note that, in computing the color-salience aftereffect from the single-central preview, we excluded all search RTs in which the target was the central item, so that the aftereffects measured were always from the central preview item to the peripheral search items as in Experiment 2.8.

We confirmed that the selectivity of the color-salience aftereffect adjusted to the task environment; the selectivity excluded a single central item by default (Experiment 2.8) presumably because a single item presented at fixation is typically search irrelevant (because there is little need to search for it), but the selectivity expanded to include it when the search display was changed so that the central, directly fixated, item was often the target of search. Note that the color-salience aftereffect was reduced for the single-central preview relative to the standard preview ($t(17) = 2.516$, $p < 0.03$) presumably because the single-central preview display still violated

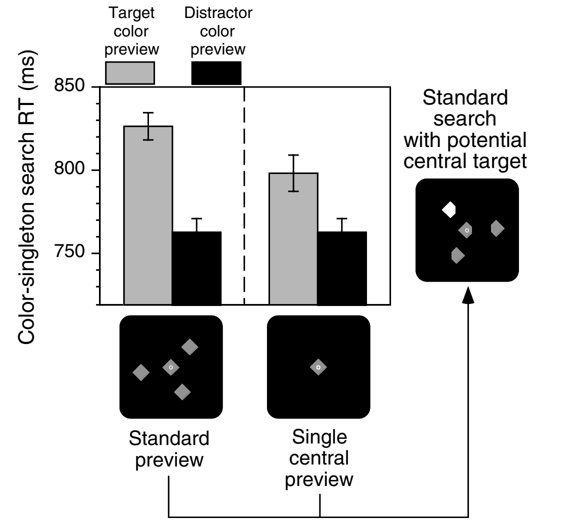

Fig. 16. *Experiment 2.10*: The color-salience aftereffect produced by the standard (with unchipped diamonds including the central diamond) and single-central preview displays (see illustrations on the bottom). The search display also had a central item (see the illustration on the right). The standard preview and search displays were randomly rotated for each presentation. The RTs from the search trials in which the central item was the target were excluded from the analysis (to avoid potential contributions from local color adaptation). The error bars represent ±1SE.

the multiplicity requirement, though the periphery requirement was eased by the task manipulation.

To summarize, pattern specificity of the color-salience aftereffect was examined in Experiments 2.1–2.10, revealing that the underlying color coding mechanism had a global-configuration selectivity for the presence of multiple peripheral objects. The fact that this selectivity coincided with a typical search context suggested a link between the color-coding mechanisms underlying the color-salience aftereffect and the mechanisms underlying visual search. This link was further confirmed by the demonstrations that the selectivity of the color-salience aftereffect flexibly expanded to include the current atypical search contexts. Hypotheses about the neural substrate of the color-salience aftereffect must take into account this task-modulated sensitivity to global configurations as well as the remarkable tolerance for changes in spatial and local features. We will suggest that the color-salience aftereffect is mediated by neural adaptation and interactions in mid- to high-level color processes in which cells are selective for both color and increasingly global form (e.g., in V4 and IT), as well as by feedback signals from brain areas that monitor and adaptively respond to task relevance (e.g., prefrontal cortex).

Before elaborating these conclusions, however, we report several control experiments to insure that the global-pattern selectivity of the color-salience aftereffect was primarily perceptual rather than cognitive. Potentially confounding contributions from observers' expectations (Experiment 3.1) and their strategic manipulations of attention (Experiments 3.2 and 3.3) were investigated. In the final experiment (Experiment 3.4), we demonstrated that the color-salience aftereffect was distinct from the seemingly related phenomenon of priming of color-singleton search (e.g., Goolsby & Suzuki, 2001b; Maljkovic & Nakayama, 1994, 2000; Suzuki & Goolsby, 2003).

5. Experiments 3.1–3.4

5.1. Control for expectancy and attention

Because the color of the preview display was equally likely to be the color of the target or of the distractors in the subsequent search, the observer's expectancy about the upcoming target color could not solely account for the color-salience aftereffect. Nevertheless, it is important to determine the degree to which the aftereffect might be influenced by expectancy.

5.2. Effect of expectancy on the color-salience aftereffect

We manipulated expectancy by making the preview color predictive of either the target color or the distractor color in the subsequent search. For one group of observers ($N = 14$), the preview color became the distractor color with 80% probability, biasing them to look for the opposite color in the subsequent search; this expectancy should augment the color-salience aftereffect. For the other group of observers ($N = 14$), the preview color became the target color with 80% probability, biasing them to look for the same color in the subsequent search; this expectancy should reduce or reverse the color-salience aftereffect.

5.2.1. Stimuli

The standard preview displays (with chipped diamonds) were used.

5.2.2. Results and discussion

Reliable color-salience aftereffects occurred whether the preview color predicted the distractor color or the target color (Fig. 17); the magnitudes of the aftereffect were 77 ms ($t(13) = 5.057$, $p < 0.0005$) for the 80% distractor-color preview, and 58 ms ($t(13) = 4.659$, $p < 0.0005$) for the 80% target-color preview. The aftereffect appears to have been smaller for the 80% target-color preview, but the difference was not significant ($t(26) = 0.925$, n.s.). This slightly diminished aftereffect could be due to the fact that the overall RT was faster for the observers in the 80%-target-color-preview condition (663 ms vs. 700 ms; $t(26) = 1.916$, $p < 0.08$). Overall, the results indicate that the color-salience aftereffect was little influenced by expectancy.

