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Colour-specific differences in attentional deployment for equiluminant pop-out colours: Evidence from lateralised potentials



Vincent Jetté Pomerleau ^a, Ulysse Fortier-Gauthier ^a, Isabelle Corriveau ^a, Roberto Dell'Acqua ^b, Pierre Jolicœur ^{a,*}

^a Université de Montréal, Montréal, Québec, Canada

^b University of Padova, Padova, Italy

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ABSTRACT

We investigated how target colour affected behavioural and electrophysiological results in a visual search task. Perceptual and attentional mechanisms were tracked using the N2pc component of the event-related potential and other lateralised components. Four colours (red, green, blue, or yellow) were calibrated for each participant for luminance through heterochromatic flicker photometry and equated to the luminance of grey distracters. Each visual display contained 10 circles, 1 colored and 9 grey, each of which contained an oriented line segment. The task required deploying attention to the colored circle, which was either in the left or right visual hemifield. Three lateralised ERP components relative to the side of the lateral coloured circle were examined: a posterior contralateral positivity (Ppc) prior to N2pc, the N2pc, reflecting the deployment of visual spatial attention, and a temporal and contralateral positivity (Ptc) following N2pc. Red or blue stimuli, as compared to green or yellow, had an earlier N2pc. Both the Ppc and Ptc had higher amplitudes to red stimuli, suggesting particular selectivity for red. The results suggest that attention may be deployed to red and blue more quickly than to other colours and suggests special caution when designing ERP experiments involving stimuli in different colours, even when all colours are equiluminant.

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1. Introduction

Colour is an effective cue for attentional selection and as such is often used in experiments probing attentional mechanisms (Bacon and Egeth, 1994; Clark, 1969; Jolicoeur et al., 2008; Posner, 1980; Von Wright, 1972; Woodman and Luck, 2003). Attentional selection enables us to concentrate our limited attentional resources on a subset of the visual information reaching the visual cortex. Selection is required to avoid the loss of relevant information at later stages of processing because higher-level visual areas can only process and/or store a finite number of relevant objects (Cowan, 2000; Dell'Acqua et al., 2012). Visual spatial attention mechanisms are believed to process visual items serially (whether individually or in small groups) at some point in the visual processing stream in order to be identified in more detail and to control further processing (Sperling, 1960; Treisman and Gelade, 1980).

1.1. Colors and visual spatial attention

Usually, colours are used as a discriminative tool for segregating visual targets from distracters. This section provides a brief overview

* Corresponding author at: Département de Psychologie Université de Montréal C.P. 6128, succursale Centre-ville Montréal QC H3C 3J7, Canada. Tel.: +1 514 343 6511: fax: +1 514 343 2285.

of the results of a few key studies in which chromaticity was shown to have an experimental effect in attentional tasks. Additional discussion can be found in a number of more detailed studies (for which we suggest key studies e.g. Carter, 1982; Treisman and Gelade, 1980; Wolfe, 1994).

Two recent papers evaluate the contributions of colour to visual spatial attention (see also Ansorge and Becker, 2013; Lennert et al., 2011, for additional evidence). The first study addresses the contribution of colour to motion processing in automatic target selection (Tchernikov and Fallah, 2010). The authors measured smooth pursuit eye movements that occur spontaneously immediately following a saccade to a circular region containing dots moving coherently either left or right. The dots were red, green, blue, or yellow (with luminance equated across colours). In two experiments, pursuit movements were initiated earlier for red dots. In Experiment 1, this was evaluated with one colour at a time. The participant's task was to move their eyes in the general direction of the colored stimulus after the disappearance of a white fixation cross. In Experiment 2, different colours were put in opposition and red tended to win over other colours (if two sets of dots moved in the region in different directions, the spontaneous pursuit movements were in the same direction as the moving red dots). Overall, a hierarchy of colours was found, from red (strongest), to green, to yellow, to blue (weakest).

A second paper also evaluated reaction times (RTs) to targets of different desaturated colours (Lindsey et al., 2010). In this study,

E-mail address: vincent.jette.pomerleau@umontreal.ca (P. Jolicœur).

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desaturated colour targets (pink, green, blue, and orange) were placed in a visual display among white and saturated distracters. Participants had to indicate the presence or absence of a target on every trial. To minimise the magnitude of difference in colour appearance, the authors chose desaturated targets (30 cd/m^2) that laid at the midpoint of a line segment between saturated distracter (12 cd/m^2), and white distracter (60 cd/m^2) in Cie L*ab colour space. Those colours were furthermore tested through two auxiliary experiments, the first involving direct heterochromatic matching, and the second based on Maximum Likelihood Difference Scaling. The authors found faster RTs for desaturated red than desaturated orange and green, and slower RTs for desaturated blue (red < orange < green < blue).

What can be retained from these studies is that there seems to be an attentional bias for some colours over others, favouring their selection by attention and hastening our response when they are target. So far, mostly RTs have been reported, but RTs effects are often coupled to observable electrophysiological effects (Brisson et al., 2007; Mazza et al., 2009a). Here we used event-related potentials (ERPs) as a way to monitor, millisecond-to-millisecond, the deployment of attention to colored targets. Our goal was to determine if, like visual search or spontaneous capture of smooth pursuit eye movements, the mechanisms that guide and engage attention reflected by the N2pc component of the ERP would show systematic variations as a function of stimulus colour. We chose colours (red, green, blue, yellow) that are frequently used in visual search task (with and without electrophysiology) involving colour. Our main interest was in the lateralised electrophysiological components known for their link to visual attention, namely the N2pc. However, we were also interested in two other lateralised components, one just before the N2pc, the Ppc (positivity posterior contralateral), and the other just after the N2pc, the Ptc (positivity temporal contralateral).

1.2. The N2pc

The N2pc is a lateralised ERP component that can be calculated by subtracting the electrical potentials measured at electrodes sites ipsilateral to a lateral attended object from the electrical potentials measured at electrode sites contralateral to that object. The N2pc is observed over the posterior scalp, with peak amplitude typically observed at or near electrodes PO7/PO8. As the name suggests, the latency of the N2pc is in the N2 time range, which is 180–280 ms following the onset of an attended stimulus (Brisson and Jolicoeur, 2007; Luck and Hillyard, 1994; Robitaille and Jolicoeur, 2006). Luck and Hillyard (1994) argued that the N2pc reflects spatial filtering of distracters, whereas Eimer (1996) and, more recently, Mazza et al. (2009a, 2009b) argued that the N2pc reflects target enhancement.

It is no surprise that, much like in behavioural attentional studies, colour is often used in ERP experiments involving the N2pc (Eimer, 1996; Hickey et al., 2009). Studies usually report conditions in which the target and distracter are equiluminant to equate bottom-up effective intensity. Then, after making sure that an equal number of participants/trials are performed with each colour, different colour trials are averaged together. Typically, the direct effect of colours on the N2pc is not discussed, with possible differences assumed to have been equated across conditions. This approach is technically sound when there are no colour-specific interactions, but has downplayed what appear to be quite substantial effects that are interesting in their own right. When experimenters do study the effect of colours on the N2pc, it is often with search questions unrelated to chromaticity (e.g., effect of language on detection/disparity between target and distracter). This results in a near absence of reports of N2pc latency or amplitude effects between colours (Liu et al., 2009; Regier and Kay, 2009).

