Research report

The role of the collicular pathway in the salience-based progression of visual attention

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HIGHLIGHTS

- Progression of visual attention is salience-based.
- The superior colliculus is involved in attention.
- S-cone stimuli prevent collicular processing.
- When presenting with S-cone stimuli, attention does not progress on the basis of salience.
- The superior colliculus is involved in salience-based progression of attention.

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ABSTRACT

Visual attention has been shown to progress from the most to the least salient item in a given scene. Cognitive and physiological models assume that this orienting of covert attention relies on the collicular pathway, involving the superior colliculus and the pulvinar. Recent studies questioned this statement as they described attentional capture by visual items invisible to the superior colliculus. Electrophysiological studies shown that there is no direct projections from short-wave receptors to the superior colliculus. S-cone stimuli can thus be employed to assess visual processing without the involvement of the collicular pathway. We have attempted to investigate whether this pathway is involved in the salience-based orientation of attention by presenting S-cone stimuli. Volunteers were asked to make a judgment regarding a target among two distractors (all items of unequal sizes). Items’ location and size varied randomly, as well as color, randomly black or calibrated for each subject to activate exclusively S-cones. The hierarchical pattern testifying of the salience-based orientation of attention was only found with black stimuli, arguing in favor of an implication of the collicular pathway in salience. In a second experiment, one item was presented at a time in order to test the item-multiplicity effect by comparing experiments. Performance was the most penalized when presenting multiple stimuli in the black condition. Results were interpreted in terms of distinct modes of processing by the collicular and geniculate pathways. The establishment of salience that determines attentional progression appeared to be only possible when the collicular pathway was solicited.

1. Introduction

Spatial attention progresses through the visual field toward the elements of interest. It is widely accepted that exogenous (i.e., automatic) orientation of attention relies on visual salience. For instance, in an experimental paradigm using multiple stimuli varying on the basis of their salience, judgment times, detection times and saccadic latencies were directly related to the salience of the target [1–3]. This implies that attention is captured by the most salient item, i.e., the item that differs the most from its neighbors as regards of at least one of its visual features, like size or luminance. It also implies that attentional progression through space and time is salience-based, i.e., visual search progresses from the most salient to the immediate least salient item, and so forth, until the target is found.

Despite this largely accepted point of view, a debate subsists about the neural mechanisms underpinning such a salience-based...
attentional attraction and progression. Indeed, structures like the pulvinar (PUL), the superior-colliculus (SC), the parietal and the occipital cortices might be involved in the generation of visual salience [4–8]. However, attention is seemingly not underlain by single structures but by largely distributed neural networks [9]. Animal and human studies have pointed the collicular pathway, involving the SC and the PUL as well as their outputs toward the occipito–parietal cortex, as being one candidate network involved in the early stages of visual attention [10–14]. This pathway was especially associated with the generation of visual salience and subsequent orienting of attention [8,12].

For instance, behavioral studies showed that performance was superior in the temporal visual hemifield [3,15], which mostly projects to the collicular pathway [16]. Also, attention effects were found in the blind field of blindsight patients whose perception depends on their intact collicular pathway [13,17,18]. Furthermore, attention effects diminish after lesions of the collicular pathway [12,14,19–21]. Other studies yet challenge this hypothesis. For instance, it was suggested that attentional capture could occur in the absence of the processing taking place within the collicular pathway [22,23]. Based on electrophysiological studies showing that there is no color-opponent cell projections reaching the SC, especially from cells coding short-wave stimuli (S-cones stimuli; [24,25]), Summer and colleagues [22,23] used stimuli to which the SC is blind and found that they did produce involuntary orienting of attention. This suggests that attention could be directed to salient items even when the collicular pathway is not involved.