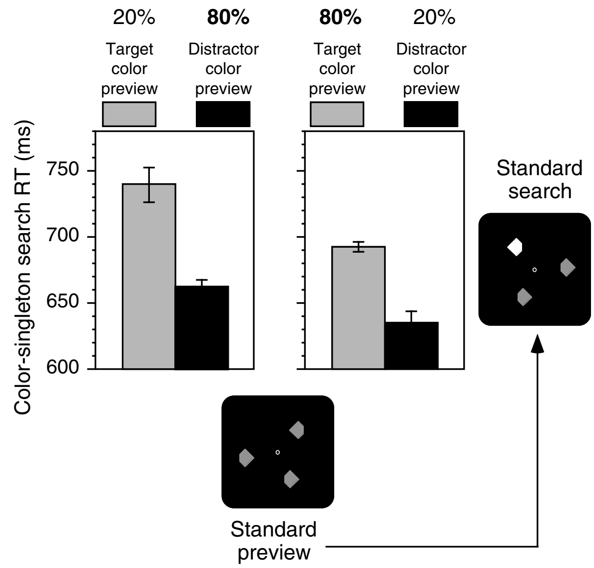

Fig. 17. *Experiment 3.1*: The color-salience aftereffect produced by the standard (with chipped diamonds) preview displays when the probability of distractor and target color repetition was manipulated. The probability of distractor-color repetition was high (80%) for one group of observers (left panel), whereas the probability of target-color repetition was high (80%) for the remaining observers (right panel). The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

A crucial property of the color-salience aftereffect was that the aftereffect was highly selective for global configuration and, at the same time, it was quite tolerant for changes in spatial and local features. A potentially trivial explanation of this global-form selectivity was that observers might have quickly looked away (despite the instruction to maintain fixation at the central marker) or withdrawn their attention from a preview display whenever it looked sufficiently different from the search display. For example, when observers saw the large patch, outline triangle, face, or the single central diamond in the preview display, they might have quickly withdrawn attention and possibly looked away because those displays appeared very different from the search display consisting of three discrete items. This strategic-ignoring account of the global-form selectivity of the color-salience aftereffect, however, did not seem tenable for the following reasons.

Some of the altered preview displays that did not violate the multiplicity and periphery requirements and thus produced reliable color-salience aftereffects, were quite distinguishable from the search displays. For example, the small items used in Experiment 2.4 appeared like three dots and thus appeared clearly distinct from the search diamonds (Fig. 10). The 8-item preview displays used in Experiment 2.6 also appeared very distinct from the 3-item search displays (Fig. 12). It is difficult to explain why observers did not rapidly withdraw attention from these distinctive preview displays.

Furthermore, we showed that a 27 ms preview was sufficient to produce reliable color-salience aftereffects (Experiment 1.3). A saccade could not have been generated within 27 ms (e.g., Fischer & Breitmeyer, 1987), and even voluntary shifts of attention would have been at most partially executed within the 27 ms preview period (e.g., Cheal & Lyon, 1989; Hikosaka, Miyauchi, & Shimojo, 1993; Suzuki & Cavanagh, 1997). Thus, even if observers voluntarily withdrew attention and initiated a saccade as soon as the preview display appeared (despite the instructions to do otherwise), they would have still seen the preview display for at least 27 ms, and that amount of preview would have been sufficient to produce reliable color-salience aftereffects. It was thus unlikely that the absence of the color-salience aftereffect from the patch, triangle, face, and central-diamond preview displays was due to strategic withdrawal of attention. Nevertheless, we conducted three control experiments to show that the color-salience aftereffect was relatively independent of observers' attention and responses during the preview period.

5.3. Experiment 3.2. Effect of withdrawing attention (preview displays cued with a tone)

The purpose of this experiment was to demonstrate that voluntary withdrawal of attention could not account for the absence of the color-salience aftereffect from the patch, triangle, face, and central-diamond preview displays. These preview displays could have produced reduced color-salience aftereffects (relative to the standard preview displays) for at least two reasons. One is that they deviated from the geometric selectivity of the color-salience aftereffect. The other is that they appeared so different from the search display that the observer rapidly recognized that it was not a search display, and consequently withdrew attention. To dissociate these possibilities, we clearly marked the preview displays without geometrically altering them. A short (200 ms) tone accompanied the onset of half of the standard preview displays. Observers were told that the tone signaled a preview display with 100% probability. Thus, if the absence of the color-salience aftereffect from the specific geometrically altered preview displays was due to the observer rapidly recognizing them as preview displays, standard preview displays accompanied by the tone should also produce no aftereffect.

5.3.1. Stimuli

The tone-cued preview was the same as the standard preview (with chipped diamonds) except that its onset coincided with a short tone. The tone-cued preview and standard preview were intermixed.

5.3.2. Results and discussion

The tone-cued preview produced a reliable color-salience aftereffect (Fig. 18); the magnitude of the aftereffect was 102 ms ($t(14) = 6.870$, $p < 0.0001$) for the standard preview, and 50 ms ($t(14) = 6.681$, $p < 0.0001$) for the tone-cued preview. The aftereffect from the tone-cued preview was reduced relative to that from the standard preview ($t(14) = 3.485$, $p < 0.005$). This reduction might be attributable to the observer's strategic withdrawal of attention. Alternatively, attention might have been involuntarily captured by the tone, interfering with visual encoding of the preview display. This question will be partially addressed in the next experiment. Nevertheless, the fact that the tone-cued preview displays produced a reliable color-salience aftereffect despite the fact that they were clearly labeled as preview displays (to be ignored), indicates that the observer's strategic withdrawal of attention cannot entirely account for the absence of the color-salience aftereffect from certain geometrically altered preview displays.