One pertinent paper regarding our research question evaluated the role of physical disparity between target and distracter items (Zhao et al., 2011). In their study, the authors modulated the physical difference (through colour in one condition) between target and distracters

while observing the effect on the N2pc. They compared conditions in which the disparity from the distracter was high (distracter light blue, target dark blue) and a condition in which it was low (distracter medium blue, target dark blue), by manipulating the RGB values of the colours while maintaining them equiluminant. Participants were asked to find the stimulus (a cross) that differed in colour and to decide whether the top or the lower segment of the vertical bar of the target was longer. A main effect of colour disparity was found, with the mean amplitude of the N2pc in the high colour disparity condition being larger (more negative) than the low-disparity condition. A marginal effect of latency was also found, with the N2pc related to low disparity being later than the high-disparity N2pc. Both ERP results dovetailed with the behavioural data in which the high disparity condition had faster RTs than the low disparity condition.

1.3. The Ppc

Rarely discussed, the posterior contralateral positivity (Ppc) is a lateralised component earlier than the N2pc, roughly from 150 to 200 ms post stimulus. In a study by Corriveau et al. (2012), neither the mean amplitude of the Ppc nor its latency depended on the lateral item status as target or distracter. This early-lateralised response appeared to reflect an attention driven spatial "attend-to-me" signal that arises in the waveforms of an unbalanced visual display containing a salient stimulus only on one side.

1.4. The Ptc

The Ptc is a *positive* component that can be observed over the *contralateral* hemisphere of the attended item. The Ptc was observed between 290 and 340 ms post stimulus in previous experiments. The label "*temporal*" follows the suggestion of Hilimire et al. (2009). Hilimire et al. (2009) suggested the Ptc might reflect local attentional competition resulting from the spatial proximity between a target and a salient distracter. The amplitude of the component generally becomes larger (more positive) as the physical separation between the target and a salient distracter decreases (Hilimire et al., 2009). This modulation of Ptc amplitude could reflect distracter inhibition after initial attentional deployment (the N2pc), in order to isolate a target once it has been identified (Hilimire et al., 2011). Their component did not vary with target-distracter saliency difference (manipulated through colour saturation of the target or the salient distracter) (Hilimire et al., 2010).

From previous ERP and behavioural experiments, we expected to see a difference in the N2pc amplitude and latency for colours that allow a better attentional deployment, possibly resulting in a colour hierarchy (Tchernikov and Fallah, 2010; Zhao et al., 2011). More precisely, we anticipated a shorter N2pc latency to red targets, based on the Tchernikov and Fallah (2010) results. However, Lindsey et al. (2010) only found an advantage for desaturated reds, and so the typical red stimuli used in most attention selection experiments may not be subject to the special effect for desaturated red. Predictions for other colours are even more difficult to make, given paucity of results and inconsistent results across studies.

Very few experiments explored the role or even the existence of the Ppc and Ptc. Previous experiments dealing with the Ppc component indicate that it reflects the representation of an unbalanced visual display (Corriveau et al., 2012). Since colour attentional bias should create an unbalanced display, we would expect for the present experiment a more positive Ppc for colours with a stronger attentional response, namely the red target compared to other targets. The Ptc reportedly representing inhibitory processing of close distracters could amplify in amplitude for colours with increased salience like red, since more inhibition should be required for more salient targets (Hilimire et al., 2010).

In most of our recent work we equated the luminance of colours using a specialised instrument (Minolta CS100 chromameter). We wondered, however, if individual differences luminance responses could produce small but systematic luminance differences that would bias attention to one or another of the colours. In order to minimise possible individual differences, we used a psychophysical luminance calibration procedure to equate luminance of the colours for each individual.

Furthermore, in order to determine if some colours were more or less discriminable from the background grey distracter stimuli used in all displays, we conducted two control experiments. These control experiments consisted in visual discrimination tasks that should not yield significant differences between colours if all colours are equally discriminable from the distracters. Given the colour singletons to which attention was to be deployed were presented only with other grey stimuli, and the colour differences across colour stimuli and grey were large, one would expect to find a pop-out pattern of rapid and effortless search.

1.5. Experiment 1

The purpose of Experiment 1 was to determine if different colours would elicit different lateralised ERPs, and most particularly different N2pc waves, under conditions in which each colour was presented on a neutral background of grey distracters. These are conditions that should minimise differences across colours, because colours were never in direct competition for selection with each other. They just had to be found among the neutral grey distracters. This is illustrated in Fig. 1.

2. Method

2.1. Participants

Sixteen paid volunteers participated in Experiment 1. Three participants were rejected, two because of HEOG activity exceeding 25 μ V on a 200 ms interval on more than 50% of trials, suggesting an eye movement towards the lateral target (see below) and one for an accuracy that was at or near chance (25%) in more than one condition. The remaining ERP



Fig. 1. Illustration of the ERP task, the Multiframe Presentation. The arrow represents the passage of time. The first visual frame, not visible here, displayed a fixation cross for 500 ms. Illustrated is a trial with vertical as a target orientation. Six frames were presented for 200 ms with an inter-stimulus interval of 600 ± 100 ms. At the end of each presentation, participants had to indicate whether 0, 1, 2 or 3 targets were presented within the MFP. White labels with the letters R, G, B, Y were added for better comprehension of the black and white version of the article. They respectively represent red, green, blue and yellow stimuli. These labels were not present in the actual experiment.

participants (9 males and 4 females) had a mean age of 23.2 years (*S.E.* = 2.8, range 19–29). All 13 participants were neurologically normal undergraduates at the Université de Montréal and had normal colour vision, and either normal or corrected-to-normal visual acuity.

2.2. Luminance calibration methodology

2.2.1. Stimuli

Stimuli for the calibration experiment consisted in two types of frames, each displaying simultaneously 10 numbered disks, as illustrated in Fig. 2. The disks could be red, green, blue or yellow, depending of the trial block. Each disk of Fig. 2A showed different shades of the same colour, while all disks of Fig. 2B were displayed with the same reference grey. Each disk had a diameter of 1.25° of visual angle and was placed 3° from a central fixation point, thus forming a circle of disks. Participants individually set luminance values through a variant of the heterochromatic flicker photometry technique, described next.

2.2.2. Procedure

In order to control for subtle individual differences in colour perception, we used a variant of the heterochromatic flicker photometry technique (Bone and Landrum, 2004; Walsh, 1953). The heterochromatic flicker photometry technique uses the alternation of two colored stimuli





Fig. 2. Illustration of the calibration task. Two altering frames containing ten numbered circles were presented at a 15 Hz frequency. Each circle of the colored frame (frame A) displayed a slightly different luminance value, while the grey circle frame (frame B) had constant luminance value in each frame. Participants had to choose which circle showed the least flickering through a numeric keypad. Colored frames could display red, green, blue or yellow circles, depending on the color being calibrated.

at the same spatial position (we alternately presented the numbered disk presented on Fig. 2A and B). Participants had to minimise their perception of flicker through luminance adjustment of one of the two colours while colours alternated. The rate (or frequency) of the alternation needs to be high enough in order to obtain a flicker but not so high that colour fuse (we used a frequency of 15 Hz). Equal luminance between colours is obtained when the perception of flicker is minimised.

We modified the usual heterochromatic flicker photometry technique in two ways (see Fig. 2). First, we only presented disks containing flickering colours to the periphery of the visual field. That allowed the presentation of stimuli at the same eccentricity as in the ERP and control experiments. Participants were instructed to pay attention to the disks while looking at a central fixation point. Only after doing this could participants directly look at the disks to make a final decision. The second modification from the original technique was in the luminance value of each circle. In our modified technique, each disk presented in periphery had a slightly different luminance (see Fig. 2A), while only a single colour is presented in the usual technique. Depending on the colour of the circle (red, green, blue, or yellow), a different RGB value was displayed within each disk. From a random disk position, a precise value was added in a clockwise manner four times, and from the same random disk, the same value was subtracted five times in an anticlockwise manner. If disks were all red, then a different value of red was present in every disk while the green and blue component values stayed the same. The same applied for the green and the blue colours, while for the vellow, both red and green component values were modified with a common value and the blue component stayed constant.