These data indicate a lack of homogeneity in the literature about the neural mechanisms of salience-based attraction and progression of visual attention. It is worth noting that different methodologies led to different conclusions. In order to contribute to this debate, we tested whether the collicular pathways is necessary for the attention to progress from the most to the least salient item of the field by using S-cones stimuli. S-cones signals are exclusively involved in color perception as their retinal ganglion cells reach the koniocellular layers of the geniculate nucleus [26]. The collicular pathway is thus blind to these stimuli. Despite the interest of this psychophysical method that allow to measure performance on the basis of a specific S-cone perception, it has never been employed to investigate the role of the collicular pathway in the deployment of attention through multiple stimuli during covert visual search. The salience-based progression of attention was assessed using a version of the Multiple Salience Levels Visual Search Task (MSLVST; [3]) in which participants are required to make a judgment about a target presented among two distractors, all items of unequal salience. Usually, performance varies as a function of the salience of the target since it is better for the most salient item and decreases as the target’s salience decreases. If the collicular pathway contribute to this phenomenon, then presenting S-cone stimuli that prevent collicular processing would not lead to this typical pattern of results. The main finding of the present study is that S-cone stimuli prevented salience-based progression of attention. In an alternative condition using items defined by luminance contrast, which are visible to both the geniculate and the collicular pathways, salience-based progression was found. These results support the hypothesis that the collicular pathway contributes to the salience-based progression of visual attention.

2. Experiment 1

2.1. Materials and methods

2.1.1. Participants

Twenty-one participants (4 males and 17 females; age: 22.7 ± 2.7 years) took part in this experiment. None of them had any history of headache, epilepsy or substance abuse. They were all right-handed according to the Edinburgh laterality inventory (mean laterality: 90 ± 0.7), all had normal or corrected-to-normal vision, were not under any medication. All participants gave their written consent for their participation. The experiment was conducted in accordance to the Helsinki declaration.

2.1.2. Stimuli and apparatus

Stimuli were three outlined (1 pixel) squares of different sizes presented on a standard gray background (24.3 cd/m²) from a viewing distance of 41 cm. Their respective sizes were .73 × .73° (surface: 25 mm²), .57 × .57° (surface: 16.81 mm²) and .49 × .49° (surface: 10.89 mm²) of angular space. Each square had a 3-pixel gap (.084°) and was rotated 0°, 90°, 180° or 270° clockwise. The target orientation was 0° (up) or 180° (down), with one distractor oriented 90° (right) and the other 270° (left). The three squares were presented at 30°, 90° and 150° clockwise in relation to the vertical (i.e., to the right of fixation) or 30°, 90° and 150° anticlockwise in relation to the vertical (i.e., to the left of fixation), at a distance of 3.8°. The distance between two neighboring squares was 3.8°. The fixation point was a small white dot (2.2 cd/m²). The stimuli were either black or calibrated in a way to only activate retinal S-cones by means of a pilot experiment (see note 2). In the Black condition, luminance of the squares was 26.9, 25.1 and 24.75 cd/m², respectively. In the S-cone condition, the stimuli and the background were adjusted for each participant as to be isoluminant by means of an initial pilot experiment (note 1).

The stimuli were presented on a cathode Sony Flat Trinitron 21” GDM F-520 calibrated monitor (1920 × 1440 resolution at 60 Hz) controlled by an Intel Core i7 3610QM, 2.30 GHz CPU with IntelG RAm processor (Intel HD Graphics 4000 1696 Mo graphic card). All luminance measures were conducted with a Minolta luminance meter LS-110. The experiment was run on PsychoPy2 [27] and took place in a dim-lighted room (.02 cd/m²). Participants had their head resting on a chinrest.

2.1.3. Procedure

The procedure is depicted in Fig. 1. Each trial started with the white fixation dot presented for 500 ms. The search display was then added for 100 ms (this short display duration, consistent with previous research, was chosen to minimize saccades toward the items) and was constituted of three squares presented either to the right or left of fixation. Each square could be located randomly and equiprobably at one of the three locations. One of the three squares was the target with 33% probability and the two others were distractors. In half of the trials, the target orientation was 0°, in the other half 180°. The stimuli color (Black or S-cone), the location of the target (30°, 90° or 150° in relation to the vertical), its size (large, medium or small) and orientation (0° or 180°), and the location of the search display (to the left or right of fixation) occurred with equal probability and were randomly chosen by the computer in each new trial. Luminance noise was used in order to, firstly, ensure that attention orientation was made on the basis of color and not luminance or color contrast [28,29]. Secondly, literature advised [29] to use such noise when stimuli are not precisely equiluminant (which was the case in the Black condition) and finally, even if there might be some small S-cone input in the SC, this channel is not chromatically opponent and could be masked using luminance noise [22,26,30,31]. This consisted in random presentation of 10 gray shades, for 16 ms (i.e., 160 ms flickering) before and after the search display. The gray shades varied randomly from 25% gray (12.2 cd/m²) to 75% gray (36.5 cd/m²), by steps of 5%. After the post-stimulus luminance noise period, the fixation dot remained on the screen for 1800 ms allowing the subject to respond, before being extinguished for 300 ms, signaling the end of the trial and the new trial to come. Each participant completed a 10-trial training
session, followed by a 288-trial session (48 trials/target size/stimuli color) split in two equivalent blocks of 144 trials with a brief pause in between. Participants were asked to gaze at the fixation dot during the whole experimental session and to indicate as quickly and accurately as possible the target’s orientation (up or down) by pressing two pre-defined vertically-arranged response buttons with the major (up button) and index (down button) fingers. They responded with one hand in the first block and the other hand in the second block and half of the participants started with the right hand. Response times (RT) and errors were recorded.