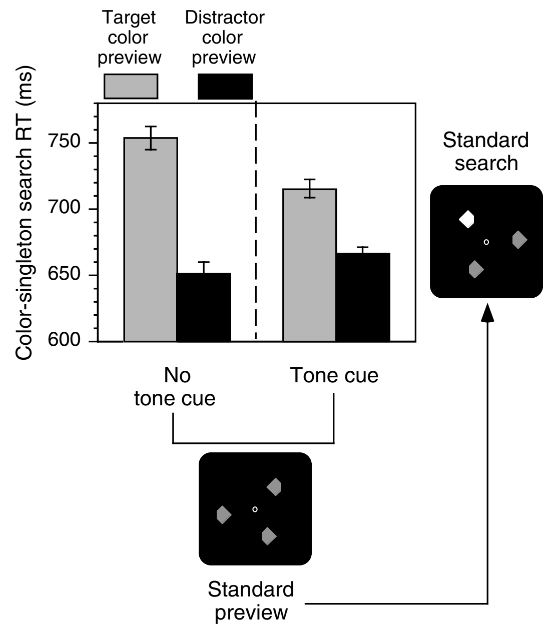

Fig. 18. *Experiment 3.2*: The color-salience aftereffect produced by the standard (with chipped diamonds) preview displays when a short tone accompanied half of the preview displays. The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

5.4. Experiment 3.3A. Effects of actively attending to the preview display

While the tone-cued preview experiment showed that the color-salience aftereffect was robust even when the to-be-ignored preview displays were clearly marked (presumably causing strategic withdrawal of attention), a complementary question was whether the aftereffect might be increased by actively attending to the preview displays. The observer was cued to either actively attend to or ignore the preview display. Because the attend/ ignore cue was presented well in advance of the preview display in this experiment, the effects of actively attending and ignoring the preview display were evaluated without potential perceptual interference from the cue.

5.4.1. Stimuli

Attention during preview was manipulated by using a secondary task of size-change detection. Each standard preview display (with chipped diamonds) was preceded (by 497 ms) by a change of the fixation marker (which remained in the changed state throughout the preview period). The open-circle fixation marker became a solid circle in the color of the upcoming preview display, or it became a plus symbol (0.42° by 0.42°) with equal probability.

When the fixation marker became a colored circle, the observer actively attended to the three preview diamonds and detected a slight size change (shrinkage by 1-pixel-wide perimeter or 12.9% in area) that occurred on a randomly chosen diamond—the *cued-to-be-attended* preview. The size change occurred with 50% probability 604 ms after the onset of the preview display. When a size change occurred, the observer responded as quickly as possible by pressing the space bar on the computer keyboard, and made no response when a size change did not occur. The preview display was terminated on response or 537 ms after the size change, yielding a total preview duration of 1141 ms (604 ms + 537 ms) when no response was made before preview offset. The overall high accuracy (87.7% correct) on this attention-demanding task of detecting a subtle size change with spatial uncertainty indicated that observers actively attended to the three diamonds.

When the fixation marker became a plus symbol, the observer passively viewed the preview display (and ignored a size change when it occurred); in other words, the plus symbol cued the observer that the upcoming display was a preview display to be ignored—the *cued-to-be-ignored* preview.

The overall preview duration was roughly comparable between the cued-to-be-attended preview displays ($M = 1069$ ms, SE = 9 ms) and the cued-to-be-ignored preview displays ($M = 1116$ ms, SE = 3 ms—shorter than the total duration of 1141 ms due to infrequent [1.9%] but erroneous responses to size change).

5.4.2. Results and discussion

The actively attended preview did not produce a stronger color-salience aftereffect than the ignored preview (Fig. 19); the magnitude of the aftereffect was 55 ms ($t(28) = 4.417$, $p < 0.0005$) for the cued-to-be-ignored preview and 38 ms ($t(28) = 2.532$, $p < 0.02$) for the cued-to-be-attended preview (averaged across the size-change and no-size-change trials). If anything, the attended preview appears to have produced a reduced aftereffect compared to the ignored preview, though this difference was not significant ($t(28) = 1.336$, n.s.).

A comparison between the size-change and no-size-change previews showed that the aftereffect from the attended preview (right panel in Fig. 19) was equivalent ($t(28) = 0.091$, n.s.) whether a size change occurred (40 ms) or did not occur (41 ms). The overall search RT, however, was significantly slower when a size change occurred (888 ms vs. 857 ms, $t(28) = 4.237$, $p < 0.0005$), indicating a general RT cost of task

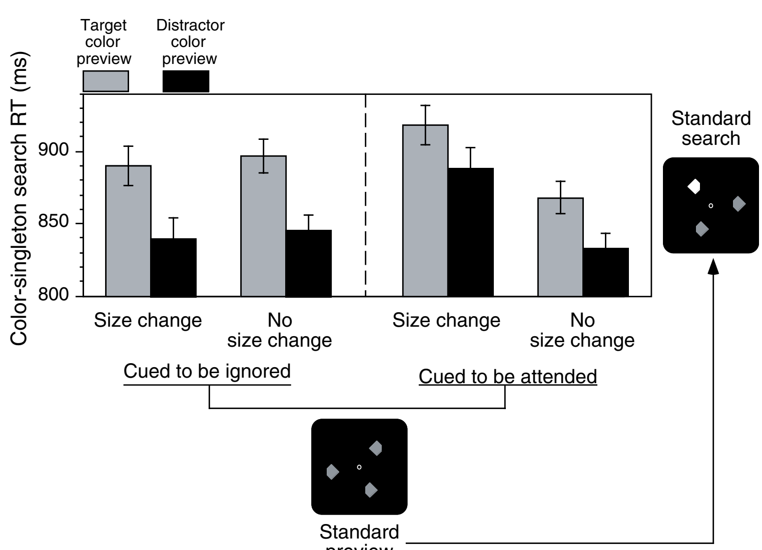

Fig. 19. *Experiment 3.3A*: The color-salience aftereffect produced by the standard (with chipped diamonds) preview displays when the observer was cued to ignore half of the preview displays and was cued to attend to the rest of the preview displays. A size change occurred on one of the preview items with 50% probability. The data from the ignored preview conditions (with and without size change) are shown on the left and the data from the attended preview conditions (with and without size change) are shown on the right. The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

switching (from responding to a size change to doing a search task). For the ignored preview (left panel in Fig. 19), size change had no effect on either the aftereffect or the overall RT (aftereffects of 68 ms [size change] vs. 61 ms [no size change], $t(28) = 0.251$, n.s.; overall RTs of 868 ms [size change] vs. 875 ms [no size change], $t(28) = 0.932$, n.s.).