The task of the participant was to choose which of the 10 numbered disks showed the least flicker. Participant's answer was recorded through the numeric keypad of a standard keyboard, key 1 corresponding to disk 1 and key 0 to disk 10. After each response, the RGB differences between circles were adjusted to represent a smaller range of RGB colours starting with stimulus chosen on the previous response, until only small (single-step) difference remained between each disks. By doing so, we selected the RGB values providing the least individual luminance difference perception for each colour. Each one of the four colours was calibrated 3 times through 4 forced choice flickering frames. The mean of each RGB component for the 3 calibrations was used as the calibrated colour.

2.2.3. Experiment 1 task

2.2.3.1. Stimuli. The visual display of a frame was very similar to the frames used in the calibration procedure, as illustrated in Fig. 1. Ten circles were displayed, at the same distance from a fixation point as the calibration procedure. The only difference from the calibration frames was the existence of three types of stimuli: distracters, targets, and decoys. Distracters consisted of circles formed with a thin grey line, and containing a grey oriented line on a black background. Oriented lines could either be horizontal, vertical, or at $\pm 45^{\circ}$ from vertical. Targets and decoys were also circles containing an oriented line, but instead of being grey, they were displayed in colour. All colours including the grey were obtained from the calibration procedure and were therefore equiluminant.

2.2.3.2. Procedure. In the search task that followed the calibration procedure, targets were defined as any colored circle containing either a vertical line (half of the participants) or a horizontal line (the other half). Every visual search display contained a colored circle (a colour singleton among grey distracters) containing a line that was either in the target or non-target orientation (one of the other three orientations). Each of the grey distracter circles also contained a line in one of the four possible orientations, chosen at random independently for each display.

Participants initiated every trial by pressing the spacebar. A fixation cross was displayed for 500 ms before the beginning of the trial. Six search displays, henceforth called frames, were then presented, one

after the other. Each frame was visible for 200 ms followed by a fixation cross for 600 ± 100 ms. Participants had to count the number of targets (from 0 to 3) in the sequence of six frames and report the count by button press at the end of the sequence. The letters 'v', 'b', 'n' or 'm' were used to respond 0, 1, 2, or 3 targets, using the middle and index fingers of the left hand (0, 1) or the right hand (2, 3). Participants had 4 s to enter their overt response after each set of 6 frames in a method we call the multiframe procedure (MFP). Feedback was displayed for 500 ms. The experiment consisted of 5 blocks of 80 trials for a total of 400 trials. Each trial consisted in six visual search frames, yielding 2400 attentional episodes.

2.2.3.3. Electrophysiological recording. A BioSemi ActiveTwo system (BioSemi Inc., Amsterdam, The Netherlands) was used for the recording of the EEG signal with 64 active Ag/AgCl electrodes mounted on an elastic cap and rereferenced to the algebraic mean of right and left mastoid signals. Electrodes were placed on the participant's scalp according to the international 10/10 system (Chatrian, 1985; Chatrian et al., 1988). Two electrooculograms were calculated to identify lateral eye movements and blinks through the comparison of pairs of electrodes. The horizontal electrooculogram (HEOG), calculated as the difference between the left and right external canthi electrodes, was used to detect horizontal eye movements. The vertical electrooculogram (VEOG) was calculated as the difference between electrode Fp1 and another electrode placed below the left eye and used to detect blinks.

The EEG was recorded at a sampling rate of 512 Hz, with an antialiasing lowpass filter of 134 Hz was applied during the recordings. An offline bandpass filter 0.05–30 Hz was also applied on the EEG signal. For one participant, that filter was replaced by an offline bandpass filter of 0.05–20 Hz to reduce the signal contamination by alpha activity.

Trials with an HEOG difference larger than 25 μ V on a 200 ms interval suggested lateral eye movements and were rejected. Trials with a variation of VEOG larger than 50 μ V over a 200 ms interval were flagged as blinks and were removed. All trials with artifactual data, identified as a variation of more than 100 μ V for any electrode, were also removed.

We averaged HEOG for left-target and right-target trials from 200 to 700 ms post stimuli presentation and used only the data of participants with residual EOG activity less than less than 3.5 mV, 3 μ V being slightly too restrictive for two participant in two different conditions. Mean HEOG exceeding 3 μ V reached that amplitude after 350 ms, and therefore could not affect our N2pc measures, which peaked between 250 and 300 ms (see Fig. 3A and B). Concerning VEOG, participants with an average difference exceeding 6 μ V were also excluded. Overall, as mentioned previously, no participants were excluded for vertical eye movement and 2 were excluded for horizontal eye movement.

2.2.4. Experiment 1 results

2.2.4.1. Calibration task results. The heterochromatic flicker photometry technique allows the selection of stimuli colours that are all equal in luminance (Walsh, 1953). Despite Walsh's previous results regarding luminance, we measured the luminance for the stimuli of Experiment 1, using a Minolta meter, and then tested for significant differences across the 4 luminance means, using a one-way ANOVA. No significant differences were observed (F(3, 36) = 1,31, p > .28). All colours are therefore equiluminant.

2.2.4.2. Main experiment

2.2.4.2.1. Behavioral results. In our multiple frame procedure (MFP), participants were required to report a target count after each set of six frames. Participants had an average success rate of 90.67 \pm 0.07%, with a range of 75% to 99%. No differences were found depending on target orientation (horizontal, n = 6, or vertical, n = 7, t(11) = 0.21, p > .80).



Fig. 3. A. Grand average of event-related lateralization waveforms (contralateral minus ipsilateral) at PO7/PO8 time-locked to the onset of the coloured item presentation. Red refers to the presentation of a red lateralised item, and so forth for green, blue and yellow. Labels R, G, B, Y respectively represent red, green, blue and yellow stimuli. Tick marks on the time axis represent 100 ms increments. 3B. Grand average of HEOG: target to the right: doted, target to the left: continuous, for each color, calculated as the difference between the left and right external canthi electrodes. Negative deflection reflects eye movement towards target.

3. ERP results

All subsequent analyses were made on electrodes PO7 and PO8. Time windows are presented in Tables 2 and 3.

3.1. Multiple frame procedure

In order to confirm the stability of attentional deployment across different frame positions in the sequence of frames, we assessed the



Fig. 4. Grand average of event-related lateralization waveforms (contralateral minus ipsilateral) at PO7/PO8 time-locked to the onset of the coloured item presentation in each frame. Tick marks on the time axis represent 100 ms increments.

presence of the N2pc on each MFP frame (1 to 6). The event-related lateralisations (ERLs) for each frame position are shown in Fig. 4, amplitudes in Table 1. A repeated measure ANOVA with Frame Position as main factor revealed no significant differences between amplitudes, F(5, 60) = 1,14, p > .35. In fact, *t*-tests revealed a negativity between 245 and 285 ms significantly different from 0 in all six frames (Frame 1: t(12) = -3.15, p < .01; Frame 2: t(12) = -3.76, p < .005; Frame 3: t(12) = -4.10, p < .005; Frame 4: t(12) = -3.94, p < .005; Frame 5: t(12) = -4.35, p < .005; Frame 6: t(12) = -2.76, p < .05).

3.2. Targets and decoys

We assumed that attention would be first deployed to the colored singleton circle, and that subsequently, the orientation of the line in that circle would be evaluated to determine if the display contained a target or a decoy. To know whether or not the electrophysiological activity arising from target and decoys are comparable (and therefore can be averaged together for further analyses), components were compared on their amplitude. In order to evaluate this, two time windows were chosen independently for both targets and decoys in order to best fit the individual conditions components (see Fig. 5). Paired-sample t-tests comparing the target and decoy mean amplitude across their respective Ppc, N2pc, and Ptc (the time range of each component is indicated in Table 2) found no significant differences; Ppc: t(12) = 1.22, p > .24; N2pc: t(12) = 1.62, p > .13; Ptc: t(12) = -1.18, p > .25. The same results were also obtained when a common window was chosen for both the target and decoy conditions of the N2pc and Ppc (Ppc: t(12) = 1.31, p > .21; N2pc: t(12) = -2.04, p > .06) confirming that for the purpose of this experiment both conditions were equivalent.¹ For subsequent analyses, these two different types of trials were merged together and are called targets from the point of view of attentional deployment.