2.2. Results

2.2.1. Response times

RT inferior to 100 ms (less than .1% of the trials) were discarded as representing anticipation errors. An analysis of variance (ANOVA) was performed on mean correct RT with the size of the target (large, medium and small) and its color (Black vs. S-cone) as within-participant factors. The interaction between these two factors was significant ($F(2, 40) = 4.06; p < .025$). A hierarchical pattern was observed in the black color condition since RT were faster when the large square was the target (745 ms), slower when it was the medium one (766 ms), and slowest of all when it was the small square (790 ms). Progression slopes ($\alpha^1$), expressed in speed gain in milliseconds per additional square millimeter, were analyzed as a way of investigating further the progression of attention. The Black condition progression slope was $-1.88$ ms/mm$^2$ which was different from zero ($t(20) = 2.14, p = .047$). As highlighted in previous research from our laboratory [3], this finding supports the hypothesis of salience-based progression of attention. This pattern did not show in the S-cone condition (large: 751 ms; medium: 731 ms; small: 725 ms) where the progression slope was $1.21$ ms/mm$^2$ which was not significantly different from zero ($t(20) = 1.64, p > .11$). The comparison between these slopes ($t(20) = 2.47, p < .022$ bicaudal) confirmed that progression from the most to the least salient item only occurred in the Black condition. Results, presented in Fig. 2a, suggest that the salience-based progression of attention fails to occur when the collicular pathway is not involved in visual processing, here due to the color of visual elements. Therefore, the collicular pathway seems involved in this phenomenon.

2.2.2. Accuracy

All participants performed above chance level in all stimuli color conditions. The proportion of correct responses, calculated on the basis of the trials in which the participants gave a response, ranged from .54 to .63 (mean and mean standard deviation: .59 ± .03). Performance was significantly different than chance level (i.e., .5) in both color conditions (Black: $t(20) = 10.41, p < .001$; S-cone: $t(20) = 6.78, p < .001$). An ANOVA was performed with the size of the target (large, medium and small) and its color (Black vs. S-cone) as within-participant factors. The main effect of color was significant ($F(1, 20) = 31.69, p < .001$), with accuracy being greater for the black color condition (.64 ± .09) than the S-cone color condition (.54 ± .06). The target size x color interaction was also significant, ($F(2, 40) = 3.3, p < .05$). A hierarchical pattern was observable in the black color condition (.67, .63 and .61 for the large, the medium and the small target, respectively). The progression slope was .34%/mm$^2$, which was reliably different than zero ($t(20) = 2.74, p < .013$), arguing in favor of a salience-based progression of attention. The S-cone condition did not reveal such a hierarchical pattern (.55, .53 and .55 for the large, the medium and the small target, respectively). The progression slope was $-0.02$%/mm$^2$, which was not different from zero ($t(20) = .23, p > .82$). Supported by a significant difference in the comparison between the two progression slopes ($t(20) = 2.11, p = .048$ bicaudal), this distinction was consistent with previous observations in support of an involvement of the collicular pathway in processing salience. Results are presented in Fig. 2b.

In order to test the presence of a RT/accuracy tradeoff that would suggest that participants would favor RT over accuracy and vice versa, the correlation between RT and accuracy was computed for

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$^1 \alpha = \text{covariance (x, y)/variance (x)}$ where $x$ is the surface of each of the three squares in mm$^2$ and $y$ is the RT when each square was the target.
each condition: none of these coefficients reached significance (all $r < .3$, all $p > .18$).

