Saliency and priority modulation in a pop-out paradigm: Pupil size and microsaccades

Chin-An Wang, Jeff Huang, Donald C. Brien, Douglas P. Munoz

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ABSTRACT

A salient stimulus can trigger a coordinated orienting response consisting of a saccade, pupil, and microsaccadic responses. Saliency models predict that the degree of visual conspicuousness of all visual stimuli guides visual orienting. By presenting a multiple-item array that included an oddball colored item (pop-out), randomly mixed colored items (mixed-color), or single-color items (single-color), we examined the effects of saliency and priority (saliency + relevancy) on pupil size and microsaccade responses. Larger pupil responses were produced in the pop-out compared to the mixed-color or single-color conditions after stimulus presentation. However, the saliency modulation on microsaccades was not significant. Furthermore, although goal-relevancy information did not modulate pupil responses and microsaccade rate, microsaccade direction was biased toward the pop-out item when it was the subsequent saccadic target. Together, our results demonstrate saliency modulation on pupil size and priority effects on microsaccade direction during visual pop-out.

1. Introduction

The appearance of a salient stimulus in the environment evokes a series of orienting responses such as shifts of gaze and attention that together are thought to prepare the body for immediate action for survival (Lynn, 1966; Sokolov, 1963a). Although the orienting response includes momentary changes in pupil size and microsaccades (Cornell & Munoz, 2014; Wang & Munoz, 2015), most research has only focused on saccadic eye movements.

Research exploring how visual saliency modulates saccadic eye movements has received extensive attention over the past few decades. An influential model has proposed the existence of a visual saliency map (Itti & Koch, 2001; Koch & Ullman, 1985) that gives rise to the degree of visual conspicuity of stimuli (or objects) available in the environment by integrating various feature maps (e.g., contrast, color, orientation, motion), resulting in a bottom-up sensory-driven map that defines the degree of conspicuity across the image. The saliency map thus serves to guide visual orienting (saccades) towards the most visually conspicuous stimuli (Itti & Koch, 2001). However, the salience computation is not only modulated by bottom-up sensory properties that render a stimulus conspicuous from its surrounding (Itti & Koch, 2001; Koch & Ullman, 1985), but also influenced by an internal goal of an observer (typically called top-down), together yielding the priority map—the combined representation of salience and relevance (Boehnke & Munoz, 2008; Fecteau & Munoz, 2006; Serences & Yantis, 2006). Although a considerable body of research has systematically demonstrated the influences of bottom-up and top-down processes on the control of saccadic eye movements (Kowler, 2011), their influences on pupil size and microsaccades are less understood.

In addition to saccadic eye movements, pupil size and microsaccades are also considered as components of orienting (Cornell & Munoz, 2014; Wang & Munoz, 2015). Transient pupil responses are induced following the presentation of salient stimuli (Loewenfeld, 1999; Sahraie & Barbur, 1997; Sokolov, 1963a), and evoked pupil responses scale with the contrast of stimuli (Barbur, 2004; Gamlin, Zhang, Harlow, & Barbur, 1998; Stelmack & Siddle, 1982; Wang & Munoz, 2014; Wang, Boehnke, Itti, & Munoz, 2014). Similarly, microsaccade generation is modulated by stimulus presentation (Hafed, 2011; Martinez-Conde, Otero-Millan, & Macknik, 2013; Rolfs, 2009), with suppression shortly after stimulus appearance (referred to as microsaccade suppression), followed with an increased rate of microsaccades (referred to as microsaccade enhancement) (e.g., Hafed & Clark, 2002; Engbert & Kliegl, 2003; Valsecchi & Turatto, 2009; Wang, Blohm, Huang, Boehnke, & Munoz, 2017). Microsaccade direction is also...
modulated by stimulus presentation because more microsaccades are directed toward the stimulus location after the stimulus presentation (Hafed, 2011; Martinez-Conde et al., 2013; Rolfs, 2009). Although the modulation of stimulus contrast on pupil responses has been demonstrated (Barbur, 2004; Gamlin et al., 1998; Stelmack & Siddle, 1982; Wang & Munoz, 2014; Wang et al., 2014), the signature of saliency computation is to integrate various stimulus features into a topographic representation of visual conspicuity, whereby certain stimuli stand out from others based on low-level features of the input image. It is thus important to investigate not only 1st order saliency computation using a single feature, but also 2nd order saliency computation that integrates various feature maps, resulting in center-surround feature contrasts that make a stimulus stand out from its neighbors. Furthermore, because there is usually more than one object in the natural environment at any moment, it is important to test the saliency predictions on other orienting components in ecologically appropriate conditions. Previous studies are limited not only in their ability to demonstrate saliency computation that renders a stimulus conspicuous from its surrounding, but also between different stimuli in an array.

