



ELSEVIER

Contents lists available at SciVerse ScienceDirect

# Neuropsychologia

journal homepage: [www.elsevier.com/locate/neuropsychologia](http://www.elsevier.com/locate/neuropsychologia)

## Saliency affects feedforward more than feedback processing in early visual cortex



Tatiana Aloï Emmanouil, Philip Avigan, Marjan Persuh, Tony Ro\*

Department of Psychology and Program in Cognitive Neuroscience, The City College and Graduate Center of the City University of New York, USA

### ARTICLE INFO

#### Article history:

Received 2 March 2013

Received in revised form

19 April 2013

Accepted 23 April 2013

Available online 30 April 2013

#### Keywords:

Early visual cortex

Saliency

TMS

Attention

Awareness

### ABSTRACT

Early visual cortex activity is influenced by both bottom-up and top-down factors. To investigate the influences of bottom-up (saliency) and top-down (task) factors on different stages of visual processing, we used transcranial magnetic stimulation (TMS) of areas V1/V2 to induce visual suppression at varying temporal intervals. Subjects were asked to detect and discriminate the color or the orientation of briefly-presented small lines that varied on color saliency based on color contrast with the surround. Regardless of task, color saliency modulated the magnitude of TMS-induced visual suppression, especially at earlier temporal processing intervals that reflect the feedforward stage of visual processing in V1/V2. In a second experiment we found that our color saliency effects were also influenced by an inherent advantage of the color red relative to other hues and that color discrimination difficulty did not affect visual suppression. These results support the notion that early visual processing is stimulus driven and that feedforward and feedback processing encode different types of information about visual scenes. They further suggest that certain hues can be prioritized over others within our visual systems by being more robustly represented during early temporal processing intervals.

© 2013 Elsevier Ltd. All rights reserved.

### 1. Introduction

It has been known for nearly a century that early visual cortex is crucial for vision in humans, with lesions to this region producing stereotypical visual field deficits (Holmes, 1918). Furthermore, neurons within areas V1 and V2 in early visual cortex have been shown to produce highly specific and consistent responses to visual information, such as edges and orientations, even in anesthetized animals (Hubel & Wiesel, 1968; Livingstone & Hubel, 1988). Based on these long-standing observations, it had originally been assumed that visual information processing in V1/V2 proceeds automatically and independently from bottom-up and top-down factors, such as stimulus feature saliency (differences in hue, size, etc.) and attentional set (attention to certain features, locations, temporal intervals, sensory modalities, etc.).

However, several studies have shown that V1/V2 does not only serve as a passive relay of information to higher-order areas, but instead amplifies responses to salient bottom-up information (Li, 1999; Li, Piech, & Gilbert 2006), is involved beyond the initial stages of visual information processing via feedback loops (Lamme & Roelfsema, 2000), and is influenced by top-down factors such as

attention (Motter, 1993; Somers, Dale, Seiffert, & Tootell 1999) and task (Huk & Heeger, 2000). The time course of these bottom-up and top-down influences, nevertheless, remains unclear. For example, some evidence suggests that bottom-up factors, such as saliency, should influence processing in V1 at early temporal intervals (for a review see Theeuwes, 2010), whereas top-down factors, such as attentional set, should affect later processing. Other evidence, however, suggests that attention may influence early neuronal responses in V1 (Ito & Gilbert, 1999) and that saliency maps are generated in the posterior parietal cortex after initial processing (Gottlieb, Kusunoki, & Goldberg 1998; but see Zhang, Zhaoping, Zhou, & Fang 2012).

In the current study we manipulated bottom-up feature saliency as well as top-down attentional set to investigate how these variables affect early visual cortex activity at different time intervals. We applied TMS over V1/V2 at varying temporal intervals after stimulus onset to assess whether the magnitude of visual suppression (Amassian, Cracco, Maccabee, Cracco, Rudell, & Eberle, 1989; Kammer, 2007) was affected by saliency and attentional set. If bottom-up saliency differences influence processing in V1/V2 only at early temporal intervals, then we should find that TMS at early temporal intervals produces different magnitudes of suppression based on stimulus feature saliency, regardless of attentional set. Furthermore, if top-down attentional set differences influence processing in V1/V2 only at later temporal intervals, then we should find that TMS at later temporal intervals produces

\* Correspondence to: NAC 7/120, Department of Psychology, 160 Convent Avenue, The City College of New York, New York, NY 10031, USA. Tel.: +1 212 650 5160.  
E-mail address: [tro@ccny.cuny.edu](mailto:tro@ccny.cuny.edu) (T. Ro).

different magnitudes of suppression based on attentional set, regardless of feature saliency differences.

## 2. Experiment 1

In Experiment 1, we compared the magnitude of visual suppression while subjects performed an orientation or a color discrimination task on stimuli that varied in saliency. According to a standard definition, saliency depends on the bottom-up distinctiveness of a physical stimulus relative to its surround (Fecteau, Chua, Franks, & Enns, 2001). In our experiment, saliency was manipulated by changing the distinctiveness of the color of a single line relative to the color of the background. More specifically we presented red and green lines on a gray background that was mostly comprised of the green phosphor, as is usually the case for grayscale stimuli on a cathode ray tube (CRT) monitor (Breitmeyer, Ro, & Singhal, 2004). We chose to compare green, which was more similar to the background, with its opposite color red, expecting red to be more salient than green under these conditions.