2.3. Discussion

The black condition in Experiment 1 confirmed the salience-based progression of attention attested by previous research [3]. As shown by the hierarchical pattern in both RT and accuracy, attention would deploy first toward the most salient item, then toward the immediately less salient item until the target was found. When the involvement of the collicular pathway was hindered because of the preferential excitation of S-cone stimuli, this hierarchical pattern did not occur in both RT and accuracy. This absence of hierarchical pattern could not have been attributable to a random answer effect since all participants performed above chance level in both Black and S-cone conditions. This indicates that either salience generation and/or processing [8] could not be achieved and that subsequent salience-based progression was impaired, or salience-based progression per se was impaired. Our results thus indicate that when the contribution of the collicular pathway in covert visual search is empirically impeded, deploying attention through space on the basis of salience is not possible.

Nevertheless, some points in the results had to be further investigated, like the overall difference in accuracy between the Black and the S-cone conditions. A drop in the overall accuracy in the S-cone condition was not expected. It could have arisen from difficulties in perceiving correctly the small gap on which the target had to be judged. Indeed, in this condition, no perception on the basis of contrast was possible due to the flickering displays, forcing a color-based processing [28,29]. The gap of the items is a kind of contrast defined by a discontinuity in one line of the squares, rendering even more difficult the discrimination between the target and the distractors. Furthermore, the koniocellular pathway to which the S-cones project is less responsive for high spatial frequencies [32] as required for correctly processing those gaps. Also, S-cones receptors are known to have a slower processing time than the other visual receptor categories [33], which could have impeded target processing. Finally, an increment in the task difficulty may have occurred due to the simultaneous presence of multiple items. Theories of visual salience (i.e., [71]) posit that items have to be processed in parallel (i.e., simultaneously) and compared so that their relative salience could emerge. A decreased or impaired processing in the collicular pathway can deprive visual perception from systems that allow processing of multiple stimuli [19]. Such crude and coarse spatial pointers [34] characterize the collicular pathway, presumably related to the large receptive field of the magnocellular cells. They would spot large areas in the visual field containing the items to process. Smaller spatial pointers characterize the geniculate pathway [35], which lead to high precision processing of specific items without the possibility to encompass neighboring items. Since S-cones stimuli are processed only by koniocellular cells, firing through the geniculate pathway, participants would not be able to process simultaneously all items, and consequently the establishment of the salience of each item and the hierarchy of salience would be prevented. Shall this hypothesis be true, then the drop in accuracy in the S-cone condition would be explained by the failure of the geniculate pointers to process multiple items. This hypothesis was tested by adapting the present design to exclude multiple stimuli. A single item in the specific S-cones color condition should show similar results than those obtained in the three-items display of Experiment 1, while better performance should be observed in the Black condition.

3. Experiment 2

Experiment 2 used only a single item presentation, whether of the large or the small square from Experiment 1. The absence of multiple items would allow investigating the pointers hypothesis as outlined above.

3.1. Material and methods

3.1.1. Participants

Sixteen participants (4 males and 12 females; age: $22.4 \pm 1.9$ years; mean laterality: $93 \pm .05$) completed Experiment 2. None of them took part in Experiment 1. The same inclusion/exclusion...
criterion as Experiment 1 were applied. The Experiment was conducted in accordance to the Helsinki declaration.

3.1.2. Stimuli and apparatus

The stimuli were the large and the small squares used in Experiment 1.

3.1.3. Procedure

The procedure was similar to the one used in Experiment 1 with the difference that the display contained only a single square (the large or the small), presented along the horizontal meridian at 3.8° from fixation. Each subject completed a 10-trial training session, followed by an experimental session consisting of 128 trials (32 trials on the size of the stimulus (Black vs. S-cone) as within-participant factors. Only the main effect of color was significant \( F(1, 15) = 31.51; p < .001 \) as participants were faster in the Black condition (532 ms) than in the S-cone condition (649 ms).

3.2. Results

3.2.1. Response times

RT smaller than 100 ms (less than .1% of the trials) were discarded as representing errors of anticipation. An ANOVA was performed on mean correct RT with the size of the target (large or small) and its color (Black vs. S-cone) as within-participant factors. Only the main effect of color was significant \( F(1, 15) = 31.51; p < .001 \) as participants were faster in the Black condition (532 ms) than in the S-cone condition (649 ms).