The goal of this study is to investigate the influence of both the saliency and priority modulation on pupil size and microsaccades using a pop-out paradigm that uses an oddball item (Fig. 1). We hypothesize that, due to the shared neural circuitry controlling pupil and saccade behaviors, similar saliency and priority modulation should be observed on pupil size and microsaccades: that is, greater pupil and microsaccadic responses should be observed in the pop-out condition compared to other control conditions, and the influence of top-down processes should be demonstrated on pupil size and microsaccades as well as on saccades.

2. Materials and methods

2.1. Experimental setup

All experimental procedures were reviewed and approved by the Ethics Board of Queen’s University and were in accordance with the principles of the Canadian Tri-Council Policy Statement (TCPS-2 2014) on Ethical Conduct for Research Involving Humans, and the Declaration of Helsinki (World Medical Association, 2001). Twenty-six participants (8 males, mean age: 21.4, SD: 2.9 years) were recruited to participate in Experiment 1 and twenty participants were recruited for Experiment 2 (10 males, mean age: 22.5, SD: 3.4 years). Participants had normal or corrected-to-normal vision and were naïve regarding the purpose of the experiment. Participants provided informed consent and were compensated financially for their participation.

Participants were seated in a dark room for all experiments. Eye position and pupil size were measured with a video-based eye tracker (Eyelink-1000 binocular-arm, SR Research, Osgoode, ON, Canada) at a rate of 500 Hz with binocular recording (left pupil was mainly used). Stimulus presentation and data acquisition were controlled by Eyelink Experiment Builder and Eyelink software. Stimuli were presented on a 17-inch LCD monitor at a screen resolution of 1280 × 1024 pixels (60 Hz refresh rate), subtending a viewing angle of 32° x 26°, with the distance from the eyes to the monitor set at 58 cm.

2.2. Experiment 1 (Fig. 1A)

The experiment consisted of 190 trials. Each trial began with the
appearance of a radial arrangement of circular stimuli (49 items, 1° diameter each, 26 cd/m²) that spanned 20° visual angle on a grey background (12 cd/m²). The 48 surrounding items were light-grey, forming three rings of items that contained 8, 16, and 24 items that were 4°, 7°, and 10° eccentricities from the central item, respectively. The central item acting as the fixation point (FP) was colored (26 cd/m²; red or green, randomized for each trial), and the level of luminance was same between the central item and other items. After a variable fixation period of 1000–1500 ms, the 48 items surrounding the FP changed in color (remained at 26 cd/m²) depending on the condition of the trial. In the pop-out condition, one item mainly from the 7° eccentricity ring changed to a new color (oddball item) while all others changed to the same color as the central FP (40 % of the trials); in the mixed-color condition, a random half of the surrounding items changed to the same color as the central FP and the other half changed to the opposite color (20 % of the trials); in the single-color condition, the surrounding items changed to the same color as the central FP (20 % of the trials). To maintain task engagement, a subset of trials (20 %) were catch trials (saccade condition), in which the FP and all but one peripheral items disappeared following the initial fixation period, and participants were required to generate a saccade toward the remaining element in the array. The four conditions (pop-out, mixed-color, single-color, saccade) were randomly interleaved. Note that because pupil size is sensitive to luminance changes (Loewenfeld, 1999), to avoid any luminance change involved after the pop-out (or others) presentation, the luminance level remained unchanged in each trial. Therefore, any observed differences in pupil size after the presentation cannot be attributed to changes in luminance.

2.3. Experiment 2 (Fig. 1B)

The identical displays were used as in experiment 1, with an initial fixation period of a radial arrangement of circular stimuli (48 grey surrounding items and one colored FP). The variable fixation period of 1000–1500 ms was followed by the same display as the pop-out condition in experiment 1 during which participants maintain fixation, but here the color of the FP instructed the condition of the trial: in the relevant condition (red FP in Fig. 1B), following the pop-out array presentation, the FP disappeared after a variable fixation length (500–2000 ms), and participants were required to generate a saccade toward the pop-out item location in the pop-out array stimulus; in the irrelevant condition (green FP in Fig. 1B), following the pop-out array presentation, the FP as well as the item array all disappeared simultaneously with the appearance of a white stimulus (so cannot be associated with neither FP colors, 32 cd/m²), and participants were required to generate a saccade toward a white peripheral stimulus presented at a random location not overlapping the pop-out array item location. Note that, although the single item in the irrelevant condition also popped out, pop-out here only referred to the pop-out item location in the array presentation. The colors of the FP denoting relevant/irrelevant conditions were counter-balanced across subjects. Participants were explicitly informed prior to the experiment which FP color indicates a relevant (or irrelevant) condition and were given enough practice trials to make sure that they understood the task. Note that only trials with more than 1500 ms pop-out stimulus presentation were included for analysis.