Despite the fact that observers were given 497 ms to prepare for the to-be-ignored preview displays, those cued-to-be-ignored preview displays still produced reliable color-salience aftereffects that were not reduced in magnitude from those produced by the actively attended preview displays. Thus, the reduced magnitude of the color-salience aftereffect from the tone-cued preview displays (Experiment 3.2) was more likely due to some form of automatic attention capture or distraction by the tone cue rather than due to the observer's strategic withdrawal of attention.

5.5. Experiment 3.3B. Effects of focused attention

In the preceding experiment, we showed that actively attending to the preview display did not increase the color-salience aftereffect relative to ignoring the preview display. To further demonstrate the insensitivity of the aftereffect to attentional state, we manipulated focused attention using an exogenous cueing paradigm.

5.5.1. Stimuli

All preview displays were standard preview displays (with chipped diamonds). Half of the preview displays were immediately preceded (by 150 ms) by a briefly flashed (27 ms) circle at the location of one of the upcoming diamonds; the circle was achromatic (the same luminance and color as the fixation marker) with a diameter of 1.94° (about 50% larger than the diameter of the diamonds) drawn with a one-pixel-thick line. This type of abrupt-onset cueing has been shown to be effective in automatically drawing observers' attention to the cued location (e.g., Cheal & Lyon, 1989; Eriksen & Collins, 1969; Nakayama & Mackeben, 1989; Suzuki & Cavanagh, 1997). Observers then responded about the side of the chip of the exogenously-cued diamond and the display was terminated upon response. When a preview display was exogenously cued, the observer's attention was captured and focused at one of the diamonds. Note that the preview duration was comparable for the exogenously-cued preview displays ($M = 571$ ms, SE = 13 ms) and passively viewed preview displays (604 ms).

5.5.2. Results and discussion

The color-salience aftereffect was reliable regardless of focused attention (Fig. 20); the magnitudes of the aftereffect were 85 ms for the passive preview ($t(21) = 4.389$, $p < 0.0005$), and 56 ms for the exogenously-cued preview ($t(21) = 2.198$, $p < 0.04$). The aftereffect appears to be reduced for the exogenously-cued preview, but the difference was not significant ($t(21) = 0.919$, n.s.). The color-salience aftereffect was thus relatively insensitive to focused attention (and response) as well as to global attention to the three items (Experiment 3.3A).

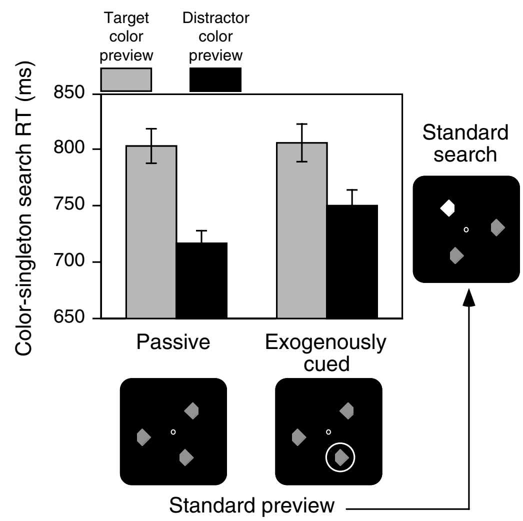

Fig. 20. *Experiment 3.3B*: The color-salience aftereffect produced by the standard (with chipped diamonds) preview displays when the observer was exogenously cued to respond to one of the diamonds in half of the preview displays (see illustrations on the bottom). The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

The results of Experiments 3.1–3.3 demonstrated that the color-salience aftereffect was a stable phenomenon that was relatively immune to effects of expectancy (predictive values of preview displays) and attention (whether the observer withdrew attention from or actively attended to the preview displays). If anything, voluntary attention to the entire preview display (Experiment 3.3A) as well as exogenously focused attention on one of the preview items (Experiment 3.3B) appear to have reduced (rather than increased) the aftereffect relative to passive preview, though these reductions were not significant. The tone-cue experiment (Experiment 3.2), however, suggests that capturing of attention to a different modality might diminish the aftereffect. It remains to be seen whether a strong capture of visual attention to an object outside of the preview display might reduce the aftereffect.

Significantly, because the color-salience aftereffect was robust whether the preview display was attended or ignored, the absence of the aftereffect from the patch, triangle, face, and central-diamond preview displays cannot be attributed to strategic withdrawal of attention. These results thus supported the idea that the global-pattern sensitivity of the color-salience aftereffect was indeed due to the global-form selectivity of the color-coding mechanisms that mediate the color-salience aftereffect.

Interestingly, the fact that the color-salience aftereffect was relatively unaffected by attention also made this phenomenon distinct from a potentially related phenomenon of "priming of color pop-out" (e.g., Goolsby & Suzuki, 2001b; Maljkovic & Nakayama, 1994, 2000; Suzuki & Goolsby, 2003). The priming of color pop-out occurs when the color combination of a color-singleton search is repeated, resulting in facilitation of the search RT. For example, responding to a red singleton target presented among green distractors facilitates a subsequent response to another red singleton target presented among green distractors (relative to a subsequent response to a green singleton target presented among red distractors). Repetition of either the target color, the distractor color, or both have been shown to contribute to this priming of color pop-out (e.g., Bichot & Schall, 1999; Maljkovic & Nakayama, 1994).