3.2.2. Accuracy

All participants performed above chance level in both Black and S-cone color stimulus conditions. The proportion of correct responses ranged from .59 to .82 (mean: .71 ± .06). Performance was significantly different than chance level in both color conditions (Black: \( t(15) = 16.4, p < .001 \); S-cone: \( t(15) = 5.4, p < .001 \). An ANOVA was performed with the size of the target (large or small) and its color (Black vs. S-cone) as within-participant factors. The main effect of color was significant \( F(1, 15) = 201.6; p < .001 \) as participants performed better in the Black condition (.85 ± .09) than in the S-cone condition (.57 ± .08). The main effect of size did not reach significance \( F(1, 15) = 3; p > .85 \) for the large (.72 ± .08) and the small target (.72 ± .08), but the size × color interaction was significant \( F(1, 15) = 5.07; p < .03 \). Despite this, no hierarchical pattern was observed in either the Black \( \text{slope} = -.15/\text{mm}^2; t(15) = 1.71, p = .11 \) or the S-cone condition \( \text{slope} = -.17/\text{mm}^2; t(15) = 1.68, p = .11 \).

3.2.3. Further analysis

In order to investigate the assumption derived from the pointer hypothesis, performance for the large and the small targets was compared between Experiments 1 and 2. The pointer hypothesis states that when luminance stimuli are used, participants would perform less well for displays with three items than for displays with one item. Reversely, performance for S-cone stimuli could be virtually unchanged whatever the display size. On the basis of our hypothesis, we focused on number-of-items × color interaction. An ANOVA was carried out with target size (large vs. small) and color (Black vs. S-cone) as within-participant factors, and the number-of-items (1 vs. 3 item) as between-group factor. As expected, the color × number-of-items interaction was significant in RT analysis \( F(1, 35) = 26.88, p < .001 \). Mean RT were not different in the three-item condition between color conditions (Black: 767 ms, S-cone: 738 ms, \( p > .15 \)) while the Black condition showed better performances than the S-cone in the one-item condition (Black: 532 ms, S-cone: 649 ms, \( p < .001 \)). The multiplicity of items would penalize performances in both color condition (Black: \( p < .001 \), S-cone: \( p < .03 \)) but RT were more affected by the multiplicity of items in the Black condition than in the S-cone condition (effect of the multiplicity of items: Black condition, 3-items − 1-item = 235 ms; S-cone condition, 3-items − 1-item = 89 ms). Results are presented in Fig. 3a. Also, the color × number-of-items interaction was significant in accuracy \( F(1, 35) = 40.42, p < .001 \), since accuracy in the black condition increased with decreasing number of items (3 items: .64; 1 item: .85, \( p < .001 \)), whereas no difference was found in the S-cone condition (3 items: .54; 1 item: .58, \( p > 2 \)). These results back-up the observation that the multiplicity of items penalizes performance more in the Black condition than in the S-cone condition. Results are presented in Fig. 3b.

3.3. Discussion

The results of Experiment 2, as well as the comparison between Experiments 1 and 2 bring some supplementary information about salience-based progression of attention. First, the hierarchical pattern found in the black condition of Experiment 1 has been interpreted as the deployment of attention toward elements as a function of their relative salience. In Experiment 2, the absence of effect of target size rules out the possibility to interpret these results a being due to any physical strength effect of the stimuli [3,36] and supports that salience emerges through comparison between multiple items [7,37]. Second, if what allows encompassing and comparing neighboring items for their relative salience to be derived are the coarse spatial pointers of the collicular pathway [34], then the discrepancy found between the black and the S-cone stimuli between multiple and single item displays can be explained by the impairment of collicular processing. Finally, in Experiment 2, performance was overall lower in the S-cone condition, and this can be explained by the lower visibility of the S-cone stimuli, but also slower processing times of the S-cone receptors [33]. In both cases, the brief exposure of the display would not leave enough time for correct processing and would therefore lead performance to drop.