### 2.1. Method

#### 2.1.1. Subjects

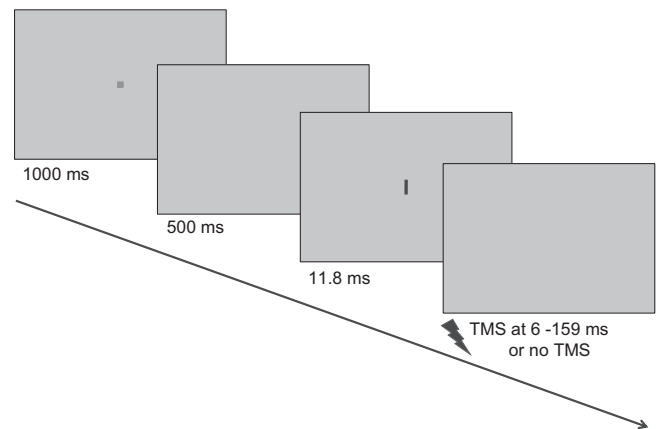
Eight subjects (5 males; mean age of 23.25 years; range of 19–30 years) gave written informed consent and took part in the experiment for monetary compensation. This study was approved by the Institutional Review Board of the City University of New York. All subjects reported normal or corrected to normal vision, which was confirmed by a short vision test using a Snellen Eye Chart.

#### 2.1.2. Stimuli

Stimuli were presented on a Sony Trinitron GS220 CRT monitor, running at an 85 Hz refresh rate, using custom software written in Visual C++ with Microsoft DirectX libraries. Luminance was measured using a UDT Instruments S370 Optometer on the particular monitor, PC computer and experiment booth where the experiment was conducted. The stimuli were oriented lines (subtending  $.25 \times .06^\circ$  of visual angle) presented at the center of the monitor on a light gray background (CIE coordinates  $L=3.96$ ,  $x=.33$ ,  $y=.36$ ). On each trial, the orientation of the line was either horizontal or vertical and the color of the line was either red (CIE coordinates  $L=12.3$ ,  $x=.62$ ,  $y=.34$ ) or green (CIE coordinates  $L=12.8$ ,  $x=.29$ ,  $y=.60$ ). In this first experiment, the colors were matched in physical luminance, but varied in hue and saturation, with the red stimulus ( $s=3.1$ ) being more saturated than the green stimulus ( $s=1.6$ ). In producing the gray background, we set all three phosphors of the monitor (red, green and blue) to equal values to produce a perceptual gray. However, because the green phosphor on CRT monitors produces more light than the red and blue phosphors (Breitmeyer et al., 2004), the gray background was largely composed of the green phosphor.

#### 2.1.3. Task and procedure

Top-down attention to specific features was manipulated by having subjects perform an orientation or a color task in separate blocks, the order of which was counterbalanced across subjects. In both tasks, the subjects made two responses on each trial. For the first response, subjects indicated whether they saw (i.e., they consciously perceived) the stimulus feature. The second response required the subjects to perform a two-alternative forced choice (2AFC) discrimination of line orientation (horizontal or vertical) or color (red or green). Subjects were encouraged to guess for the second response, even when they were not aware of the stimulus



**Fig. 1.** Stimuli and design: A fixation spot was presented for 1000 ms and was followed after a 500 ms blank period by a small line stimulus. The line, which appears dark gray in the figure, was colored in the experiment. It varied in saliency (more salient red or less salient green) and in orientation (horizontal, vertical) and was presented for 11.8 ms. A TMS pulse followed at one of 14 SOAs. On 1/15th of the trials, no TMS was applied. In separate blocks, subjects judged either the orientation or the color of the line. Awareness and discrimination performance were measured on every trial.

feature, to assess TMS-induced blindsight as observed in our previous studies (Boyer, Harrison & Ro, 2005). All responses were made using the buttons on a standard computer mouse; the button response assignment was counterbalanced between subjects.

Each trial (Fig. 1) began with the presentation of a fixation square for 1000 ms followed by a 500 ms blank interval. The colored line was then presented for 11.8 ms (one frame). After the visual stimulus was presented, a TMS pulse was delivered on 14/15th of the trials at one of 14 different SOAs between 6 and 159 ms (6, 18, 29, 41, 53, 65, 76, 88, 100, 112, 124, 135, 147, and 159 ms). There were 24 trials per SOA and 24 control trials on which no TMS was delivered (the remaining 1/15th of the trials). The three conditions of main interest, saliency (more salient red, less salient green), task (orientation, color), and TMS (14 stimulation intervals and no TMS) were orthogonally manipulated. Overall, subjects completed 360 trials, the order of which was random. Subjects were given a short break every 15 trials, which also allowed for cooling of the TMS coils. The two measures of interest were the proportion of aware responses and discrimination accuracy.

#### 2.1.4. TMS procedure

TMS was conducted using a Cadwell Laboratories MES-10 polyphasic stimulator connected to a 9 cm circular coil. The site of stimulation was V1/V2, which was functionally localized by adjusting the position and intensity of the TMS until each subject was unable to detect the visual stimuli. Some indirect evidence that this type of occipital stimulation affects areas V1/V2 comes from studies that modeled the effects of occipital stimulation to visual cortex (Salminen-Vaparanta, Noreika, Revonsuo, Koivisto, & Vanni, 2012; Thielscher, Reichenbach, Ugurbil, & Uludag, 2010).

The coil was initially placed with its base approximately 1 cm above theinion and its intensity set at 50%. The position and intensity were then adjusted while subjects performed two different localization and intensity setting tasks. In the first, subjects were presented with four random numbers for 10 ms within a box frame in the center of the screen, after which a TMS pulse was administered at a fixed SOA of 95 ms. Subjects reported the numbers and subsequently received feedback by clicking the mouse and seeing the numbers again. The position and intensity of the TMS was adjusted until subjects could not see the numbers

(missed any of the four numbers in at least 3 out of 5 displays). Using the position and intensity parameters obtained in the first task, we next tested suppression of the actual stimuli used in the main experiment. We presented the stimuli and delivered the TMS at 3 optimal suppression SOAs (76, 88 and 100 ms), similar to those commonly used in studies of V1/V2 stimulation (Amassian et al., 1989; Ro et al., 2003). Further adjustments to the site and the intensity of TMS were made to produce optimal visual suppression (suppression of at least 3 out of 5 stimuli). This final location and intensity was then used for the remainder of the experiment. The mean intensity of the TMS across all participants was 70.8% of the maximum 2.2 T stimulator output.