3.3. Electrophysiology-N2pc

Fig. 3A presents grand-averaged event-related lateralisations (ERLs) obtained by subtracting the ispilateral ERP waveform from the contralateral ERP waveform for each singleton colour. These averages were time-locked to the onset of the visual search display presentation and included a 200-ms pre-stimulus baseline and extended 700 ms after onset.

Analyses of mean amplitudes were performed on the average voltage in a window starting 20 ms before and extending to 20 ms after the grand average waveform peak for each conditions of the N2pc. The time window boundaries can be found in Table 3 and the mean amplitudes, in Table 4. A repeated measure ANOVA for the Colour factor (red, green, blue, or yellow) showed no amplitude main effect, *F*(3, 36) = 1.23, *p* > .31. All N2pc components had an amplitude significantly different from zero (one-sample *t*-tests versus 0, red: *t* (12) = -4.10, *p* < .005; green: *t* (12) = -4.48, *p* < .005; blue: *t* (12) = -3.88, *p* < .005; yellow: *t* (12) = -3.69, *p* < .005).²

We examined the latency of the onset of lateralised activity across colour conditions. These analyses used repeated-measures ANOVAs combined with the jackknife method (Kiesel et al., 2008; Miller et al., 1998). The use of the repeated measure ANOVA with the jackknife required some corrections to the F value. These corrections compensated for the artificial deflation of the error variance associated with sets of jackknife waveforms ($F = F/(n-1)^2$) (Ulrich and Miller, 2001). Latency was estimated as the time at which the waveform first reached amplitude of -0.75 microvolt. The N2pc showed significant latencies differences depending on the colour of the singleton, as shown in Fig. 3A, F' (3, 36) = 11.57, p < .0001.³ Tukey's post-hoc test revealed that conditions in which a potential target was red or blue had an earlier N2pc compared to conditions in which the potential target was green or yellow; while the red and blue N2pc did not differ in latency (R < GY; B < GY; $R \sim B$; $G \sim Y$). The estimated mean latency for each singleton

¹ We intended here to openly expose the verification that both waveforms were actually identical. We chose both a common window and a maximum difference window (to maximize a difference between conditions), in order to demonstrate that even without presuming a common window for the ERP components we still failed to get a significant difference between target and decoys. Since both items reflected the same activity, trials where attentional deployment was to a target or to a decoy were averaged together in subsequent analysis.

² That result was explored further because of the apparent amplitude differences visible by eye in Fig. 3A. A subsequent paired *t*-test evaluated the presence of a difference between the red-blue average and green-yellow average, but still revealed no significant difference, t(12) = -1.65, p > .12.

³ The different filter between one participant and the rest did not introduce any side effect. When using the same filter parameters for all participants, the more susceptible result to change (the jackknife) showed similar results F'(3, 36) = 10.31, p < .0001). The Tukey test also showed the same color hierarchy.

Table 1 Mean amplitude and

Mean amplitude and standard deviation of the N2pc in microvolt ($\mu V)$ for each frame position.

	N2pc (s.d.)
Frame 1	98 (1.12)
Frame 2	-1.21 (1.16)
Frame 3	-1.21 (1.07)
Frame 4	-1.21 (1.10)
Frame 5	-1.23 (1.02)
Frame 6	81 (1.05)

colour can be found in Table 5. Tukey's post-hoc test also required some correction $(H'=H^*(n-1))$ for jackknife measurements (Ulrich and Miller, 2001).

Condition specific voltage maps shown in Fig. 6 were produced to examine the scalp distribution of lateralised activity for the N2pc in each colour conditions. The distributions were quite similar, overall, all showing a typical N2pc-like peak near PO7–PO8, as expected from previous research (e.g., Jolicoeur et al., 2008)

3.4. Electrophysiology—Ppc

We also performed analyses on the mean amplitude of the Ppc depending on the colour of the singleton for windows shown in Table 3. The waveforms are in Fig. 3A and mean amplitudes are in Table 4. These results were submitted to a repeated measure ANOVA with singleton colour as a within-subjects factor. The mean amplitudes were different, F(3, 36) = 6.08, p < .005), and Tukey's post hoc tests showed significant differences with the Ppc for red more positive than for blue or green, and the red–yellow difference missing significance.

The red and yellow Ppc waves were confirmed to be present by *t*-tests against zero, while the two others were not (red: t(12) = 3.94, p < .005; green: t(12) = 1.13, p > .55; blue: t(12) = 1.42, p > .15; yellow: t(12) = 2.52, p < .05). In Fig. 7 we show the voltage distribution map of the Ppc for red and yellow singletons. The distribution is posterior and resembles a polarity-inverted N2pc, although somewhat more inferior and lateral than N2pc. Although the red and yellow Ppcs did not significantly differ at PO7–PO8, our activation maps suggest a more positive red Ppc due to the similar larger amplitude trend found on

Table 2

Time windows for targets and potential targets (color singleton containing a non-target line orientation) for the N2pc Ppc, and Ptc components, in milliseconds, post stimulus.

	N2pc	Ррс	Ptc
Potential target	240–280	130–170	335–375
Real target	235–275	145–185	335–375

Table 3

Time windows for N2pc. Ppc, and Ptc in milliseconds, post stimulus, for each singleton color.

	N2pc	Ррс	Ptc
Red	215-255	130-170	330-370
Green	260-300	160-200	340-380
Blue	240-280	130-170	335-375
Yellow	260-300	160-200	340-380

the surrounding electrodes. That hypothesis was confirmed through a paired sample *t*-test comparing the red and yellow Ppcs from a pooling of electrodes PO3–PO7 and electrodes PO4–PO8 (t(12) = 3.87, p < .005).

For the subsequent analyses, we measured the Ppc latency at a threshold set at 50% of the average waveform maximum amplitude between 120 and 200 ms. We found the colour factor to be significant (F' (3, 36) = 5.89, p < .005). Tukey's post-hoc tests revealed that the blue Ppc reached its 50% threshold significantly before the green and yellow Ppcs, but not before the red Ppc (B ~ R; B < GY; R ~ G ~ Y; Mean R: 130.1 ms; G: 149.2 ms; B: 112.4 ms; Y: 158.6 ms). In order to verify the presence of a pattern similar to the N2pc, we grouped together the red and blue (RB) as well as the green and yellow (GY) Ppc waves. Comparing these two averaged components, we observed that RB reached its 50% threshold significantly earlier than the GY component (F' (1, 12) = 15,56, p < .005); (Mean RB: 121.2 ms; GY: 153.8 ms).

3.5. Electrophysiology-Ptc

The Ptc component can be seen in the waveforms in Fig. 3A as a greater positivity contralateral to the colour singleton, mainly for red



Fig. 5. Grand average of event-related lateralization waveforms (contralateral minus ipsilateral) at PO7/PO8 time-locked to the onset of the coloured item (dotted lines refer to lateralised targets, continuous lines refer to lateralised decoys). Tick marks on the time axis represent 100 ms increments.

Table 4

Mean amplitude ($\mu V)$ and standard deviation for the N2pc Ppc, and Ptc, for each singleton color.