Though both the priming of color pop-out and color-salience aftereffect manifest as RT modulations in color-singleton search, they seem to have different influences on color salience. Priming of color pop-out is attention-dependent, facilitating the processes of attending to the previously attended color and ignoring the previously ignored color. Consistent with this characterization, when the observer attended to a distractor item in the preceding color-singleton display, the priming of color pop-out was eliminated (Goolsby & Suzuki, 2001b). In terms of color salience, the priming of color pop-out *increases* the salience of the previously attended color while it reduces the salience of the previously ignored color. In contrast, the color-salience aftereffect *reduces* the salience of the previously viewed color regardless of whether that color was attended or ignored.

This distinction is consistent with the idea that, whereas the color-salience aftereffect is likely to involve adaptation of color processing, the priming of color pop-out is likely to involve facilitation of a particular direction of color segmentation (e.g., green as the attended foreground color and red as the ignored background color). This characterization of the priming of color pop-out suggested that it would not be a pop-out specific effect, and that the priming should occur as long as the prior display had two colors and observers attended to the items of one color while they ignored the items of the other color. This prediction was tested in the next experiment.

5.6. Experiment 3.4. Effect of attending to one color and ignoring the other color in the preview display

In Experiments 3.2, 3.3A and 3.3B, three uniform-colored items produced a color-salience aftereffect regardless of whether they were attended or ignored. Here, we mixed these three uniform-colored (e.g., green) preview items with an additional set of three items of the other color (e.g., red). Because there were the same number of items for each color and the colored items were evenly intermixed (e.g., red, green, red, green, ...) along the invisible iso-acuity ellipse (Fig. 1A), neither color perceptually popped out. The observer attended either to the green items or to the red items.

If the priming of color pop-out required a prior pop-out experience, no priming should occur from attending to the three items of one color while ignoring the three items of another color. In contrast, if the priming of color pop-out was actually driven by facilitation of a specific direction of color-based segmentation (e.g., attending to green items while ignoring red items), a subsequent search which required the same direction of color segmentation (e.g., finding the green target among red distractors) should be facilitated. Such a result would provide a boundary condition between the priming of color pop-out and the color-salience aftereffect, the former being engaged in multi-color displays when one color is attended, and the latter being engaged in single-color displays regardless of attention.

5.6.1. Stimuli

The preview display always contained three green items and three red items (all chipped diamonds). These items were randomly placed at the twelve positions along the invisible iso-acuity ellipse (Fig. 1A) with the constraint that the six items were evenly spaced (2 position steps or 60° rotation apart) and the adjacent items had different colors. The to-be-attended color was indicated by a color change in the fixation marker, which occurred 497 ms prior to onset of the preview display. When the fixation marker became a solid green (or red) circle, the observer attended to the green (or red) items in the preview display to detect a slight size change in one of the attended items (see Experiment 3.3). Observers responded to the size change (which occurred 604 ms after the onset of the preview display as in Experiment 3.3) as soon as they detected it by pressing the space bar on the computer keyboard. The preview display was terminated on response or 537 ms after the size change. The cue validity was 80% in that the size change occurred on one of the attended diamonds 80% of the time. There was a 10% chance that the size change occurred on one of the ignored diamonds. These invalidly-cued previews were included to validate the attentional manipulation. In the remaining 10% of the preview displays, the size change did not occur, ensuring that observers pressed the space bar only when they detected a size change.

5.6.2. Results and discussion

Size changes were detected significantly faster (420 ms vs. 483 ms, $t(14) = 2.895$, $p < 0.02$) and more often

(86.6% vs. 73.0%, $t(14) = 3.465$, $p < 0.005$) when they occurred on a color-cued diamond than when they occurred on an uncued diamond. This confirmed that observers successfully attended to the cued color during preview. We will not discuss priming effects from the invalidly-cued previews; in these previews, the observer would initially attend to the cued color, but as soon as a size change was noticed on an uncued diamond, attention would switch to the uncued color. Any effects from these invalidly-cued previews would be difficult to interpret, and in fact we found no significant priming effect from these previews. We will discuss influences from previews in which the size change either did not occur or occurred on one of the color-cued diamonds. In these previews, the observer presumably attended to the color-cued diamonds throughout the preview duration; the durations of these previews were 1028 ms (SE = 14 ms) with size change and 1141 ms (the full display duration) without size change.

We clearly obtained a priming effect where a color-singleton search was faster when the target-colored items were previously attended while the distractor-colored items were previously ignored in the preview display (relative to when the distractor-colored items were previously attended while the target-colored items were previously ignored). We obtained this priming effect from both the size-change preview (in which observers responded to the size change on one of the attended diamonds) and the no-size-change preview (in which observers attended to the color-cued diamonds but a size change did not occur). The RT facilitation (RT for previously attending to distractor color −RT for previously attending to target color; see Fig. 21) was significant for the size-change preview ($M = 36$ ms, SE = 15 ms, $t(14) = 2.342$, $p < 0.04$) and marginal ($M = 47$ ms, SE = 26 ms, $t(14) = 1.808$, $p < 0.093$) for the no-size-change preview (probably due to the low statistical power because only 10% of previews were the no-size-change previews). As in Experiment 3.3, the overall RT was slower following a size-change preview than following a no-size-change preview (845 ms vs. 806 ms, $t(14) = 2.111$, $p < 0.054$; Fig. 21), presumably due to a cost from task switching (i.e., responding to a size change prior to doing a search task).