## 2.2. Results

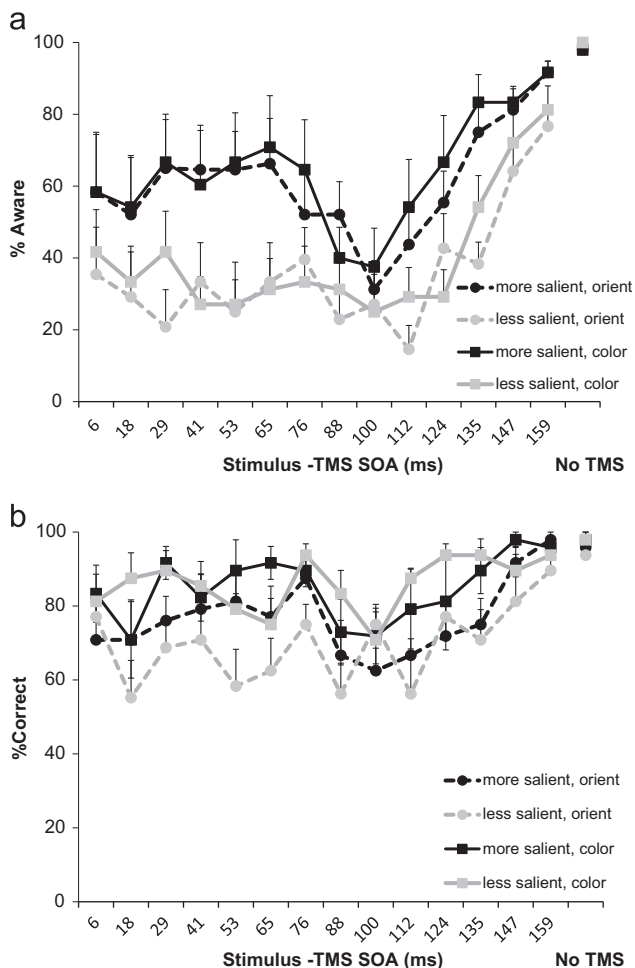
Trials in which the first response was slower than 4 s were excluded from the analysis (.7% of all trials). The awareness data (Fig. 2a) were submitted to a  $2 \times 2 \times 14$  ANOVA with bottom-up saliency (more salient red, less salient green), top-down attentional set (attention to color vs. orientation), and TMS condition (14 SOAs) as the three within-subject factors. There was a significant main effect of saliency ( $F(1,7)=42.34, p<.001$ ), with the more salient red stimuli showing more resistance to TMS-induced visual suppression than the less salient green stimuli. We also observed a main effect of TMS SOA

( $F(13,91)=7.54, p<.001$ ), replicating previous results of visual suppression with a peak at around 100 ms. However, there was no significant main effect of task ( $F(1,7)=.5, p=.50$ ) and no interaction of task with saliency ( $F(1,7)=.06, p=.81$ ) indicating that the color saliency effects were present regardless of whether subjects were attending to the color or the orientation. Importantly, there was a significant interaction between color saliency and TMS SOA ( $F(13,91)=2.81, p=.002$ ), which was due to less suppression of the more salient red color at earlier SOAs. There were no other significant effects. Thus, the main result of this experiment was that feature saliency influenced the magnitude of visual suppression more at early than at late TMS intervals.

A trends analysis corroborated the results of the omnibus ANOVA. We observed a significant quadratic trend for TMS SOA ( $F(1,7)=29.43, p=.001$ ), which was a consequence of the characteristic peak of visual suppression at 100 ms and slow recovery thereafter. In addition, there was a significant quadratic trend for the interaction between saliency and TMS SOA ( $F(1,7)=6.98, p=.03$ ). This quadratic trend was significant because the difference in visual suppression between the more salient red stimuli and less salient green stimuli was reduced at later time intervals.

The data from the 2AFC discrimination task (Fig. 2b) were also submitted to a  $2 \times 2 \times 14$  ANOVA with saliency, task, and TMS SOA as within-subject factors. The main effect of saliency was not significant ( $F(1,7)=1.37, p=.28$ ). The fact that we did not obtain similar saliency effects in discrimination as in awareness might be expected since discrimination, as opposed to our subjective awareness measure, is a 2AFC measure in which participants often employ strategies. For example, participants in the color task they may have strategically responded that a stimulus was green when they failed to perceive a salient red line. In this case, responses to a given stimulus are influenced by the entire set of stimuli in the experiment, thus making it difficult to examine the effect of each stimulus separately. The discrimination results did show a main effect of task ( $F(1,7)=20.58, p=.003$ ), with overall more accurate performance in the color task than in the orientation task, likely because discrimination between a horizontal and a vertical line was harder than discrimination between a more salient and a less salient color. As in the awareness results, there were no interactions of task with saliency ( $F(1,7)=2.52, p=.16$ ). There was also a main effect of TMS SOA ( $F(1,7)=4.31, p<.001$ ) suggesting that discrimination varied at different TMS SOAs. Furthermore, we found a significant quadratic trend for the effect of TMS SOA ( $F(1,7)=19.32, p=.003$ ); the discrimination results at the different TMS SOAs followed a similar pattern to the awareness results, with reduced performance at intermediate TMS SOAs.