2.4. Data analysis

To maintain an accurate measure of pupil size, trials with an eye position deviation of more than 2° from the central FP or with detected saccades (> 2° amplitude) during the required period of central fixation were excluded from analysis. When blinks were detected, following the literature, pre- and post-blink pupil values were used to perform a linear interpolation to replace pupil values during the blink period (Karatekin, Bingham, & White, 2010; Nassar et al., 2012; Wang, McInnis, Brien, Pari, & Munoz, 2016). Trials were discarded when two blinks occurred within a time interval of less than 500 ms. The above criteria resulted in the removal of less than 2% of trials in both experiments. Note that trials with blinks that occurred around the array presentation (~400 to 1500 ms of array onset) were excluded from microsaccade analysis (~5%). There were at least 20 trials for each condition remaining for analysis. Saccade reaction time (SRT) was defined as the time from the FP disappearance to the first saccade away from central fixation that exceeded 30°/s and its amplitude was greater than 2°. In the saccade condition, failure to initiate a saccade within 1000 ms after the disappearance of FP or failure to make a saccade to the correct location (within 2.5° radius around the target) were marked as errors.

Following the procedures of baseline pupil correction used previously (Wang & Munoz, 2014; Wang et al., 2017), for each trial a baseline value was determined by averaging pupil size from 200 ms before to the appearance of the array presentation. Pupil values were subtracted from this baseline value. We also computed instantaneous pupil velocity to further examine moment-to-moment pupillary changes. As mentioned, we hypothesized that the SC is importantly involved in initiating all components of orienting, and the phasic and sustained responses of the SC occur in many tasks, including pop-out tasks (White, Kan, Levy, Itti, & Munoz, 2017). Moreover, transient and sustained pupil responses are evoked by SC microstimulation (Wang, Boehnke, White, & Munoz, 2012). And these responses are similar to the responses observed in the current study. We therefore selected 2 epochs to capture transient and sustained pupil responses: an epoch of 300–450 ms after the array presentation (initial epoch) was selected for the transient responses because the time to peak response was ~375 ms, and an epoch of 700–1300 ms (second epoch) was selected to capture the sustained responses. Two velocity epochs were also selected accordingly to measure the transient and sustained responses separately: epoch of 200–300 ms (initial epoch) for the transient responses was used because the time to peak velocity was ~245 ms, and epoch of 450–850 ms (second epoch) was used for the sustained responses.

Microsaccades were detected using the established algorithm (Engbert & Kliegl, 2003; Engbert & Mergenthaler, 2006) that has been implemented in our lab previously (Watanabe, Matsuo, Zha, Munoz, & Kobayashi, 2013; Yip et al., 2018). Briefly, the velocity threshold of fixational saccades was defined flexibly depending on the noise level on each trial (threshold: 6 SDs). The minimum duration of fixational saccades that exceeded the velocity threshold was set to 6 ms. This analysis was limited to a temporal period in which eye positions were relatively stable (required central fixation period). The amplitude, direction, and peak velocity of microsaccades were analyzed. Microsaccade rate was first calculated on an individual subject (averaged all trials in each condition), then rates for the corresponding conditions were averaged across participants. Following previous research (e.g., Engbert & Kliegl, 2003; Laubrock, Engbert, & Kliegl, 2005; Valsecchi & Turatto, 2009), the histogram of microsaccades was scaled to a rate-per-second measure (computed within a moving window of 100 ms). Analysis of microsaccade direction (or called orientation) was also conducted to examine the modulation of microsaccade direction by the pop-out item location. Analysis was performed in different time windows. In each condition, the number of microsaccades that occurred in a selected time window was first identified (N), and the number of microsaccades made toward the pop-out location (Npopout), i.e. orientation angle −π/12 < φ < π/12 (φ: microsaccade orientation relative to the pop-out item angle), or to the opposite location of the pop-out item location (Naway), i.e. orientation angle φ < −π/12 or π/12 < φ, was further classified (probability densities computed from 24 bins). Frequency of microsaccade toward (Npopout / N) or away (Naway / N) from the pop-out item in different conditions was then compared statistically. Microsaccade suppression and enhancement are well-documented (Hafed, 2011; Martínez-Conde et al., 2013; Rolfs, 2009). Therefore, two epochs across experiments were selected to capture microsaccade
suppression (150–200 ms after array onset) because the time to peak response was $\sim 195$ ms, and the enhancement epoch of 225–400 ms was selected because the time to peak response was $\sim 395$ ms.