	N2pc	Ррс	Ptc
Red	-1.50 (1.32)	0.88 (.80)	0.98 (.89)
Green	-1.17 (.94)	0.16 (.52)	-0.10 (.85)
Blue	-1.60 (1.49)	0.24 (.63)	0.18 (1.14)
Yellow	-1.13 (1.10)	0.49 (.71)	-0.04 (1.15)

singletons. The mean amplitude of the Ptc for each participant and condition in a window of 20 ms around peak amplitude for the component (see Table 3 for time ranges) were submitted to a repeated measure ANOVA with Colour as a within-subjects factor that revealed a significant main effect, F(3, 36) = 8.64, p < .001. Tukey's post hoc tests showed significant differences between the red and all other colours, the red being more positive (see Table 4 for mean voltages). Although windows of analysis were set to assess the highest visible peak of each colour Ptc component, only the red Ptc differed from zero (one-sample *t*-tests versus 0, red: (t(12) = 3.94, p < .005; green: <math>t(12) = -0.42, p > .65; blue: t(12) = 0.57, p > .55; yellow: t(12) = -0.13, p > .85). A voltage distribution map of the red Ptc can be seen in Fig. 8. The voltage distribution map of the Ptc is similar to the Ppc in position and polarity.

3.6. Discussion-Experiment 1

Through ERPs we evaluated how different colours influenced lateralised event-related potentials (ERLs) that reflect preattentional and attentional processes, particularly attentional deployment. We designed a visual search task in which a single colored item, a singleton target or decoy was shown in red, green, blue, or yellow among grey items (distracters). Singletons and grey distracters all had the same luminance (which was equated psychophysically for each participant). The experimental design left only attention and colour-specific differences as probable causes of the observed effects.

There were two main findings in Experiment 1. Firstly, we observed that red or blue singletons triggered an earlier N2pc compared to green or yellow singletons (red ~ blue < green ~ yellow). Secondly, significantly higher amplitudes for the red Ppc and Ptc suggest a stronger attentional signal by the red target singleton.

Our first results regarding the N2pc latency confirms and extends earlier findings (Fortier-Gauthier et al., 2013), in showing that the N2pc has an earlier onset latency for red than for green singletons, which we here extended here to show a significantly earlier response to blue than to yellow. The colour attentional hierarchy we obtained differs from previous behavioural results (Lindsey et al., 2010; Tchernikov and Fallah, 2010). Even considering the small differences in methodology, the shorter N2pc latency for a blue target singleton differs from previous results. Interestingly, the grouped Ppc waves show the same colour hierarchy showed with the N2pc. These results were not as robust as for the N2pc results probably because of the smaller amplitude of the Ppc component. However, from these results, we can postulate a mechanism differentially sensitive to variations in stimulus colour that responds prior to the onset of the N2pc.

Table 5

Mean	latency	of	the	onset	of	the	N2pc	in
millise	conds (m	ns), a	and s	tandard	dev	viatio	n, for ea	ach
singlet	on color.							

	N2pc (s.d.)
Red	205 (3.15)
Green	250 (2.48)
Blue	223 (2.76)
Yellow	253 (4.06)



Fig. 6. Grand average scalp voltage distributions of the N2pc for each color.

A few hypotheses could explain our colour hierarchy. First, it could be that some colours may be easier to discriminate from grey. That possibility is evaluated later in Experiments 2a and 2b. Second, regarding solely the results to blue targets, we could hypothesise that a non equiluminant blue target could explain its shorter latency. Previous results showed that the bleaching of S-cones (or "blue" cones) does not affect in a large way results of tasks such as the heterochromatic flicker photometry results (Cavanagh et al., 1987). Knowing this, one could propose that our calibration task, a modified version of the heterochromatic flicker photometry, did not yield equiluminant colours. That proposal can be discounted for two reasons. Firstly, resulting luminance values, after adjustment, were measured with an instrument and the measured values were submitted to statistical analysis. The observed luminances were not statistically different across colours. Secondly, the results of Cavanagh et al. (1987)



Fig. 7. Grand average scalp voltage distributions of the Ppc for each color.



Fig. 8. Grand average scalp voltage distributions of the Ptc for each color.

showed that the contribution of blue cone activity to the luminance channel is considerably weaker than for the two other cone populations. This reduces the likelihood that luminance differences across blue singletons and green or yellow singletons was the main cause of the attentional differences across colours, particularly given that the luminances differences were small, at best (given the results of the flicker photometry and physical photometry).

Another hypothesis for our colour hierarchy could be derived based on earlier result on linear separability between colours in colour space (Bauer et al., 1996). In the present experiment, only two dimensions in colour space need to be considered because all colours were equiluminant (luminance being one of the three dimensions). Furthermore, throughout the experiment, only one colour was shown at a time, so the creation of a single linear separation per trial was sufficient to perform the task.⁴ Considering the experimental results presented, it could be surmised that the creation/activation of a two dimensional linear separation is faster for the colours that trigger faster attentional deployment (red and blue) than for the other colours (green and yellow). That possibility is further investigated in Experiments 2a and 2b.

A third hypothesis for our colour hierarchy would be that red is furthest, and blue farther from grey, in an appropriate colour space, than yellow or green. This would mean that yellow or green would be less discriminable from grey than red or blue (Bauer et al., 1996, see page 1453 & 1464). Previous research showed that, as the distance between target and distracters expands in a colour space, the cost in RTs of adding more distracters in a visual search task becomes increasingly small. Fig. 9 shows a 2 dimensional representation of the mean of the colours obtained from the calibration task in the Cie L*ab colour space (the figure is two dimensional because of equiluminance). This colour space was designed so as to optimise the relationship between distance in the space and differences in discriminability among nearby colours. That figure shows differences in the distance of the different colours and grey, which might provide a basis to explain our results. For example, the advantage for red over other colours could be explained because red is further from grey than the other colours. One problem for this account, however, is that blue was not further from grey than green or yellow. Moreover, the threshold for the perception of different colours in the Cie L*ab space is very low (i.e., is reached at a short distance, see Nagy et al., 1990; Olds et al., 1999). Considering the actual colours position in colour space (see Fig. 9) a distance factor to the grey colour of this magnitude is an unlikely candidate to explain differences of N2pc latency between colours because a ceiling effect for the discrimination of the colours is most likely in place for much closer (to grey) colours than our particular yellow or green (further explored in Experiments 2a and 2b).

Our second main result suggests increased salience for red targets, as red target trials showed higher Ppc and Ptc amplitude. Concerning the Ppc results, it has been verified that the red target had higher amplitude than the green and blue targets. This suggests that the imbalance in the visual display caused by the red target had larger attentional repercussions than for blue or green target colours. The absence of amplitude effect between the red and yellow Ppc is somewhat puzzling and does not reflect the effects observed on the N2pc or the Ptc (and is likely due to noise associated with the measurement of a component with a relatively small amplitude).

Studies interested in exploring the Ptc have not considered colour as a possible factor up until now (Hilimire et al., 2009, 2010, 2011). Although colour saturation was a factor in a previous study, different colours were not compared (Hilimire et al., 2010). Hillimire et al. suggest that a more positive Ptc component reflects higher distracter inhibition in order to isolate a target. That would imply that the distracters surrounding red targets needed more inhibition after initial deployment in order for the task to be completed successfully, which is unlikely since the distracters are identical between colour condition and that red was the most easily separable colour used (based on distance from grey, Fig. 9). This would in turn suggest that the red triggers both a faster attentional deployment, but also enhances the distracter inhibition process. It is not clear that this is the most coherent interpretation of the results. Another fact that needs to be put forward is that, while our component has the same approximate latency, and follows the N2pc, it does not seem as anterior as the one reported by Hilimire et al. (2010), and thus it could reflect a different underlying process.

Interestingly, these results also contribute to confirm that the Ppc and Ptc reflect the ERP representation of an unbalanced visual display but that these mechanisms do not simply reflect an imbalance in luminance.