We also analyzed the discrimination data separately for aware and unaware trials. For this analysis, we collapsed across TMS SOA because of the few number of unaware trials for the longer SOAs and the few number of aware trials for the shorter and intermediate SOAs. We obtained a large number of both aware and unaware responses, which allowed us to calculate discrimination accuracy for both types of responses with sufficient statistical power. The mean number of aware and unaware trials was similar both in the orientation (Aware:  $M=85.88, SD=36.41$ , Unaware:  $M=92.25, SD=37.64$ ) and the color (Aware:  $M=80.38, SD=33.5$ , Unaware:  $M=98.88, SD=34.15$ ) tasks. For aware trials, not surprisingly, performance was at ceiling for both the color ( $M=96.85\%, SD=2.87\%$ ) and the orientation ( $M=90.71\%, SD=9\%$ ) tasks. For unaware trials, which allowed an assessment of discrimination performance without awareness (i.e., TMS-induced blindsight), we examined whether performance exceeded the 50% level expected by chance. If discrimination is above chance for unaware trials, this would suggest the existence of TMS-induced blindsight, similar to that observed in our previous TMS studies (Boyer, Harrison, & Ro, 2005) and in patients with V1 damage (Poppel, Held, & Frost, 1973; Weiskrantz, Warrington, Sanders, & Marshall, 1974). Based on this previous



**Fig. 2.** Awareness and discrimination results for Experiment 1: (a) Awareness performance for the two levels of saliency (more salient red and less salient green, shown in black and light gray) and the two tasks (orientation and color, shown in dashed and solid lines) for each TMS SOA and the No TMS condition. Visual suppression was reduced for the salient red stimuli, especially at early SOAs. (b) Discrimination performance was reduced at intermediate SOAs. Error bars indicate one standard error of the mean.

evidence demonstrating above chance discrimination without awareness we performed one-tailed *t* tests. Accuracy was significantly better than chance in the color task (75.41%,  $SD=15.08\%$ ;  $t(7)=4.78$ ,  $p=.002$ ) and approached significance in the orientation task (57.23%,  $SD=13.3\%$ ;  $t(7)=1.48$ ,  $p=.09$ ). Blindsight for color was greater than blindsight for orientation ( $t(7)=4.43$ ,  $p=.003$ ). These results suggest that color, and perhaps the more difficult orientation judgments, can be accurately performed in the absence of awareness and of early visual cortex activation. Note that the blindsight effects reported here may be underestimated since we analyzed unaware trials from all SOAs, even the later SOAs that have been shown to produce no blindsight (Koivisto, Mantyla, & Silvanto, 2010). The fact that we observed blindsight including after including these later SOAs suggests that the blindsight effect in this study was quite robust.

The results of Experiment 1 showed that saliency influences processing in V1/V2 and that this effect varies with time. We found that salient red stimuli were more resistant to TMS-induced visual suppression (i.e., not as strongly suppressed) than green stimuli, especially during early intervals of stimulation and regardless of top-down attentional set to color or orientation. At later processing intervals however, the advantage of red stimuli was reduced. These differences between early and later intervals suggest that saliency differences in V1/V2 are more prominent during feedforward as opposed to feedback processing.

### 3. Experiment 2

In Experiment 2 we tested the possibility that the saliency effect we observed in Experiment 1 was due to an inherent processing advantage of red over other hues, as opposed to just the color contrast with the green-dominated surround. Several studies point to a possible advantage of the color red. For example red hues receive priority in visual search (Lindsey, Brown, Reijnen, Rich, Kuzmova, & Wolfe, 2010), have reduced inattentive blindness (Mack & Rock, 1998), and show decreased masking (Breitmeyer & Williams, 1990). Therefore, we reasoned that saliency in the first experiment might have been at least partly driven by the red color itself.

In order to test this hypothesis, in Experiment 2 we eliminated color contrast by introducing a black background that was no more similar to green compared to red. Subjects were presented with red, green, and blue lines that were horizontal or vertical in orientation. The blue stimulus was included in order to (1) compare red with an additional color, and (2) control for saturation effects, since the blue stimuli were similarly saturated to the red stimuli, and both the red and blue stimuli were more saturated than the green stimuli. Because we found no differences between the color and orientation tasks in Experiment 1, subjects only performed the color task in Experiment 2.

Furthermore, in Experiment 2 we manipulated discrimination difficulty by separating the three colors into two different block difficulty conditions: in the easy blocks participants saw only red and green lines, which were highly discriminable from each other, whereas in the difficult block they saw blue and green lines, which were harder to discriminate from one another. Importantly, the green stimuli used in the two blocks were identical. This experiment thus also allowed us to address the question of whether task difficulty, independent of stimulus features, plays a role in visual suppression.

#### 3.1. Method

##### 3.1.1. Subjects

Sixteen subjects (13 males; mean age of 22.9 years; range of 19–36 years), five of whom participated in the previous experiment, completed this experiment, which was approved by the

Institutional Review Board of the City University of New York. All gave informed consent, reported normal or corrected-to-normal vision, which was confirmed by a short vision test using a Snellen Eye Chart, and received monetary compensation for their participation.

##### 3.1.2. Stimuli, task, and procedure

The stimuli and procedures used in Experiment 2 were identical to Experiment 1, except for the following. The lines were red ( $L=10$ ,  $x=.62$ ,  $y=.34$ ), green ( $L=10.4$ ,  $x=.29$ ,  $y=.60$ ) or blue ( $L=9.7$ ,  $x=.16$ ,  $y=.09$ ) on a black background. The red and blue stimuli used in this experiment were similar in saturation and more saturated than the green stimuli (for red  $s=3$ , for green  $s=1.57$  and for blue  $s=3.4$ ). The functional localization of visual cortex was performed as described for Experiment 1 except for the use of the new red and green colors, which were of lower luminance than those of Experiment 1 and were presented on a black background. The mean intensity of TMS in this experiment was 75.6% of maximum stimulator output.