To specifically examine our hypothesis that the pop-out condition should evoke greater pupil as well as microsaccadic responses than other conditions, the planned comparisons between the pop-out condition and the mixed-color or single-color condition in Experiment 1 were performed using Student t-test after one way repeated-measure ANOVA. To correct alpha levels for multiple t-tests for different time epoch data, p values of planned comparisons from two time epoch results were corrected using Bonferroni-Holm method (Holm, 1979; White, Berg et al., 2017). In Experiment 2, the student two-tailed t test was used for the comparison between the relevant and irrelevant condition. Nonparametric test (Wilcoxon signed-rank two-tailed) was performed on analyses for microsaccade direction due to the deviation from normality of the data. The Bonferroni-Holm method was used to perform on analyses for microsaccade direction due to the deviation from normality of the data. The Bonferroni-Holm method was used to correct multiple t-tests for different time epoch data. Effect sizes, where appropriate, were also reported. In addition, Bayesian t tests, where appropriate, were performed to inform statistical significance for pairwise comparisons, with a scale factor $r = 0.707$ (Rouder, Speckman, Sun, Morey, & Iverson, 2009). Note that microsaccade direction analysis in the inhibition epoch was unable to perform because of a very limited number of observations resulted from microsaccade suppression. Statistical tests were performed using JASP Team (JASP Team, 2019), SPSS (SPSS IBM, New York, NY, USA) and MATLAB (The MathWorks Inc., Natick, MA, USA).

3. Results

3.1. Exp 1: Larger pupil dilation observed in the pop-out stimulus presentation

Participants performed well in the saccade condition with correct saccadic responses generated on 92 % of trials and a mean SRT of 331 ms. Fig. 2A illustrates pupil dynamics after the stimulus presentation, showing initial pupil dilation following with pupil constriction in all three fixation conditions (pop-out, mixed-color, single-color). Differences in pupil size in the initial epoch (300–450 ms after stimulus onset) were significantly different, with mean pupil size being 0.06 mm, 0.073 mm, and 0.062 mm in the pop-out, mixed-color, and single-color conditions, respectively (Fig. 2B, F(2,50) = 6.56, $p = 0.004$). As mentioned, the comparisons between the pop-out and mixed-color or single-color conditions are of theoretical interest because the most conspicuous stimulus can only be computed in the pop-out condition according to the saliency model (e.g., Koch & Ullman, 1985; Itti & Koch, 2001), not other two “control” conditions, given that there was no more salient stimulus among all stimuli in the mixed-color or single-color condition. The results revealed significant differences between the pop-out and mixed-color conditions ($p = 0.006$, $r = 0.61$, BF = 43.109), and no differences between the pop-out and single-color conditions ($p = 0.593$, $r = 0.11$, BF = 0.237). Analysis of the differences in pupil size in the second epoch (700–1300 ms) also revealed significant differences among three conditions (Fig. 2C, F(2,50) = 10.827, $p < 0.001$). Mean pupil sizes were $-0.0055$ mm, $-0.030$ mm, and $-0.051$ mm in the pop-out, mixed-color, and single-color conditions, respectively, with significantly larger pupil size in the pop-out than the mixed-color condition ($p = 0.046$, $r = 0.48$, BF = 4.151) or the single-color condition ($p = 0.004$, $r = 0.65$, BF = 119.092).

Similarly, analysis of pupil velocity demonstrated the same pattern of results. Pupil velocity was slightly increased in the initial epoch after stimulus presentation and was then followed with a sharp decrease (Fig. 2D). Mean pupil velocities in the initial epoch (200–300 ms) were 0.15 mm/s, 0.17 mm/s, and 0.17 mm/s in the pop-out, mixed-color, and single-color conditions, respectively (Fig. 2E, F(2,50) = 2.027, $p = 0.15$), with similar pupil velocities between the pop-out and mixed-color conditions ($p = 0.196$, $r = 0.34$, BF = 0.876) and between the pop-out and single-color conditions ($p = 0.196$, $r = 0.34$, BF = 0.876) and between the pop-out and single-color conditions ($p = 0.196$, $r = 0.34$, BF = 0.876) and between the pop-out and single-color conditions ($p = 0.196$, $r = 0.34$, BF = 0.876) and between the pop-out and single-color conditions ($p = 0.196$, $r = 0.34$, BF = 0.876). Mean pupil velocities in the second epoch (450–850 ms) were $-0.14$ mm/s, $-0.24$ mm/s, and $-0.23$ mm/s in the pop-out, mixed-color, and single-color condition, respectively (Fig. 2F, F(2,50) = 26.042, $p < 0.001$), with significantly larger pupil velocities in the pop-out condition than in the mixed-color condition ($p = 0.004$, $r = 0.73$, BF = 1687.681) or in the single-color condition ($p = 0.004$, $r = 0.77$, BF = 7794.635). Overall, the results showed less reliable differences in the transient pupil responses, but more reliable differences in the sustained pupil responses, with significantly larger pupil response sizes in the pop-out condition than in the mixed-color or single-color conditions. These results were consistent with our previous study of SC recording in behaving monkeys, showing reliable pop-out saliency modulation in the sustained but not transient SC activity (White, Kan et al., 2017).