Two inferences can be made from these results. First, the phenomenon known as the priming of color pop-out does not require a prior experience of color pop-out; when an observer attends to items (or an item) of one color while ignoring items of another color, this attention-based "figure-ground" color segmentation is subsequently facilitated such that it is easier to attend to the previously attended color while ignoring the previously ignored color. Second, the results also suggest a boundary condition between the color-salience aftereffect and the color-segmentation priming.

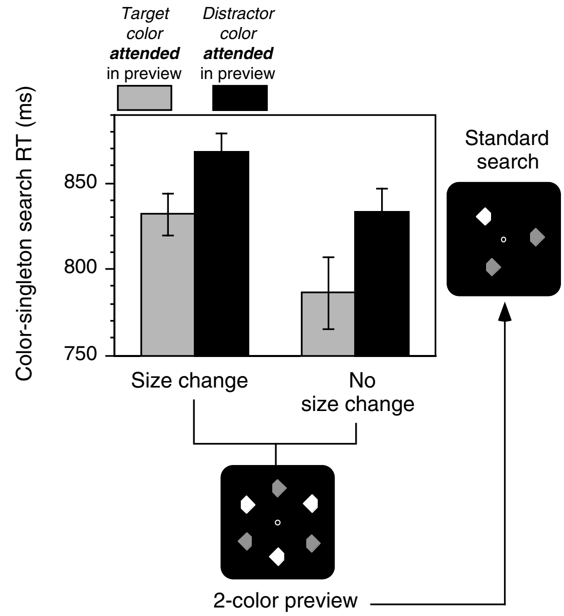

Fig. 21. *Experiment 3.4*: A color-segmentation priming effect (i.e., a priming of pop-out effect) produced by attending to items of one color while ignoring items of the other color in the 6-item preview displays (see the illustration on the bottom). A size change occurred on one of the attended items with 80% probability and one of the ignored items with 10% probability, and did not occur with 10% probability. Only the cases where a size change occurred on one of the attended items or did not occur have been included in the analysis because in those cases observers consistently attended to one color during preview (see text for details). The color-segmentation priming effect is reflected in faster RT when target color was previously attended (gray bars) relative to when distractor color was previously attended (black bars) in the preview display. The preview and search displays were randomly rotated for each presentation. The error bars represent ±1SE.

On the one hand, when a preview display contains items of more than one color and the observer selectively attends to the items of one color, a color-segmentation priming (i.e. priming of color pop-out) occurs. On the other hand, when a preview display contains items of only one color, a color-salience aftereffect occurs regardless of whether the observer ignores, actively attends to, or responds to the preview items. In other words, color-segmentation priming appears to be priming of attentional color selection, whereas the color-salience aftereffect appears to be a global-form-dependent adaptation of color salience. These are opposite phenomena in that the previously attended color becomes easier to find in color-segmentation priming, whereas the previously viewed color (attended or ignored) becomes more difficult to find in the color-salience aftereffect.

6. General discussion

We have demonstrated that brief (27–1200 ms) previewing of uniform-colored items makes the previewed color less salient in a subsequent color-based visual search (Experiments 1.1–1.3). This color-salience aftereffect is relatively independent of cognitive strategies such as expectancy (Experiment 3.1) and attentional state (e.g., actively attending to, explicitly responding to, or ignoring the preview display). The color-salience aftereffect thus appears to reflect automatic adaptive mechanisms of the visual system that direct attention to a new color in a search context. In contrast, the seemingly related phenomenon of the priming of color pop-out occurs on the basis of the prior state of attentional segmentation (i.e., attending to items of one color while ignoring items of another color; Experiment 3.4; also see Goolsby & Suzuki, 2001b).

Significantly, the color-salience aftereffect exhibited a characteristic dependence on geometric features. Although the color-salience aftereffect was relatively unaffected by variations in spatial and local features of the individual preview items (position, eccentricity, size, shape, and the number of items; Experiments 1.3, 2.3–2.6), the aftereffect was eliminated when the preview items were grouped into a perceptually unitized global form (a large patch, a closed triangle, or a face; Experiments 2.1 and 2.2) even when colored regions (and contours) were added in inducing perceptual unitization. These results suggested that the color-salience aftereffect was modulated by visual neurons that processed color in conjunction with global form, and was unlikely to be mediated by adaptation of cells that processed local color contrasts (e.g., cells in V1 and V2). [4] The overall pattern of geometric selectivity of the color-salience aftereffect (Experiments 2.1–2.8) suggested that the neural mechanisms underlying the aftereffect possessed a geometric preference for a typical visual configuration encountered during visual search (e.g., presence of multiple peripheral objects). This selectivity, however, was adaptively flexible in that it expanded to accommodate deviant stimulus configurations when they were made search relevant on the basis of task demands (Experiments 2.9 and 2.10).

The featural and temporal properties of the color-salience aftereffect suggest potential involvement of IT cells. As we found for the color-salience aftereffect, IT cells are broadly tuned to color and selective for global (rather than retinotopic) form features (e.g., Brincat & Connor, 2004; Kayaert et al., 2003, 2004; Komatsu et al., 1992; Komatsu & Ideura, 1993; Tanaka, 1996; Tanaka et al., 1991; Tsunoda et al., 2001; Wang, Fujita, & Maruyama, 2000). Both physiological and psychophysical studies indicate that IT cells adapt to briefly presented stimuli (e.g., Leopold et al., 2001; Lueschow, Miller, & Desimone, 1994; Miller, Li, & Desimone, 1993b; Suzuki, 2001, 2003, in press; Suzuki & Cavanagh, 1998; Vogels, Sary, & Orban, 1995; Vogels & Orban, 1994). Short-term plasticity of color-form multiplexing IT cells might thus contribute to the color-salience aftereffect. According to this idea, the global-form dependency of the color-salience aftereffect derives from the global-form selectivity of IT cells (i.e., the aftereffect would not occur unless the preview and search displays activated overlapping pools of IT cells). Because IT cells adjust and develop pattern selectivity through long-term experience (e.g., Jagadeesh, Chelazzi, Mishkin, & Desimone, 2001; Kobatake, Wang, & Tanaka, 1998; Logothetis & Sheinberg, 1996; Sakai & Miyashita, 1994; Sigala & Logothetis, 2002) and visual search is a ubiquitous aspect of human behavior, some IT cells may have developed geometric selectivity for search-relevant configurations. However, the particular geometric selectivity we found for the color-salience aftereffect (presence of multiple peripheral objects) has not been reported for IT cells. Even if such "multiple-item-tuned" and color-tuned IT cells were found in the future, it is not apparent as to how their adaptation might affect the relative salience of the target and distractor colors in the search display.