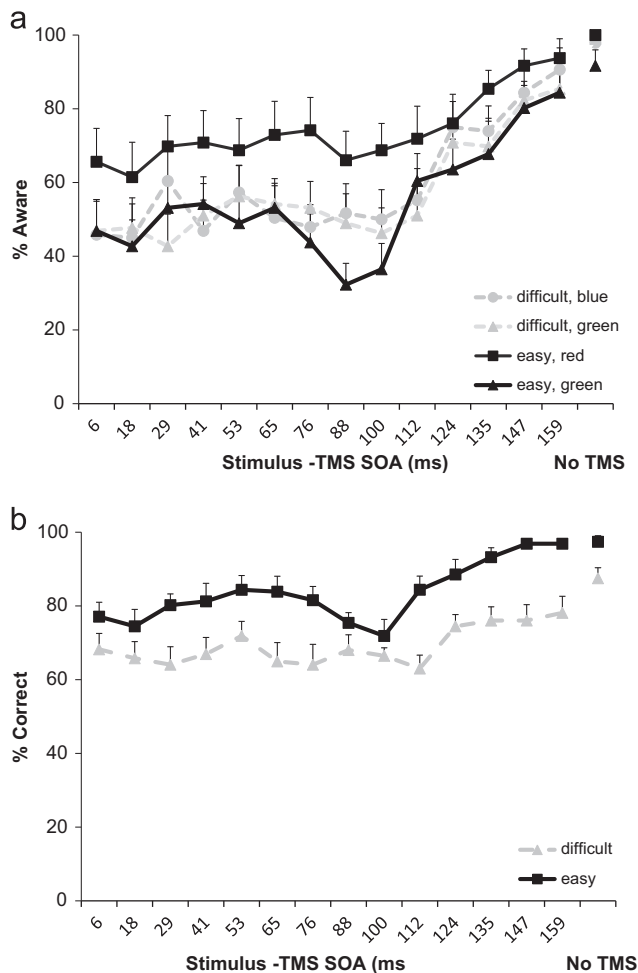
Since we found no effect of task in Experiment 1, subjects performed only the color task in Experiment 2 in two different discrimination difficulty blocks: easy perceptual discrimination blocks, in which the line hues were farther from each other in color space (red and green), and difficult perceptual discrimination blocks, in which the hues were closer to each other in color space (green and blue). The order of the blocks was counterbalanced across subjects. As before, the task required subjects to make two responses, first indicating their awareness of color and then discriminating/guessing which color was presented. The orientation of the lines was still orthogonally manipulated, but remained task-irrelevant throughout this experiment. The overall number of trials was the same as in Experiment 1. However, due to the addition of a difficult discrimination block, the number of trials per color was halved compared to Experiment 1. In order to compensate for this, we ran twice as many subjects in Experiment 2 than in Experiment 1.

#### 3.2. Results

The two measures of interest were the proportion of aware responses and discrimination accuracy. Trials in which the awareness (first) response was slower than 4 s were excluded from the analysis (.2% of all trials).

The awareness data (Fig. 3a) were analyzed separately for each block (easy, difficult) with color (red and green in the easy discrimination block or blue and green in the difficult discrimination block) and TMS SOA (14 intervals) as the within-subject factors. For the easy discrimination block, there was a main effect of color ( $F(1,15)=66.8$ ,  $p<.001$ ) as well as a main effect of TMS SOA ( $F(13,195)=7.16$ ,  $p<.001$ ). As in Experiment 1, the more salient red stimuli were less suppressed than the green, and this difference was stronger at the early SOAs. Although the interaction between color and TMS SOA did not reach significance ( $F(13,195)=1.53$ ,  $p=.11$ ), the trend analysis showed a significant interaction for the quadratic trend ( $F(1,15)=9.37$ ,  $p=.008$ ). For the difficult discrimination block, the ANOVA showed only an effect of TMS SOA ( $F(13,195)=7.97$ ,  $p<.001$ ), with no differences between the green and blue colors ( $F(1,15)=.37$ ,  $p=.55$ ) indicating that the green and blue colors were equally susceptible to TMS-induced suppression.

Next, we investigated the role of discrimination difficulty on awareness by comparing visual suppression for the identical green stimulus in the easy and difficult discrimination blocks. If discrimination difficulty has an effect on visual suppression, then we should observe differences in the magnitude of suppression for the same green stimulus when it was easier to discriminate (i.e., when



**Fig. 3.** Awareness and discrimination results for Experiment 2. (a) Awareness performance for three colors (red, blue and green, shown in dark, medium, and light gray respectively) in the two contextual discrimination difficulty tasks difficult and easy shown in solid and dashed lines respectively. Visual suppression was again reduced for the red stimulus. In addition, the green stimulus showed similar suppression regardless of contextual difficulty. (b) Discrimination was better for the easy compared to the difficult task. Error bars indicate one standard error of the mean.

it had to be discriminated from a more distinct red stimulus) compared to when it was harder to discriminate (i.e., when it had to be discriminated from a more similar blue stimulus). The awareness data from the trials with the green stimulus were submitted to a  $2 \times 14$  ANOVA with discrimination difficulty (easy, difficult) and TMS SOA (14 intervals) as within-subject variables. There was an effect of TMS SOA ( $F(13,195)=7.17$ ,  $p < .001$ ), but no main effect of discrimination difficulty ( $F(1,15)=.85$ ,  $p=.37$ ) suggesting that discrimination difficulty does not differentially influence the magnitude of TMS-induced visual suppression.