3.2. Microsaccade responses evoked by stimulus presentation

Fig. 3A illustrates microsaccade response dynamics after the stimulus presentation, showing microsaccadic suppression followed by microsaccade enhancement after the stimulus presentation. Frequency of microsaccade generation in the suppression epoch (150–200 ms) was similar among three conditions, with mean frequencies being 0.13

Fig. 2. Effect of salience on pupil responses. A) Change in pupil diameter following the array presentation in different conditions. B-C) The mean pupil size at initial epoch (B) and second epoch (C) in different conditions for each individual participant. D) Pupil velocity following the array presentation in different conditions. E-F) The mean pupil velocity at initial epoch (E) and second epoch (F) in different conditions for each individual participant. In A,D, the shaded regions surrounding the pupillary response represent ± standard error range (across participants) for different conditions. In B,C,E,F, the error-bars represent ± standard error across participants. n: number of participants. * indicates $p < 0.05$. 


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counts/s, 0.046 counts/s, and 0.025 counts/s in the pop-out, mixed-color, and single-color conditions, respectively (Fig. 3B, F(2,50) = 2.199, p = 0.132). Pair-comparisons showed similar microsaccade generation frequencies between the pop-out and mixed-color conditions (p = 0.784, r = 0.33, BF = 0.454) or between the pop-out and single-color conditions (p = 0.208, r = 0.79, BF = 2.996). Frequency of microsaccade generation in the enhancement epoch (225–400 ms) was not different among the three conditions, with mean frequencies being 0.52 counts/s, 0.40 counts/s, and 0.46 counts/sec in the pop-out, mixed-color, and single-color conditions, respectively (Fig. 3C, F(2,50) = 1.442, p = 0.247). Pair-comparisons showed non-significantly larger microsaccade generation frequency in the pop-out than the mixed-color condition (p = 0.594, r = 0.59, BF = 1.014), and no differences were observed between the pop-out and single-color conditions (p = 0.784, r = 0.087, BF = 0.253). Overall, microsaccade generation was not modulated by different presentation conditions, with some insignificant differences in generation frequency between the pop-out than the mixed-color or single-color conditions. Because microsaccade direction can be modulated by exogenous or endogenous cues (stimulus presented in the periphery or in the center to inform the target location) (Hafed, 2011; Martinez-Conde et al., 2013; Rolfs, 2009), we further analyzed microsaccade direction relative to the pop-out item location (see Methods for details) in the pop-out condition to examine whether microsaccade direction was biased by the pop-out item location. The results showed no biases between toward and away microsaccade direction relative to the pop-out stimulus location in the enhancement epoch (Fig. 4, z = 0.0162, p = 0.8264, r = 0, BF = 0.216).

3.3. Exp 2: SRT differences between the relevant and irrelevant pop-out condition

The pop-out item was goal-irrelevant to participants in Experiment 1, but it is known that top-down processes influence behaviors including saccadic eye movements (Fecteau & Munoz, 2006; Munoz & Everling, 2004; Talsma, Coe, Munoz, & Theeuwes, 2010; Theeuwes, 2010). To understand the influence of top-down processes in the pop-out condition, we further manipulated the relevance of the pop-out item in the array in Experiment 2 (Fig. 1B) by sometimes making the pop-out item a subsequent saccadic goal (relevant condition) or sometimes keeping it irrelevant (irrelevant condition).