It is also important to note that the geometric selectivity of the color-salience aftereffect was modulated by task demands, indicating that the color-salience aftereffect could not be due solely to activation-based adaptation of visual neurons. Instead, the underlying color suppression must also involve higher cortical areas that evaluate task-relevance of stimuli. Prefrontal cortex might be a good candidate because this cortex has extensive connections with IT and other visual areas (e.g., Ungerleider, Gaffan, & Pelak, 1989), and the cells there respond in a task-specific manner, classifying stimuli

[4] One possible concern is that the color-salience aftereffect might be a spatial-frequency-contingent color-aftereffect. However, it is unlikely that the specific pattern of geometric dependencies we obtained for the color-salience aftereffect was due to spatial-frequency selectivity. For example, when the thick lines were added to connect the preview items into a closed triangle (Experiment 2.1), eliminating the aftereffect, the primary spatial frequency introduced by the lines (i.e., the spatial frequency along the axis orthogonal to each added line) was similar to the spatial frequency of the items themselves (because the lines were about the same width as the items). In the small-item display (Experiment 2.5), the aftereffect was robust despite the fact that the spatial frequency of the dot-like small items was substantially changed from the spatial frequency of the standard items. In the face-preview display (Experiment 2.2) that eliminated the aftereffect, the local spatial frequency of the preview items was not changed; though the overall spatial frequency was increased by the addition of the three arcs, the similar addition of items had no effect when perceptual unitization did not occur in the 8-item display (Experiment 2.6). It is also difficult to explain, on the basis of spatial frequency selectivity, why the color-salience aftereffect was equivalent for preview displays containing 2, 3, and 8 items, but it became unreliable for 1-item preview and disappeared when that item was presented at the fixation point (Experiments 2.6–2.8). Finally, the geometric selectivity of the color-salience aftereffect expanded with task demands (Experiments 2.9 and 2.10). However, there has been no evidence that spatial frequency selectivity, which is an intrinsic property of low-level cortical neurons, can be substantially modified by manipulations of task relevance of the stimuli.

based on behavioral significance (see Miller & Cohen, 2001, for a review).

The color-salience aftereffect, however, is unlikely to be mediated entirely within the prefrontal cortex. Even cells in the ventro-lateral prefrontal cortex (VLPFC), which receives direct input from the ventral visual pathway (e.g., Ungerleider et al., 1989), generally do not respond to stimulus color per se. Instead, they tend to respond according to the task-based behavioral categories of colors (e.g., Lauwereyns et al., 2001; Sakagami & Tsutsui, 1999; Sakagami et al., 2001). For example, VLPFC cells that preferred behavioral "go" responses, responded strongly to green and weakly to red when green was associated with "go" responses and red was associated with "no-go" responses. However, the same VLPFC cells responded strongly to purple and weakly to yellow when purple was associated with behavioral "go" responses and yellow was associated with "no-go" responses; VLPFC cells that preferred behavioral "no-go" responses exhibited the opposite pattern (Sakagami et al., 2001). VLPFC cells thus respond to the color's behavioral value (association with "go" or "no-go" responses) rather than to color. Because the color-salience aftereffect exhibited broad tuning to the stimulus color when colors were not associated with responses, the locus of color suppression seems more likely to be color-tuned cells in the visual areas.

What kind of interactions between the visual areas and the prefrontal cortex might account for our results? The definitive answer must await future studies in which neural recordings are made in conjunction with behavioral demonstrations of the color-salience aftereffect. Here, we offer a simple hypothesis. We speculate that the site of color adaptation may be V4, where cells are broadly tuned to color (e.g., Schein & Desimone, 1990), and their receptive fields tolerate some variation in position, size, and spatial frequency as well as preserve some degree of retinotopy (e.g., Desimone & Schein, 1987) suitable for guiding attention to the search target. Furthermore, most V4 cells have a large antagonistic surround (outside the "classical" receptive field) such that their response to the preferred color is inhibited when the surround region is also illuminated by the same color. V4 cells are thus likely to contribute to color-based image segmentation (e.g., Schein & Desimone, 1990) which is a crucial component of color-based visual search. For example, a red-tuned V4 cell would respond strongly to a red stimulus surrounded by green stimuli, that is, when the red item perceptually segregates and pops out from the green items, but it would respond poorly to a red stimulus surrounded by other red stimuli. We speculate that the color-salience aftereffect occurs because viewing uniform-colored items temporarily suppresses V4 cells tuned to that color. As we are agnostic about the exact mechanism of this suppression effect (e.g., activation-based adaptation and/or inhibitory interactions), we will refer to it simply as V4 adaptation.