As with the awareness data, discrimination performance (Fig. 3b) was analyzed using a  $2 \times 14$  ANOVA with task difficulty and TMS interval as within-subject variables. There was a main effect of task ( $F(1,15)=21.24$ ,  $p < .001$ ) with the easy task producing better performance than the difficult task. As in Experiment 1, there was also an effect of TMS SOA ( $F(13,195)=6.98$ ,  $p < .001$ ). The trends analysis showed both a linear ( $F(1,15)=11.28$ ,  $p=.004$ ) and a quadratic ( $F(1,15)=12.60$ ,  $p=.003$ ) trend for the effect of TMS SOA on discrimination performance. In addition, there was an interaction between task and TMS SOA ( $F(13,195)=1.78$ ,  $p=.049$ ). Discrimination

performance for the separate colors was not analyzed because, as discussed in the results of Experiment 1, discrimination performance is difficult to evaluate for each color separately, since it is affected by both colors. The analysis of the discrimination data shows that our difficulty manipulation was successful.

As in Experiment 1, we also analyzed discrimination performance, collapsed across all SOAs, separately for aware and unaware trials. We obtained a large number of aware and unaware trials both in the difficult (Aware:  $M=110.13$ ,  $SD=33.40$ , Unaware:  $M=69.5$ ,  $SD=33.10$ ) and the easy tasks (Aware:  $M=119.69$ ,  $SD=36.19$ , Unaware:  $M=60.13$ ,  $SD=36.08$ ), which allowed us to calculate discrimination performance separately for each task and awareness condition. In the aware trials, not surprisingly, discrimination performance was high for both the difficult ( $M=80.65\%$ ,  $SD=12.07\%$ ) and the easy blocks ( $M=94.48\%$ ,  $SD=6.41\%$ ). As expected, discrimination performance in the easy blocks was significantly higher than in the difficult blocks ( $t(15)=4.65$ ,  $p < .001$ ). For unaware trials, we again observed above-chance performance for the difficult ( $55.7\%$ ,  $SD=10\%$ ;  $t(15)=2.18$ ,  $p=.02$ ) and the easy ( $62.97\%$ ,  $SD=16.66\%$ ;  $t(15)=3.11$ ,  $p=.004$ ) discrimination tasks. The difference between unaware discrimination performance in the hard and easy tasks did not reach significance ( $t(15)=1.75$ ,  $p=.10$ ). Overall, the unaware discrimination results are consistent with Experiment 1 and with previous reports of blindsight in normal subjects under TMS-induced suppression of awareness (Boyer et al., 2005).

#### 4. Discussion

In the current study, we used TMS to examine bottom-up (color saliency) and top-down (attentional set) influences on processing in early visual cortex. The results show that color saliency influences the magnitude of TMS-induced visual suppression regardless of whether or not subjects attended to the color dimension.

Importantly, saliency effects were more prominent during early compared to later intervals of stimulation, suggesting differential representations of visual information at the early feedforward as compared to the later feedback stages of processing (Lamme & Roelfsema, 2000). Note that this result cannot be explained by TMS having overall larger effects on visual processing at earlier time intervals of stimulation after visual stimulus presentation because our suppression curves show that TMS of V1/V2 is most detrimental to vision at later time intervals (around 100 ms), when visual suppression reaches a peak. Furthermore, previous evidence suggests that visual suppression can differ at later post-stimulus TMS intervals depending on the attended feature (de Graaf et al., 2012). Taken together, these findings suggest an important difference between the types of information that are processed during the feedforward vs. the feedback sweep and that the early differential TMS effects observed here are driven by our saliency manipulation.

Even though each TMS pulse has an extended effect over time, making it difficult to determine which processes are disrupted at each exact point in time, we measured a larger effect of saliency at the earlier compared to later intervals. This greater influence of saliency on V1/V2 processing at earlier times is consistent with the claim that vision is predominantly stimulus-driven during the feedforward sweep (Theeuwes, 2010) and that top-down influences on more complex aspects of perceptual processing, such as figure-ground segmentation (Lamme, 1995) and visual awareness (Lamme & Roelfsema, 2000), may only be reflected during later feedback processing. According to this view, salient stimuli will always be processed at first glance, and only after the initial feedforward sweep will top-down influences such as attentional set affect subsequent processing by selecting what is

relevant. Several psychophysical and EEG experiments corroborate this view by showing robust attentional capture for salient but task-irrelevant stimuli during short intervals after visual stimulation (Theeuwes, 1992; Hickey, McDonald, & Theeuwes, 2006). Our results are consistent with this framework; salient stimuli are represented in V1/V2 more robustly at early intervals after stimulus onset, which may be the signature for attentional capture. However at later intervals, top-down attention may act to disregard these bottom-up effects.

Alternatively, but not mutually exclusive with this account, is the possibility that during feedback processing, TMS may be more disruptive because it interferes with the representation of integrated objects. Evidence suggests that at the feedforward stage, the visual system extracts information about features and their statistical summaries (Treisman, 2006; Chong, Joo, Emmanouil, & Treisman, 2008), whereas at the feedback stage it integrates features into objects (Bouvier & Treisman, 2010). Disruptions at later processing intervals may thus eliminate the whole object regardless of the saliency of individual features that compose it. Some evidence for this claim comes from object substitution masking, which has been suggested to disrupt feedback processing resulting in the inability to detect entire objects (Di Lollo, Enns, & Rensink, 2000). It may therefore be the case in our experiments that feedback disruption interfered with the whole object representation, which was qualitatively different than a combination of features of varying saliency.