Participants were required to generate a saccade to the saccadic target in both relevant and irrelevant conditions, so we first compared SRT between the relevant (saccade to the array pop-out stimulus) and irrelevant (saccade to a white peripheral stimulus) conditions. Because neural discharge of a single neuron in the SC is larger following presentation of a single item presentation compared to a pop-out item in the array presentation (White, Kan et al., 2017), SRT to the single stimulus should be faster than that to the array pop-out stimulus. Moreover, the luminance level of a saccadic target in the irrelevant condition was brighter than in the relevant condition (see Methods), thus further enlarging SRT differences between the two conditions. Fig. 5 illustrates the distribution of SRTs in the relevant and irrelevant conditions. Consistently, SRTs were significantly slower in the relevant condition (pop-out item in the array) than those in the irrelevant conditions (high contrast single white item), with mean SRT being 333 ms and 282 ms in the relevant and irrelevant conditions, respectively (t(19) = 3.34, p = 0.0035, r = 0.61, BF = 12.1627). Despite the general differences in SRT, the frequency of short latency saccades (160–180 ms) was higher in the relevant than in the irrelevant condition (sign test: z = 3.2, p = 0.0015, BF = 9.3621), suggesting some influences of goal-relevant processing.

3.4. No goal-relevant modulation on pupil responses

Pupil dynamics after the stimulus presentation in Experiment 2 are displayed in Fig. 6A. Similar to Experiment 1, initial pupil dilation was followed by pupil constriction. Identical epochs were used to compare the differences between the two conditions, showing similar pupil responses in the initial epoch (300–450 ms), with mean pupil sizes being 0.041 mm and 0.041 mm in the relevant and irrelevant conditions, respectively (Fig. 6B, t(19) = 0.079, p = 0.94, r = 0.018, BF = 0.2382). No differences between the two conditions were observed in the second epoch (700–1300 ms), with mean pupil sizes being 0.036 mm and 0.045 mm in the relevant and irrelevant conditions, respectively (Fig. 6C, t(19) = 1.07, p = 0.6, r = 0.24, BF = 0.3920). Similar results were obtained for the velocity analysis (Fig. 6D), there were no differences in the initial epoch (200–300 ms), with mean pupil velocities being 0.55 mm/s and 0.58 mm/s in the relevant and irrelevant conditions.

![Fig. 3. Effect of salience on microsaccade responses. A) Change in microsaccade generation frequency following the array presentation in different conditions. B-C) The mean microsaccade rate at suppression epoch (B) and enhancement epoch (C) in different conditions for each individual participant. In A, the shaded regions surrounding the microsaccadic response represent ± standard error range (across participants) for different conditions. In B, C, the error-bars represent ± standard error across participants. n: number of participants.](image1)

![Fig. 4. Effect of salience on microsaccade direction on the pop-out condition. Normalized microsaccade direction density (microsaccade direction vector – pop-out item angle) in the enhancement epoch. Plotted in these polar histograms is the relative frequency of microsaccades (per cue direction and time window) in a given direction. Direction is defined by the angle of the polar coordinates of the microsaccade vector. Twenty-four equally spaced directional bins were used to produce the histogram.](image2)
conditions, respectively (Fig. 6E, t(19) = 0.5, p = 0.62, r = 0.11, BF = 0.2657), or in the second epoch (450–850 ms), with mean pupil velocities being −0.13 mm/s and −0.038 mm/s in the relevant and irrelevant conditions, respectively (Fig. 6F, t(19) = 1.21, p = 0.48, r = 0.11, BF = 0.4485). Together, these results suggested that there was no modulation of goal-relevance on the pupil responses.

3.5. Goal-relevant modulation on microsaccadic responses

Fig. 7A illustrates microsaccade response dynamics after the array presentation, similar to Experiment 1, showing microsaccadic inhibition following by enhancement. Dissimilar to the pupil results, microsaccade occurrence was slightly modulated by goal-relevance of the pop-out item. Mean microsaccade generation rates in the suppression epoch (150–200 ms) were 0.12 counts/s and 0.33 counts/s in the relevant and irrelevant conditions, respectively, with lower rates in the relevant condition than that in the irrelevant condition, though these effects were only approaching significance (Fig. 7B, t(19) = 2.21, p = 0.08, r = 0.45, BF = 1.6764). There were no differences between the two conditions in the enhancement epoch (225–400 ms), with mean microsaccade generation rates being 0.84 count/s and 0.87 count/s in the relevant and irrelevant conditions, respectively (Fig. 7C, t(19) = 1.38, p = 0.18, r = 0.3, BF = 0.5380).

Analysis of microsaccade direction revealed significant differences between the two conditions. Fig. 8 illustrates the frequency polar plot for microsaccade direction relative to the pop-out item in the array (0°: toward the pop-out item; 180°: away the pop-out item) between the relevant and irrelevant conditions (see Methods for details). Microsaccade direction relative to the pop-out item location in the enhancement epoch (225–400 ms) was significantly modulated by goal-relevance (Fig. 8A), with higher frequencies of “toward” microsaccades in the relevant condition than those in the irrelevant condition (z = 2.7, p = 0.0142, r = 0.427, BF = 6.228), and no frequency differences in “away” microsaccades between the two conditions (z = 0, p = 1, r = 0, BF = 0.233).