To explain the global-form selectivity of the color-salience aftereffect, we note that the preview patterns that did not produce the color-salience aftereffect were ones that would have produced strong responses from IT cells. For example, the face display would have elicited strong responses from "face-tuned" IT cells (e.g., Desimone, Albright, Gross, & Bruce, 1984; Kobatake & Tanaka, 1994; Perrett et al., 1982), the patch display from "circle-tuned" IT cells (e.g., Sato, Kawamura, & Iwai, 1980), and the triangle display from "triangle-tuned" IT cells (e.g., Hikosaka, 1999). Because a diamond is a common shape, it is reasonable to speculate that the single diamond would have elicited strong responses from "diamond-tuned" IT cells. Because IT cells tend to have "hot spots" at the center despite their large receptive fields (e.g., Desimone & Gross, 1979; Gross et al., 1972; Lueschow et al., 1994; Richmond, Wurtz, & Sato, 1983), the face preview, patch preview, triangle preview, and the central-diamond preview, which were all centered at fixation, would have elicited strong responses from the corresponding IT cells. We thus hypothesize that adaptation of V4 cells was inhibited by strong activation of IT cells through feedback connections such as those described by Rockland et al. (Rockland & Van Hoesen, 1994; Rockland, Saleem, & Tanaka, 1994).

This activation-based feedback from IT cells could explain the multiple-item selectivity of the color-salience aftereffect without invoking specific IT cells tuned to the presence of multiple items. This is because IT cells' responses to their preferred patterns tend to be reduced when there are multiple patterns present within their large receptive fields (e.g., Chelazzi, Duncan, Miller, & Desimone, 1998; Miller, Gochin, & Gross, 1993a; Sato, 1989). Even if some IT cells were preferentially tuned to a chipped diamond, a whole diamond, or to a circle, the presence of several of these shapes would have attenuated their responses. Thus, multi-item preview displays with no unitized interpretation would have produced only weak responses from IT cells, allowing V4 cells to adapt.

This IT-to-V4 feedback hypothesis could also account for some of the seemingly idiosyncratic aspects of our results. We noted that global attention to the three preview items (Experiment 3.3A) modestly reduced the color-salience aftereffect. It is possible that global attention to the overall preview display might have promoted unitized perception of the three items as a triangle, increasing responses from the triangle-tuned IT cells. A slightly reduced aftereffect obtained from the low-eccentricity preview (Experiment 2.3 and Fig. 9) might also be explained by stronger perceptual grouping of items due to their compact arrangement. It is also known that even if multiple objects are present, an IT cell responds strongly to its preferred pattern (almost as if it was the only pattern present) when attention is focused on that pattern (e.g., Chelazzi et al., 1998). Thus, the reduced aftereffect from focusing attention to one of the items (Experiment 3.3B) is also consistent with the hypothesis that increased activity from IT cells reduces the color-salience aftereffect. Note that the aftereffect was also reduced when the preview display contained heterogeneous shapes (Experiment 2.5 and Fig. 16); this might have been due to the fact that one of the shapes (e.g., the plus shape) attracted attention due to its figural salience.

To account for the task-dependence of the color-salience aftereffect, we hypothesize that, when perceptually unitized displays became search relevant, the prefrontal cortex reinstated the color-salience aftereffect by inhibiting IT cells that responded strongly to the unitized patterns. This inhibitory role is broadly consistent with the view that a primary function of the prefrontal cortex is to inhibit inappropriate cognitive and behavioral responses (e.g., Fuster, 1997; Hauser, 1999; Iversen & Mishkin, 1970; Sakagami et al., 2001). For example, in order to perform search within a face, the initial holistic interpretation of a face must be broken, and the prefrontal cortex might do so by inhibiting the face-tuned IT cells that respond to a unitized face (the prefrontal cortex has been implicated in switching conceptual framework, perceptual interpretation, and attention; e.g., Hauser, 1999; Lumer & Rees, 1999; Nagahama et al., 1998). If this inhibition of face-tuned IT cells during search in face contexts persists during the face preview, V4 cells could be adapted by the face preview displays (without inhibition from IT) to produce the color-salience aftereffect. Similarly, when a search display includes a central diamond, the prefrontal cortex might inhibit the strong responses of the diamond-tuned IT cells to the central diamond (IT cells tend to respond strongly to a central object even in the presence of peripheral objects; e.g., Sato, 1989), so that the peripheral diamonds could also be processed. If this inhibition of the diamond-tuned IT cells during search persists during preview of a single central diamond, V4 cells could be adapted by the single-central-diamond displays (without inhibition from IT) to produce the color-salience aftereffect.

To summarize, we hypothesize that (1) the color-salience aftereffect is primarily mediated by adaptation of color-tuned cells in V4, (2) the global-form selectivity of the aftereffect derives from inhibitory feedback from global-form-tuned cells in IT to V4 (preventing V4 adaptation), and (3) the task dependency of the aftereffect derives from inhibitory feedback from task-monitoring cells in the prefrontal cortex to IT (preventing strong IT responses that signal unitized perceptual interpretation). Future physiological research might examine the specific predictions that strong activations of IT cells prevent adaptation of V4 cells, and that performing visual search within unitized patterns inhibits IT cells that preferentially respond to those patterns.

In conclusion, we have demonstrated that brief previewing of uniform-colored items reduces the salience of the previewed color in a subsequent color-based visual search. This color-salience aftereffect was broadly tuned to color and generally insensitive to cognitive factors such as expectancy, attention, and behavioral response. Although the aftereffect was relatively insensitive to color energy as well as local and spatial features, it was crucially dependent on global geometric configuration in a task-dependent manner. These results suggest that (1) color salience is adaptively modulated within the time scale of individual fixations, drawing attention to a new color in a search context, and (2) these modulations seem to be mediated by adaptation of moderately retinotopic and color-tuned cells (perhaps in V4) whose activities are crucially influenced by global-form-dependent feedback (perhaps from IT to V4) and task-dependent feedback (perhaps from prefrontal cortex to IT).

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