3.7. Experiments 2a and 2b

Experiments 2a and 2b were behavioural control experiments designed to determine whether the discriminability of stimuli from grey could account for the results of Experiment 1. In these two experiments, two items were shown simultaneously in a same/different task, in which participants had to indicate whether two coloured disks were the same colour or not. We expected to find no colour effects when comparing the RTs in the same/different task. Such results would allow us to reject the possibility that some colours may be easier to discriminate from grey. Experiments 2a and 2b solely differed in the stimulus design (see below).

4. Method

4.1. Participants

Participant for Experiment 2a (8 males and 16 females) had a mean age of 22.21 years (S.E. = 2.6, range 19–27), and participants Experiment 2b (12 males and 14 females) had a mean age of 22.96 years (S.E. = 2.6, range 22–28) for a total of 50 control participants.

4.2. Control tasks

4.2.1. Stimuli

The visual display of both tasks differed from the ERP task (see Fig. 10AB (first task, with circles) and Fig. 10cd (second task, with disks)). In both control tasks, only two stimuli instead of ten were displayed. Visual properties of the circles/disks (size, distance from fixation) were the same as disks from the ERP task. The only difference between the first and second control tasks, each stimulus could be of five

⁴ For that reason, the creation of a linear separation is always possible, as the creation of a line separating only two different points in space was always possible.





Fig. 9. Illustration of the mean results of the calibration task for the ERP task. The colors are represented in the Cie L*ab color space. The x axis corresponds to the a value and the y axis to the b value. The L value, referring to luminance is not illustrated since all colors are equiluminant. Points are positioned according to coloured markers and not labels.

possible colours: grey or one of the four colours obtained through our calibration task.

Two visual conditions could be shown. For the *same* condition, stimuli could either be both grey or both coloured (Fig. 10A and C). For the *different* condition, one stimulus would be grey while the other was coloured (Fig. 10B and D). Two different coloured stimuli were not shown simultaneously, as a similar condition was not present in Experiment 1. Although two conditions were needed for the task, the condition of greatest interest for the purpose of our inquiry was the



Fig. 10. Illustration of the Experiments 2a and 2b. Not shown here, a fixation cross that preceded every trial for 500 ms. After the fixation cross, participants were shown either a frame of the same (exp 2a: frame A or C) or different (exp 2b: frame B or D) condition. Disks and circles stimuli are from in a different task. White labels with the letters R, G, B, Y were added for better comprehension of the black and white version of the article. They respectively represent red, green, blue and yellow stimuli. These labels were not present in the actual experiments.

different condition, which evaluated colour discriminability from grey distracters, which was also required from participants in Experiment 1.

4.2.2. Procedure

First, a 500 ms fixation cross was shown. Then, two stimuli were displayed above and under the cross for 200 ms. After that display, participants were instructed to simply press "v" if both stimuli were the same colour and "b" if colours differed. The experiment consisted in 455 trials of which 70 compared a grey stimulus to a *different* colour, for a total of 280 colour-to-grey pairings.

4.2.3. Experiments 2a and 2b-behavioural results

The average error rate for Experiment 2a was 3.5% (s.d. = 2.4) while average error rate for Experiment 2b was 4.3% (s.d. = 3.4). Outliers, defined as trials with RTs two and a half standard error longer or shorter than the mean, were rejected from all analyses. Experiment 2a had 3.5% outliers and Experiment 2b 3.3%. From the initial 455 trials, an average of 93.1% (s.d. = 2.5) were kept for Experiment 2a and an average of 92.5% (s.d. = 3.4) were kept for Experiment 2b once errors and outliers were removed.

For each control experiment a repeated measure ANOVA evaluated the RTs using a 2 levels factor Type (conditions *same* vs. *different*) by 4 levels factor Colour (red, green, blue, or yellow) design.

4.2.4. Experiment 2a–Circles

Mean RTs for each condition can be found in Table 6. Analyses did not reveal any interaction, F(3, 75) = 1.97, p > .15, nor any main effect, Type: F(1, 25) = 0.45, p > .51; Colour: F(3, 75) = 1.90, p > .16.

4.2.5. Experiment 2b–Disks

We found the Type (*same* or *different*) factor main effect to be marginally significant, F(1, 25) = 3.40, p < .07, and the Colour factor main effect to be significant, F(3, 75) = 5.42, p < .01, but no significant interaction effect was present, F(3, 75) = 1.40, p > .25. We performed

Table 6					
Mean response time	(ms) and standard	deviation for each	control tasks,	from Expe	eriment 2

	Exp. 2a—same	Exp. 2b—same	Exp. 2a—different	Exp. 2b-different
Red	446 (94.6)	477 (135.8)	459 (142.3)	529 (207.2)
Green	498 (189.1)	487 (133.9)	469 (150.4)	524 (172.6)
Blue	473 (118.0)	520 (160.7)	493 (186.8)	561 (213.1)
Yellow	516 (228.7)	515 (159.2)	466 (146.9)	526 (188.9)

additional repeated measure ANOVAs for the colour factor separately for each Type (*same* and the *different* conditions) in order to establish if the Colour main effect was present across both conditions. These analyses did not show any significant differences between colours, F(3, 75) = 2.10, p > .13, for the *different* condition. No significant results were also obtained with one-tailed paired sample *t*-test comparing together a group formed of the averaged red and blue RTs and the averaged green and yellow RTs for the *different* condition, t(25) = 1.43, p > .16, which were the colour grouping that were observed in our ERP Experiment (see Fig. 5 for the ERL waveforms). However, a significant effect of colour for the *same* condition, F(3, 75) = 5.96, p < .01, was found. Tukey's post-hoc tests revealed significantly shorter RTs for the red disks compared to blue and yellow disks (see Table 6 for mean RTs by condition).

5. Discussion

Experiment 2 acted as a control task, evaluating participant's capacity to discriminate two coloured circle (Experiment 2a) or disk (Experiment 2b) as *same* or *different. Same* condition consisted in two items of the same colour (either red, green, blue, yellow or grey) shown simultaneously and *different* condition consisted in a grey item and a differently coloured item, also shown simultaneously. Our results confirm that all colours have the same discriminability from grey, since no significant differences were found for the *different* condition which reproduced, especially the circle experiment (2a), the colour contrast present in our experimental task. Furthermore, the equivalent mean RT between colours in the *different* condition do not support the hypothesis that a different discriminability explains the N2pc latency effect in our experimental task. The control experiments did not reveal any RT pattern that would lead us to believe the red and blue colours had a higher discriminability than other colours during the Experiment 1.

The *same* condition was added to our control tasks in order to have a multiple choice task. The main objective of the control tasks was therefore to evaluate the eventual RT effect that could be present in the *different* condition. The colour main effect in the *same* condition is hard to explain and requires further investigations.

In the following lines, we will emphasise the absence of a colour effect in the *different* condition because finding a difference seems closer to what was required in the ERP search task than deciding that two colours were the same. In order to locate potential targets in the ERP experiment, a colour difference had to be detected and used to guide attention.

As mentioned earlier in Experiment 1, it could be surmised that the creation/activation of a two dimensional linear separation is faster for the colours that trigger faster attentional deployment (red and blue) than for the other colours (green and yellow). We reject that possibility on the basis of the results of both control tasks. If separation was easier for a colour, we would obtain faster RTs for that colour in one of the control task for the *different* condition. Given that no significant RT differences were observed in the *different* condition, the hypothesis of faster separations—or any discriminative filter activation/creation—for some colours versus others needs to be ruled out. These results from Experiment 1. Indeed, Experiment 2 shows that that the Ppc amplitude effect could not be caused by properties that would automatically lead to shorter reaction times (i.e. luminance or discriminability), as this would have been reflected in RT differences for the *different* conditions.