4. Discussion

A repertoire of orienting responses, including not only saccades, but also pupil responses and microsaccades, is evoked after the appearance of a salient stimulus in the environment (Cornell & Munoz, 2014). The current study examined how salience and goal-relevance modulate pupil size and microsaccades in a visual pop-out paradigm. In Experiment 1, our results revealed larger pupil size in the second epoch in the pop-out condition than in the mixed-color or single-color conditions (Fig. 2). Microsaccadic responses, however, were not modulated by the saliency manipulation, with similar rates of microsaccades between the pop-out and mixed-color or single-color conditions (Fig. 3). Microsaccade direction was not modulated by the pop-out item location either, with similar frequencies of microsaccade directions between “towards” and “away” conditions relative to the pop-out item location (Fig. 4). In Experiment 2, we further manipulated the goal-relevance of the pop-out item, so that the pop-out item in the array was either a subsequent saccadic target (relevant) or not (irrelevant). We found no differences in pupil responses between the two conditions (Fig. 6), and there was an insignificant trend with higher microsaccade suppression in the relevant compared to irrelevant condition (Fig. 7). Significantly higher frequencies of microsaccades directed toward the pop-out item
in the relevant than irrelevant condition in the enhancement epoch were observed (Fig. 8). Overall, our results demonstrated that pupil size in Experiment 1 was modulated by the bottom-up saliency manipulation, while microsaccade direction was modulated by the goal-relevancy priority in Experiment 2.

4.1. Relationship between pupil size and salience

Pupil size has long been characterized as a component of orienting (Lynn, 1966; Sokolov, 1963a). A series of studies have shown that pupil dilation is consistently observed after the appearance of a salient stimulus (Bala & Takahashi, 2006; Loewenfeld, 1999; Netser, Ohayon, & Gutfreund, 2010; Qiyuan, Richer, Wagoner, & Beatty, 1985), and the modulation is not simply due to changes in overall luminance, because similar pupil responses can be evoked by presentation of acoustic stimulation (Gutfreund, 2010; Qiyuan, Richer, Wagoner, & Beatty, 1985), and the pupil dilation is consistently observed after the appearance of a salient stimulus (Bala & Takahashi, 2006; Loewenfeld, 1999; Netser, Ohayon, & Gutfreund, 2010; Qiyuan, Richer, Wagoner, & Beatty, 1985), and the pupil responses scale with stimulus contrast (Stelmack & Siddle, 1982; Wang & Munoz, 2014; Wang et al., 2014). Notably, pupil constriction after presentation of salient stimuli? Pupil dilation after stimulus presentation is thought to increase visual sensitivity to heighten perception to efficiently discern what is happening for appropriate actions required for survival (Sokolov, 1963b). This function could explain the differences between fovea and non-fovea presentation because a salient stimulus presented on fovea may have strong enough visual sensitivity, resulting pupil constriction. But this account still cannot explain why the pupil constricts after peripheral stimulus presentation (e.g., Binda et al., 2013, 2017). It is important to note that because pupil size is controlled by the balanced activity between para-sympathetic and sympathetic systems (Loewenfeld, 1999; McDougall & Gamlin, 2015), factors such as background luminance, task requirements that could have a biased influence on the activity level of either system are not identical across these studies, These factors may in turn change reaction of the pupil towards a salient presentation. Although it is to be determined under what situations the pupil dilates or constricts following the appearance of a salient stimulus in the environment, the pupil clearly associates to salient presentation.

Here, we further extended the relationship between salience and pupil size by presenting multiple stimuli with carefully controlled luminance level during the task. Salience modulation in pupil responses was observed in the second epoch, and not in the initial epoch, which are consistent with our previous studies describing the responses of neurons recorded in the SC of monkeys performing similar tasks (White, Kan et al., 2017). These monkey neurophysiological results show that the discharge of individual neurons was modulated by a pop-out item during the sustained epoch. Together, these results demonstrated saliency modulation on pupil size. The absence of goal-relevance effects in Experiment 2 may suggest that pupil size was less sensitive to the top-down (priority) processes in the pop-out paradigm. It is also possible that top-down modulation of pupil size is relatively small, and pronounced transient pupil responses evoked by the presentation of the pop-out array masked any subtle top-down response that can be observed on pupil size. Future study is required to explore these possibilities in the context of the pop-out paradigm.