4. General discussion

The main purpose of the present study was to investigate the controversial [3,12,16,17,19,20,22,23,34] involvement of the collicular pathway, including the SC, the PUL and their projections to the occipito–parietal cortex, in the progression of visual attention through space following an hierarchical ordering of element on the basis of their salience. In an adapted version of the MSLVST [3], we used a psychophysical procedure to impede processing taking place within the collicular pathway. Stimuli to which cells of this pathway respond (Black stimuli) or not (S-cone stimuli; [24,25]) were used. It was expected that if the collicular pathway were involved in salience processing, then attention would fail to progress in a salience-based fashion in conditions where this pathway is not solicited.

In Experiment 1, it was shown that when the search display contained stimuli that could be processed by both the geniculate and the collicular pathway (i.e., black stimuli), attention was first drawn toward the most salient element, then the immediately less salient, etc., testifying on a hierarchical ordering of elements on the basis of their relative salience. This result supports salience-based theories of attention [7,38] and sustains previous work arguing in favor of the salience-based progression of attention [1,3]. By contrast, when the search displays contained stimuli that could not be processed by the collicular pathway (i.e., S-cone stimuli), no evidence on any hierarchical pattern was found. However, as far as RT were concerned, no difference was found for the most salient item between the black and the S-cone conditions. Overall, the results of Experiment 1 support that the collicular pathway plays a crucial
role in salience-based progression of attention, but whether the collicular pathway is involved in attentional capture by the most salient item of the field [22] remains an open issue. Based on performance of patients with lesions of the pulvinar, it was suggested that the geniculate and the collicular pathways would both participate in attention through specific spatial pointers [34]. Geniculate pointers would allow accurate processing within a narrow area, whereas collicular pointers would be large and coarse allowing the processing of a larger area. Their combination would generate highly spatially precise spikes of activity surrounding coarsely defined patterns of activity representing respectively the location of the target, along with the neighboring items. Encompassing and processing simultaneously several items is one condition for generating salience and the hierarchy of salience [7]. Since the color transition between the S-cone stimuli and the gray background prevents those stimuli to be correctly processed through the collicular pathway, only geniculate pointers would have been involved in the S-cone condition. To this respect, the results of Experiment 1 are reminiscent of what was found with patient lesions of the pulvinar since in both cases, target surround was not adequately processed, leading either to decreased distraction [19,34] or a lack of hierarchy of salience (Experiment 1 of the present study).

The comparison between Experiments 1 and 2 indicate that performance change as a function of target size in the Black condition is not the physical strength of the stimuli (i.e., their size per se) but the presence of multiple items. Contrariwise, the S-cone stimuli did not yield any difference in performance as a function of the number of stimuli. This suggests, in agreement with the abovementioned hypotheses, that geniculate pointers solicited by using S-cone stimuli are indeed finer-grained [35] and are not able to encompass multiple stimuli. We therefore tentatively propose that the contribution of the geniculate pathway in the generation of salience [39] and the salience-based progression of attention is limited.

An alternative interpretation would be based on an asynchrony hypothesis [40]. This hypothesis posits that the two pathways discussed in the present study support the same functions, but in a delayed manner: the collicular pathway would be faster than the geniculate pathway, leading to overall faster progression of attention throughout the search displays (see for behavioral data [34,42]). However, on the basis of this account it would be expected that a hierarchical pattern in the S-cone condition would also be found. The delayed processing would be shown either through slower progression slopes (see [3]), or through the presence of a hierarchical pattern only for the first items that have been explored, e.g., the large and the medium targets, testifying of an incomplete deployment of attention through the whole display. None of these patterns was observed. Nevertheless, the temporal proprieties of both pathways are to consider for further understanding of the phenomena described here [43].

The present study showed that, in the absence of direct collicular contribution, no salience-based progression of attention occurred. It is generally admitted that this phenomenon involves two stages: the establishment of a hierarchy of the items present in the visual field on the basis of their salience, and an attentional deployment involving an initial capture by the most salient item, with a subsequent progression toward other items on the basis of the pre-established hierarchy. Among the numerous structures that have been pointed out through the literature, we can mention the SC [18,21,45] which has been shown to respond specifically during target detection and visual search [45], and probably guides visual search in an involuntary fashion in response to unconsciously perceived cues [18]. Our results concur with these observations as far as S-cone stimuli that are not processed by the SC did not yield any hierarchical effect probably because of impairments in the establishment of salience or and the deployment of attention from the most toward the least salient element. Also, specifically sensitive to luminance variation information, the PUL would respond to stimulation from any location in the visual field, due to its large cell receptive fields [46]. It would contain neurons that generate signals related to the salience of visual locations [8] and would improve efficiency of visual processing by engaging attention at the location of interest [12].