5.1. General discussion

Generally, red targets tended to produce a larger Ppc, an earlier N2pc, and a larger Ptc—all lateralised ERP components relative to a lateral stimulus—relative to targets in other colours. Blue targets also produced an earlier N2pc relative to yellow and green. We equated luminance using a psychophysical procedure in a subject-by-subject

manner to minimise possible luminance differences between colours. Although the electrophysiological results appear to be robust, our attempts to relate them to a simple discriminability account were somewhat inconclusive. Previous research that found colour hierarchy used evolutionist theories or cone proportion in the retina to explain the importance of the red (Lindsey et al., 2010; Tchernikov and Fallah, 2010). The present results, without refuting past observations, cannot use similar hypotheses because of the presence of the early blue N2pc. This likely reflects either a non-controlled variable or some gap in the sparse research dedicated to colour-specific differences in attention. Despite this, the present conclusions should be a warning for ERP researchers that equiluminance is not sufficient for nulling out all colour relatedbias in a visual search display. Similarly, equating distance in a colour space like the Cie L*ab space may also not provide a complete solution.

Some of the present results may be related to the koniocellular pathway. Although first described in the late forties, this pathway has been neglected for a long time in terms of its contribution to visual perception. New data shows that the koniocellular pathway links S-cones, and consequently mostly blue-on responses, to multiple visual areas, including the colour selective blobs in the primary visual cortex of monkeys (Hendry and Reid, 2000; Komatsu, 1998). These new results challenge the notion that colour information is essentially carried by the parvocellular pathway, which contains only a small proportion of input from S-cones (Chatterjee and Callaway, 2002; Martin et al., 1997). In that way, our results could be explainable by an early integration of the blue-on responses in visual areas. As to why this effect would only show on ERPs and not in behavioural data remains unclear. Despite this uncertainty, other results have shown a rapid integration of magnocellular and koniocellular information in motion perception, which could suggest such an early integration also occurs in attentional selection based on colour cues (Morand et al., 2000).

Some apparent discrepancies exist between results from Experiments 1 and 2. In our ERP task, we observed a N2pc delay between different colours, but in Experiment 2, we observe no corresponding systematic RT difference (particularly in the different colour conditions). The two tasks used colored circles obtained through the same calibration procedure and displayed at the same eccentricity from a fixation cross, so these factors cannot be used to explain the dissimilarities. What differs between tasks are 1) the number of items; 2) the nature of the task; 3) the distance between each item; and 4) the specific position of the items in the visual displays. About the number of items, one could be concerned by the transition of strategy or differences in difficulty between tasks. In the present case, because the colours were very different, a significant difficulty difference due to the number of items between both tasks is unlikely because all colours were easily distinguishable from the grey items (Bauer et al., 1996). For the same reason, a change in strategy is unlikely to be related to the number of items present since in both tasks, colored items likely popped-out from the grey items, likely reducing disruptive effects of the grey items (Nagy et al., 1990; Olds et al., 1999; Treisman and Gelade, 1980). Regarding the difference in the nature of the task, Experiments 2a and 2b, implying simple colour discrimination, was generally easier than Experiment 1, which required both a colour discrimination and the identification of line orientation within the selected item. This difference in task difficulty may have resulted in less effort exerted in Experiments 2a and 2b, which may have attenuated possible discriminability effects across colours. The distance between each target and non-salient items would tend to make the task RTs slower for closer distracters (Mazza et al., 2009b). In their study, Mazza et al. (2009b) did not match this RT effect with neither an amplitude nor a latency effect on the N2pc. This would tend to disqualify this factor as a possible explanation to our discrepancies. The effect would also need to be colour selective, which was not reported in previous research. Finally, the fact that control items were presented on the vertical midline instead of lateral in each hemifield was another difference between the presentation conditions in Experiment 1 and the control conditions in Experiment 2. Although there are

many electrophysiological and behavioural effects related to visual fields (upper vs. lower, left vs. right), it is not clear in the present case that such differences would enhance possible colour discriminability effects in left-right lateral presentations (Experiment 1) or reduce them in upper-lower presentations (Experiment 2), although this remains possible.

Although the results from the *different* conditions of Experiments 2a and 2b did not reveal a greater ability to discriminate red from grey than for other colours, results from the *same* conditions produced shorter RTs to respond that two colored stimuli where the same when they were red than for other colours (Table 6). This pattern, particularly evident in Experiment 2b, could reflect the same advantage of red over other colours as observed in Experiment 1 if attention is more quickly deployed to a red target. This advantage would be present for both red stimuli in the same condition than for other colours, even if subsequent operations (such as colour comparison or response selection) unfolded at the same rate for all colours). Although red seemed special in some of the results of Experiment 2, we found no equivalent evidence for blue. Overall, the results converge in suggesting that red has a special status in guiding attention in a variety of situations that require attentional deployment to visual stimuli.

6. Conclusion

The colour effects observed on the N2pc, Ppc, and Ptc, along with results obtained from Experiments 2a and 2b, suggest careful evaluation of chromatic factors in subsequent studies making use of colored stimuli. Equiluminant colours do not have an equivalent effect on attentional mechanisms, as reflected by amplitude and latency effects observed across different target colours in the present study. Red stimuli appear to attract attention more efficiently than stimuli of other colours (particularly green or yellow), even under pop-out conditions. The present results reinforce earlier finding and suggest that the red advantage deserves further study.

References

- Ansorge, U., Becker, S., 2013. Contingent capture in cueing: the role of color search templates and cue-target color relations. Psychol. Res. 1–13. http://dx.doi.org/10.1007/ s00426-013-0497-5.
- Bacon, W.F., Egeth, H.E., 1994. Overriding stimulus-driven attentional capture. Percept. Psychophys. 55 (5), 485–496.
- Bauer, B., et al., 1996. Visual search for colour targets that are or are not linearly separable from distractors. Vision Res. 36 (10), 1439–1466. http://dx.doi.org/10.1016/0042-6989(95)00207-3.
- Bone, R.A., Landrum, J.T., 2004. Heterochromatic flicker photometry. Arch. Biochem. Biophys. 430 (2), 137–142. http://dx.doi.org/10.1016/j.abb.2004.04.003.
- Brisson, B., Jolicoeur, P., 2007. The N2pc component and stimulus duration. Neuroreport 18 (11), 1163–1166. http://dx.doi.org/10.1097/WNR.0b013e3281e72d1b.
- Brisson, B., et al., 2007. Stimulus intensity affects the latency but not the amplitude of the N2pc. Neuroreport 18 (15), 1627–1630. http://dx.doi.org/10.1097/ WNR.0b013e3282f0b559.
- Carter, R.C., 1982. Visual search with color. J. Exp. Psychol. Hum. Percept. Perform. 8 (1), 127–136. http://dx.doi.org/10.1037/0096-1523.8.1.127.
- Cavanagh, P., et al., 1987. Equiluminance: spatial and temporal factors and the contribution of blue-sensitive cones. J. Opt. Soc. Am. A 4 (8), 1428–1438. http://dx.doi.org/ 10.1364/JOSAA.4.001428.
- Chatrian, G.E., 1985. Ten percent electrode system for topographic studies of spontaneous and evoked EEG activity. Am. J. Electroencephalogr. Technol. 25, 83–92.
- Chatrian, G.E., et al., 1988. Modified nomenclature for the "10%" electrode system. J. Clin. Neurophysiol. 5 (2), 183–186.
- Chatterjee, S., Callaway, E.M., 2002. S cone contributions to the magnocellular visual pathway in macaque monkey. Neuron 35 (6), 1135–1146 (doi:S0896627302008747 [pii]).
- Clark, S.E., 1969. Retrieval of color information from preperceptual memory. J. Exp. Psychol. 82 (2), 263–266. http://dx.doi.org/10.1037/h0028135.
- Corriveau, I., et al., 2012. Electrophysiological evidence of multitasking impairment of attentional deployment reflects target-specific processing, not distractor inhibition. Int. J. Psychophysiol. http://dx.doi.org/10.1016/j.ijpsycho.2012.06.005.
- Cowan, N., 2000. The magical number 4 in short-term memory: a reconsideration of mental storage capacity [Comment/Reply]. Behav. Brain Sci. 24 (1), 87–185. http://dx.doi.org/10.1017/S0140525X01003922.
- Dell'Acqua, R., et al., 2012. Sparing from the attentional blink is not spared from structural limitations. Psychon. Bull. Rev. 19 (2), 232–238. http://dx.doi.org/10.3758/s13423-011-0209-3.