4.2. Modulation of microsaccades by salience and priority

Research on microsaccades has received considerable attention over the past decade, and converging evidence has found a reliable link between microsaccade dynamics and cognitive processes, particularly in the allocation of attention (Hafed, 2011; Martinez-Conde et al., 2013; Rolfs, 2009). Microsaccade dynamics are linked to salience because microsaccade occurrence is modulated by presentation of salient stimuli, with initial suppression followed by enhancement in frequency after salient stimuli (e.g., Engbert & Kliegl, 2003; Hafed & Clark, 2002; Valsecchi & Turatto, 2009). Furthermore, similar microsaccade dynamics after stimulus presentation are observed between presentation of visual and auditory stimuli (Valsecchi & Turatto, 2009; Wang et al., 2017). Microsaccade direction is also modulated by stimulus presentation: more microsaccades are directed toward the stimulus location (exogenous attention) (Hafed, 2011; Martinez-Conde et al., 2013;
Rolfs, 2009). Here, we found that microsaccade direction in Experiment 2 was also biased toward the pop-out array item location when the pop-out item was a subsequent saccadic target, compared to when it was not. However, we found that microsaccade frequencies were not modulated by both saliency and priority signals. The absence of some microsaccade modulations could be due to a number of reasons. First, to maintain the luminance level across multiple-array displays during the trial, an array of isoluminant gray stimuli was present in the beginning of the trial. The pop-out effects could thus be reduced because the locations of stimuli were already revealed before the pop-out display. Second, the involvement of multiple displays with a large number of items reduced the occurrence of microsaccades (typically less than 1/s). Expected effects of saliency and priority on microsaccades could be eliminated due to the resulting lower rate of microsaccades (Engbert & Kliegl, 2003; Tse, Shinberg, & Logothetis, 2002). Lastly, to examine various responses in the context of orienting, saccadic eye movements were required to engage participants’ attention during the task. The requirement of these saccades may have changed the dynamics of microsaccade responses because of involving saccade preparation during presentation of the array, as differences in task performance have been reported between saccade and key–press responses (e.g., Geiger, Niessen, Bente, & Vogeley, 2017). Although previous research has found consistent microsaccade effects on tasks with or without saccades (Engbert & Kliegl, 2003), our results may not be generalized to the task involving no saccades. Future study is required to address these questions.

4.3 A coordinated role of the SC on pupil size and microsaccades

Through several lines of evidence, research has suggested that the superior colliculus (SC) is essential not only in the generation of saccadic eye movements, but also in coordinating pupil size and microsaccades (Cornell & Munoz, 2014; Hafed, Goffart, & Krauzlis, 2009; Hafed, 2011; Wang & Munoz, 2015). Transient pupil dilation can be evoked by weak electrical microstimulation of the SC of behaving monkeys (Wang et al., 2012). Furthermore, the effects of stimulus contrast, modality, and saccade preparation on the pupil response (Wang, Brien, & Munoz, 2015; Wang & Munoz, 2014; Wang et al., 2014, 2016) are similar to those observed on activity recorded from single neurons in the SC (Everling, Dorris, Klein, & Munoz, 1999; Marino et al., 2012; Wise & Irvine, 1983). Moreover, the SC has been implicated in the generation of microsaccades, showing movement-related neural activity prior to microsaccade onset, with each neuron spatially tuned to a certain microsaccade direction and amplitude similar to tuning observed for macrosaccades (Hafed & Krauzlis, 2012; Hafed et al., 2009).

The SC has also been suggested as a promising neural candidate for the computation of visual salience (Fecteau & Munoz, 2006; White & Munoz, 2011). It has recently been shown that SC activity is modulated by an oddball item in the pop-out paradigm (White, Kan et al., 2017). Large activity is observed when an oddball item than when a non-oddball item is in the responsive field of a corresponding neuron. Importantly, the differences in discharge are particularly pronounced in the sustained activity. These results are consistent with our pupil results, showing the reliable saliency modulation on sustained pupil responses. However, if microsaccade generation is also coordinated through the SC, how can it explain that saliency effects were not reliably observed in our paradigm, and that the priority modulation was also dismissed in pupil size and microsaccade rate? These results may suggest similar, but not identical, mechanisms in the involvement of the SC between pupil size and microsaccades because pupil size is additionally modulated by the autonomic nervous system. Furthermore, how does activity throughout the SC map transform to one-dimension space to modulate pupil size and microsaccade occurrence, but transform to two-dimension space to modulate microsaccade direction? Future research is needed to address the distinctive role of the SC between pupil size and microsaccades, and transformation processes between SC activity and changes in pupil size and microsaccade generation frequency.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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