Note that our effects were obtained using a TMS intensity that was determined in the beginning of the experiment based on a standard functional localization of V1/V2 in which TMS pulses are applied at SOAs most sensitive to visual suppression (76–100 ms; Amassian et al., 1989; Ro et al., 2003). If we used a less sensitive SOA during functional localization, this would result in higher TMS intensities, which, according to previous studies, would produce overall more suppression at earlier SOAs (Beckers & Homberg, 1991; Kammer, Puls, Strasburger, Hill, & Wichmann, 2005). Higher TMS intensities would have also complicated our experiment by producing muscle twitches and subject discomfort and would have likely obscured differences between our conditions.

In Experiment 2, there was an advantage for red stimuli over green, even when differences with respect to the background and saturation were accounted for. This indicates that red is inherently salient and the advantage we observed in Experiment 1 was not due solely to increased color contrast with the surround. Several studies have reported greater saliency for red compared to other colors. It has been shown that we are more sensitive to red compared to green flashes of light presented in the periphery (Stromeyer, Lee, & Eskew, 1992). Also, red objects appear larger than objects of other colors (Tedford, Bergquist, & Flynn, 1977), evoke a larger finger aperture during grasp movements (Gentilucci, Benuzzi, Bertolani, & Gangitano, 2001), and change the magnitude of metacontrast masking (Breitmeyer & Williams, 1990). Additionally, red stimuli affect bottom-up attention in different ways: an asymmetry in search times for desaturated red as opposed to other desaturated colors was recently reported (Lindsey et al., 2010) and a red stimulus on a green background is less prone to inattention blindness than a green stimulus on a red background (Mack & Rock, 1998). Red may be inherently more salient due to its correlation with objects of relevance or importance in the natural environment (dangerous objects such as blood as well as edible objects such as fruits), but further studies are needed to systematically clarify the exact origin of the red color effects.

Note that in Experiment 1 the saliency effect on suppression was identical regardless of whether subjects attended to color or orientation. This suggests that saliency effects were not modulated by top-down attention to feature dimensions. The fact that visual suppression followed an identical time course for color and

orientation tasks seems surprising if one considers that anatomically the visual networks engaged in the processing of these features are partly separate (Hubel & Wiesel, 1968; Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998). Perhaps this synchrony appears only in the processing of features that belong to the same object, and therefore is specific to the processing of bound objects (Singer & Gray, 1995). Future experiments will compare processing times for features that are either bound in the same object or separated across different objects.

Experiment 2 also provides some insight into a question that is relevant to many studies of visual suppression, namely whether suppression functions are affected by perceptual or task discrimination difficulty. A number of studies assume that the magnitude of TMS-induced suppression is influenced by stimulus factors (Miller, Fendrich, Eliassen, Demirel, & Gazzaniga, 1996), but not by the task subjects are performing. In Experiment 2 we evaluated this assumption by comparing visual suppression for the same green stimuli within an easy and a difficult discrimination condition. The suppression results for these two green stimuli were identical, showing that awareness of a stimulus is not influenced by the difficulty of perceptually discriminating it from another stimulus. These results are reassuring in showing that processing in V1/V2 is unaffected by task difficulty, which in a given experiment is often arbitrary.

Note that our results cannot be explained by non-specific TMS effects produced by auditory and scalp stimulation. The results of previous studies have consistently shown that visual suppression is obtained under spatially specific parameters. Indeed, studies using a control site or sham stimulation do not provide any evidence for visual suppression (e.g. Jacobs, de Graaf, Goebel, & Sack, 2012; Koivisto, Henriksson, Revonsuo, & Railo, 2012). This is consistent with our observation that it is extremely challenging to position a TMS coil to produce visual suppression. Thus, the pattern of results of the current study can be attributed only to the neural effects of TMS over V1/V2.

In summary, two experiments showed that processing in V1/V2 is affected by color saliency and that the magnitude of this saliency effect depends on the stage of visual processing. These results indicate that different factors contribute to visual awareness at different stages of processing, with bottom-up feature saliency influencing awareness at earlier temporal processing intervals in visual cortex than later ones. These results also suggest that disruptions during feedback stages may occur at the level of object files that have formed based on bottom-up features but do not inherit the saliency advantages of these features.

## Acknowledgments

This research was supported by NSF Grants BCS 0843148 and EFRI 1137172 to TR. The authors declare no competing financial interests.

## References

- Amassian, V. E., Cracco, R. Q., Maccabee, P. J., Cracco, J. B., Rudell, A., & Eberle, L. (1989). Suppression of visual perception by magnetic coil stimulation of human occipital cortex. *Electroencephalography and clinical neurophysiology*, 74(6), 458–462.
- Beckers, G., & Homberg, V. (1991). Impairment of visual perception and visual short term memory scanning by transcranial magnetic stimulation of occipital cortex. *Experimental brain research. Experimentelle Hirnforschung. Experimentation cerebrale*, 87(2), 421–432.
- Bouvier, S., & Treisman, A. (2010). Visual feature binding requires reentry. *Psychological science*, 21(2), 200–204.
- Boyer, J. L., Harrison, S., & Ro, T. (2005). Unconscious processing of orientation and color without primary visual cortex. *Proceedings of the national academy of sciences USA*, 102(46), 16875–16879.