- Eimer, M., 1996. The N2pc component as an indicator of attentional selectivity. Electroencephalogr. Clin. Neurophysiol. 99 (3), 225–234. http://dx.doi.org/10.1016/0013-4694%2896%2995711-9.
- Fortier-Gauthier, U., et al., 2013. The "red-alert" effect in visual search: evidence from human electrophysiology. Psychophysiology 50 (7), 671–679. http://dx.doi.org/ 10.1111/psyp.12050.
- Hendry, S.H.C., Reid, R.C., 2000. The koniocellular pathway in primate vision [Review]. Annu. Rev. Neurosci. 23, 127–153. http://dx.doi.org/10.1146/annurev.neuro.23.1.127.
- Hickey, C., et al., 2009. Electrophysiological indices of target and distractor processing in visual search. J. Cogn. Neurosci. 21 (4), 760–775. http://dx.doi.org/10.1162/ iocn 2009 21039.
- Hilimire, M.R., et al., 2009. Competitive interaction degrades target selection: an ERP study. Psychophysiology 46 (5), 1080–1089. http://dx.doi.org/10.1111/j.1469-8986. 2009.00846.x.
- Hilimire, M.R., et al., 2010. Event-related potentials dissociate effects of salience and space in biased competition for visual representation. PLoS ONE 5 (9), e12677. http://dx.doi.org/10.1371/journal.pone.0012677.
- Hilimire, M.R., et al., 2011. Dynamics of target and distractor processing in visual search: evidence from event-related brain potentials. Neurosci. Lett. 495 (3), 196–200. http://dx.doi.org/10.1016/j.neulet.2011.03.064.
- Jolicoeur, P., et al., 2008. Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. Brain Res. 1215, 160–172. http://dx.doi.org/ 10.1016/j.brainres.2008.03.059.
- Kiesel, A., et al., 2008. Measurement of ERP latency differences: a comparison of single-participant and jackknife-based scoring methods. Psychophysiology 45 (2), 250–274. http://dx.doi.org/10.1111/j.1469-8986.2007.00618.x.
- Komatsu, H., 1998. Mechanisms of central color vision. Curr. Opin. Neurobiol. 8 (4), 503–508. http://dx.doi.org/10.1016/s0959-4388(98)80038-x.
- Lennert, T., et al., 2011. Attentional modulation of neuromagnetic evoked responses in early human visual cortex and parietal lobe following a rank-order rule. J. Neurosci. 31 (48), 17622–17636. http://dx.doi.org/10.1523/jneurosci.4781-11.2011.
- Lindsey, D.T., et al., 2010. Color channels, not color appearance or color categories, guide visual search for desaturated color targets. Psychol. Sci. 21 (9), 1208–1214. http://dx.doi.org/10.1177/0956797610379861.
- Liu, Q, et al., 2009. The N2pc component in ERP and the lateralization effect of language on color perception. Neurosci. Lett. 454 (1), 58–61. http://dx.doi.org/10.1016/j. neulet.2009.02.045.
- Luck, S.J., Hillyard, S.A., 1994. Spatial filtering during visual search: evidence from human electrophysiology. J. Exp. Psychol. Hum. Percept. Perform. 20 (5), 1000–1014. http://dx.doi.org/10.1037/0096-1523.20.5.1000.
- Martin, P.R., et al., 1997. Evidence that blue-on cells are part of the third geniculocortical pathway in primates. Eur. J. Neurosci. 9 (7), 1536–1541. http://dx.doi.org/10.1111/ j.1460-9568.1997.tb01509.x.
- Mazza, V., et al., 2009a. An electrophysiological assessment of distractor suppression in visual search tasks. Psychophysiology 46 (4), 771–775. http://dx.doi.org/10.1111/ j.1469-8986.2009.00814.x.
- Mazza, V., et al., 2009b. Attention selection, distractor suppression and N2pc. Cortex 45 (7), 879–890. http://dx.doi.org/10.1016/j. cortex .2008.10.009.
- Miller, J., et al., 1998. Jackknife-based method for measuring LRP onset latency differences. Psychophysiology 35 (01), 99–115 (doi:doi:null).
- Morand, S., et al., 2000. Electrophysiological evidence for fast visual processing through the human koniocellular pathway when stimuli move. Cereb. Cortex 10 (8), 817–825. http://dx.doi.org/10.1093/cercor/10.8.817.
- Nagy, A.L., et al., 1990. Visual search for color differences with foveal and peripheral vision. J. Opt. Soc. Am. A 7 (10), 1995–2001.
- Olds, E., et al., 1999. Stimulus-determined discrimination mechanisms for color search. Atten. Percept. Psychophys. 61 (6), 1038–1045. http://dx.doi.org/10.3758/bf03207611.
- Posner, M.I., 1980. Orienting of attention. Q. J. Exp. Psychol. 32 (1), 3–25. http://dx.doi.org/ 10.1080/00335558008248231.
- Regier, T., Kay, P., 2009. Language, thought, and color: Whorf was half right. Tics 13 (10), 439–446. http://dx.doi.org/10.1016/j.tics.2009.07.001.
- Robitaille, N., Jolicoeur, P., 2006. Effect of cue-target interval on the N2pc. NeuroReport: For Rapid Communication of. Neurosci. Res. 17 (15), 1655–1658. http://dx.doi.org/ 10.1097/01.wnr.0000236859.16457.34.
- Sperling, G., 1960. The information available in brief visual presentation. Psychol. Monogr. 74 (11, Whole No. 498), 29.
- Tchernikov, I., Fallah, M., 2010. A color hierarchy for automatic target selection. PLoS ONE 5 (2), e9338. http://dx.doi.org/10.1371/journal.pone.0009338.
- Treisman, A.M., Gelade, G., 1980. A feature-integration theory of attention. Cogn. Psychol. 12 (1), 97–136. http://dx.doi.org/10.1016/0010-0285%2880%2990005-5.
- Ulrich, R., Miller, J., 2001. Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. Psychophysiology 38 (05), 816–827. http://dx.doi.org/ 10.1017/S0048577201000610.
- Von Wright, J.M., 1972. On the problem of selection in iconic memory. Scand. J. Psychol. 13 (1), 159–171. http://dx.doi.org/10.1111/j.1467-9450.1972.tb00064.x.
- Walsh, J.W.T., 1953. Photometry. Constable and Company Limited, London.

Wolfe, J.M., 1994. Guided search 2.0: a revised model of visual search. Psychon. Bull. Rev. 1 (2), 202–238.

- Woodman, G.F., Luck, S.J., 2003. Serial deployment of attention during visual search. J. Exp. Psychol. Hum. Percept. Perform. 29 (1), 121–138. http://dx.doi.org/10.1037/ 0096-1523.29.1.121.
- Zhao, G., et al., 2011. The amplitude of N2pc reflects the physical disparity between target item and distracters. Neurosci. Lett. 491 (1), 68–72. http://dx.doi.org/10.1016/ j.neulet.2010.12.066.