According to Koch and Ullman’s model [7], salience would be represented in a topographical saliency map that would combine information from individual feature maps into one global measure of conspicuity. This cognitive function that needs to encompass the overall visual field for orderly exploring conspicuous locations according to their salience could be undertaken by the cooperative
processing of individual structures within the collicular pathway since it is unlikely that such a complex processing takes exclusively place within a single structure, be it subcortical (e.g., SC and PUL; [4,8]) or cortical (i.e., parietal cortex; [6]). Furthermore, such a processing should be underlain by a retinotopic cell organization [7,38]. Contrary to the SC, the PUL is mainly reported as non-retinotopic [46] even if some of its sub-divisions present a retinotopic organization. On the other hand, the lateral geniculate nucleus and the primary visual cortical area have a fine retinotopic organization that could greatly contribute to the generation of salience [39], but the fine-grained resolution of this pathway is rather difficult to reconcile with the need to encompass multiple items in order to compute salience. Thus, generating salience and establishing a hierarchy for subsequent deployment of attention would need different contribution from each pathways.

A noteworthy unpredicted divergence was observed between response speed and response accuracy in the S-cone condition of Experiment 1: RT were globally faster in the Black condition, while accuracy was globally lower. Yet no evidence on any speed/accuracy tradeoff was found. Behavioral models [47] for two-choice decisions – as the decisions made by participants in the present study – posit that performance should be homogeneous between response speed and response accuracy since they assume the existence of a single decision threshold. We believe that the discrepancy can be explained by two different phenomena. First, the pattern of chromatic performance in the Black condition testified that attention progressed according to the salience of items, meaning that the least the target is salient, the slower to take a correct decision about it. The absence of such a progression in the S-cone condition did not produce such a slowing, leading therefore to overall faster RT. Second, the overall lower accuracy in the S-cone condition can be attributed either to lower visibility of the stimuli due to impaired processing of contrast, or to the lower responsive capacity of the S-cone for high spatial frequencies.

The specific psychophysical approach used in this study aimed at impeding processing in the collicular pathway for identifying how the collicular and the geniculate pathways contribute to the salience-based progression of attention through space. Our aim was not to list the potential neural candidates involved in this phenomenon, an objective that can be achieved through other techniques. Despite the rigorous method that allowed drawing several inferences on mechanisms underlying salience-based progression of attention, these inferences are limited. First of all, while it was possible to outline the contribution of each pathway, it is difficult to distinguish the specific role of the SC, the PUL or the lateral geniculate nucleus. Another limitation would reside in the impairment not only of the koniocellular pathway. The magnocellular pathway, involved in the perception of changes in luminance, in the processing of low-frequency signals, and in attention [48] is also blind to S-cone stimuli [22]. The use of static size/luminance variations to investigate collicular/geniculate differences is another limit because this technique may prevent specific control of the feature-based creation of salience. Movement is probably a better feature as it has been long known to elicit strong responses in the collicular pathway and to capture attention [46,49,50]. Finally, in order not to restrain any inference on neuronal mechanism from this paradigm to the S-cone technique, monocular viewing techniques could be useful since they allow observing temporal vs. nasal hemifield asymmetries which are attributable to differential processing between the pathways under investigation [3,16].

5. A debated method

The initial electrophysiological observations of Marrocco and Li [24] and De Monasterio [25] have yielded the lack of retinal S-cone input to the SC, which have led many clinical and behavioral studies to exploit the fact that S-cone stimuli would not activate the SC and therefore produce responses without collicular functional implication. In a recent report, Hall and Colby [44] challenged this and described collicular activation for S-cone stimuli in old world monkeys. The authors postulated that such observations would rule out any conclusions made upon the S-cone stimuli isolation technique. This claim is in contradiction with the results obtained in the present Experiment since activation of the SC would lead performance to be equivalent in both Black and S-cone conditions. Yet, the color condition interacted with target size. Our main concern regarding Hall and Colby’s study is that it did not distinguish whether the activation of the SC recorded after presentation of S-cone stimuli arises from a direct retinal or a cortical (striate and extrastriate) input. This leaves open the possibility of a retroactivation from cortical areas which, probably, would take place later on. It is thus fairly conceivable that the short presentation time used in this study would allow differences in color conditions to emerge from the failure of the SC to process direct retinal S-cone signals. To our knowledge, it never has been postulated that the SC would not process in fine the overall visual information conveyed through S-cone signals, but only that S-cone stimuli would prevent signals from the retina to reach directly the SC.