- Breitmeyer, B. G., Ro, T., & Singhal, N. S. (2004). Unconscious color priming occurs at stimulus – not percept – dependent levels of processing. *Psychological science*, 15(3), 198–202.
- Breitmeyer, B. G., & Williams, M. C. (1990). Effects of isoluminant-background color on metacontrast and stroboscopic motion: interactions between sustained (P) and transient (M) channels. *Vision research*, 30(7), 1069–1075.
- Chong, S. C., Joo, S. J., Emmanouil, T. A., & Treisman, A. (2008). Statistical processing: not so implausible after all. *Perception and psychophysics*, 70(7), 1327–1334 (discussion 1335–1326).
- Di Lollo, V., Enns, J. T., & Rensink, R. A. (2000). Competition for consciousness among visual events: the psychophysics of reentrant visual processes. *Journal of experimental psychology general*, 129(4), 481–507.
- Fecteau, J. H., Chua, R., Franks, I., & Enns, J. T. (2001). Visual awareness and the on-line modification of action. *Canadian journal of experimental psychology*, 55(2), 104–110.
- Gentilucci, M., Benuzzi, F., Bertolani, L., & Gangitano, M. (2001). Influence of stimulus color on the control of reaching-grasping movements. *Experimental brain research*, 137(1), 36–44.
- Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, 391(6666), 481–484.
- Hadjikhani, N., Liu, A. K., Dale, A. M., Cavanagh, P., & Tootell, R. B. (1998). Retinotopy and color sensitivity in human visual cortical area V8. *Nature neuroscience*, 1(3), 235–241.
- Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of cognitive neuroscience*, 18(4), 604–613.
- Holmes, G. (1918). Disturbances of Vision by Cerebral Lesions. *British journal of ophthalmology*, 2(7), 353–384.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of physiology*, 195(1), 215–243.
- Huk, A. C., & Heeger, D. J. (2000). Task-related modulation of visual cortex. *Journal of neurophysiology*, 83(6), 3525–3536.
- Ito, M., & Gilbert, C. D. (1999). Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron*, 22(3), 593–604.
- Jacobs, C., de Graaf, T. A., Goebel, R., & Sack, A. T. (2012). The temporal dynamics of early visual cortex involvement in behavioral priming. *PLoS one*, 7(11), e48808.
- Kammer, T. (2007). Masking visual stimuli by transcranial magnetic stimulation. *Psychological research*, 71(6), 659–666.
- Kammer, T., Puls, K., Strasburger, H., Hill, N. J., & Wichmann, F. A. (2005). Transcranial magnetic stimulation in the visual system. I. The psychophysics of visual suppression. *Experimental brain research*, 160(1), 118–128.
- Koivisto, M., Henriksson, L., Revonsuo, A., & Railo, H. (2012). Unconscious response priming by shape depends on geniculostriate visual projection. *European journal of neuroscience*, 35(4), 623–633.
- Koivisto, M., Mantyla, T., & Silvanto, J. (2010). The role of early visual cortex (V1/V2) in conscious and unconscious visual perception. *Neuroimage*, 51(2), 828–834.
- Lamme, V. A. (1995). The neurophysiology of figure-ground segregation in primary visual cortex. *Journal of neuroscience*, 15(2), 1605–1615.
- Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in neurosciences*, 23(11), 571–579.
- Li, W., Piech, V., & Gilbert, C. D. (2006). Contour saliency in primary visual cortex. *Neuron*, 50(6), 951–962.
- Li, Z. (1999). Contextual influences in V1 as a basis for pop out and asymmetry in visual search. *Proceedings of the national academy of sciences of the United States of America*, 96(18), 10530–10535.
- Lindsey, D. T., Brown, A. M., Reijnen, E., Rich, A. N., Kuzmova, Y. I., & Wolfe, J. M. (2010). Color channels, not color appearance or color categories, guide visual search for desaturated color targets. *Psychological science*, 21(9), 1208–1214.
- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, 240(4853), 740–749.
- Mack, A., & Rock, I. (1998). *Inattention blindness*. Cambridge, MA: MIT press.
- Motter, B. C. (1993). Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *Journal of neurophysiology*, 70(3), 909–919.
- Miller, M. B., Fendrich, R., Eliassen, J. C., Demirel, S., & Gazzaniga, M. S. (1996). Transcranial magnetic stimulation: delays in visual suppression due to luminance changes. *Neuroreport*, 7(11), 1740–1744.
- Poppel, E., Held, R., & Frost, D. (1973). Leter: Residual function after brain wounds involving the central visual pathways in man. *Nature*, 243(5405), 295–296.
- Ro, T., Breitmeyer, B., Burton, P., Singhal, N. S., & Lane, D. (2003). Feedback contributions to visual awareness in human occipital cortex. *Current biology*, 13(12), 1038–1041.
- Salminen-Vaparanta, N., Noreika, V., Revonsuo, A., Koivisto, M., & Vanni, S. (2012). Is selective primary visual cortex stimulation achievable with TMS? *Human brain mapping*, 33(3), 652–665.
- Singer, W., & Gray, C. M. (1995). Visual feature integration and the temporal correlation hypothesis. *Annual review of neuroscience*, 18, 555–586.
- Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the national academy of sciences of the United States of America*, 96(4), 1663–1668.
- Stromeyer, C. F., 3rd, Lee, J., & Eskew, R. T., Jr. (1992). Peripheral chromatic sensitivity for flashes: a post-receptoral red-green asymmetry. *Vision research*, 32(10), 1865–1873.
- Tedford, W. H., Jr., Bergquist, S. L., & Flynn, W. E. (1977). The size-color illusion. *Journal of general psychology*, 97, 145–149 (1st Half).
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception and psychophysics*, 51(6), 599–606.
- Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta psychologica (Amst)*, 135(2), 77–99.
- Thielscher, A., Reichenbach, A., Ugurbil, K., & Uludag, K. (2010). The cortical site of visual suppression by transcranial magnetic stimulation. *Cerebral cortex*, 20(2), 328–338.
- Treisman, A. (2006). How the deployment of attention determines what we see. *Visual cognition*, 14(4–8), 411–443.
- Weiskrantz, L., Warrington, E. K., Sanders, M. D., & Marshall, J. (1974). Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain*, 97(4), 709–728.
- Zhang, X., Zhaoping, L., Zhou, T., & Fang, F. (2012). Neural activities in v1 create a bottom-up saliency map. *Neuron*, 73(1), 183–192.