6. Conclusion

The central aim of the present study was to investigate the implication of the collicular pathway in the salience-based deployment of attention by the presentation of stimuli to which it is blind. We differentiated two attentional phenomena, namely an initial capture and direction of attention towards the locus of the most salient item, and a subsequent progression in space from the most to the least salient item. RTs indicated that the use of S-cone stimuli is not detrimental for capture but is detrimental for salience-based progression of attention. When the processing of the collicular pathway was involved in a visual search task, performance testified of a deployment through space as a function of salience. These results are in line with the well-supported hypothesis that posits a strong involvement of this pathway in either the generation of salience or the attention orientation on its basis. These results are also arguing in favor of a distinct processing of the visual field by the collicular and geniculate pathways in terms of specialized visual pointers.

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Appendix A. Methodological notes

S-cone stimuli consist in a color transition that activate exclusively short wave sensitive retinal rods. This specific color transition that leaves large and medium rod cells unchanged differ between individuals and between retinal locations because of retinal sensitivity, macular pigmentation, lens density and chromatic aberrations variations. Therefore, S-cone stimuli were individually calibrated by means of two short pilot experiments. Short wave receptors are classically known to be specialized in blue color perception, responding for a transition from gray to lilac-blue. The aim of this pilot session was to determine the exact color transition
between the standard gray background (the exact point between black and white: 0°, 0%, 50% for hue, lightness and chroma in the MunSELL’s model [51]) and the color that only activates S-cones among numerous color candidates. Those candidates were chosen according to the literature (e.g., [23,41]) to span color variations from deep blue (250°, 100%, 100%) to pink (300°, 100%, 100%) since the expected color variation, at 3.8° of visual angle, would be slightly shifted from blue toward pink. The calibration procedure consisted in two pilot protocols of 15 min each in order, first, to select isoluminant candidates compared to the standard background, and second, to assess among isoluminant color candidates which variation specifically activated S-cones. 121 Color candidates were chosen, from 250° to 300° color angle by 5° angle steps, or 11 hue angles, by 11 chroma variations, from 50% to 100% saturation. Lightness was maintained constant.

A.1. Note 1: Isoluminant selection

The first pilot protocol was set up in order to select the isoluminant variation of every hue angle. The minimum motion technique [52] was used. In this procedure, vertical color bars were presented on the screen, their color being alternatively standard gray and randomly one of the color candidate at each trial. This display flickered at a rate of 4Hz and was periodically substituted by gray bars of respectively 0°, 0%, 25° and 0°, 0%, 75% chroma, slightly horizontally off by half a bar distance. From this flickering emerged an optical illusion: vertical bars seemed to move from left to right when the used color was brighter than the background and from right to left when it was darker. In the isoluminant condition, no motion illusion appeared. Participants were asked to report either the direction of the motion illusion or the absence of illusion. The computer then selected the isoluminant chroma variation of each hue variation, resulting in a selection of 11 isoluminant color candidates.

A.2. Note 2: S-cone calibration

The second pilot protocol aimed to select among isoluminant color candidates the specific color transition that would leave the L- and M-cone activity unchanged. The transient trianopria procedure [53] was used. Participants were asked to detect a color item while the S-cone chromatic pathway was made insensitive. This transient desensitization was produced with a homogeneous yellow screen presentation (60°, 100%, 100%; 78.1 cd/m²) prior to the detection task, for an initial adaptation duration of 2 min and for 6 s before each trial. Then the target to detect, a 73° × 73° square colored with a randomly selected color candidate, appeared with 50% chance at a random location. Potential target locations were the same as describe in Experiment 1. The color transition that solicited both the least detection and the highest RT detection was the most affected by S-cone desensitization for detection, this transition could not be processed by L- and M-cone chromatic pathways and the S-cone receptivity was made transiently ineffective. Thus, this color candidate was then selected for the following MSLVST protocol.

References