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Intra- and interocular colour-specific activation during dichoptic suppression

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Abstract

A new psychophysical method, based on dichoptic suppression, is introduced to study intra- and interocular colour activations. An experiment is performed which shows that activation of a specific colour in one eye may cancel suppression of the same colour in the ipsi-lateral eye or in the contra-lateral eye at non-corresponding retinal locations. A control experiment shows that the effect is not due to an overall response-bias to the activated colour. The colour-specific intra- and interocular activation might play a role in various colour-based percepts known in the literature.

Keywords: Binocular rivalry; Colour vision; Dichoptic suppression

1. Introduction

When two eyes receive different monocular stimuli, binocular rivalry may occur. In this situation the subjective experience is that, in an alternating fashion, some parts are visible while other parts are suppressed (e.g., Blake, 1989; Blake & Logothetis, 2001; Helmholtz, 1924; Levelt, 1965). Recent research in binocular rivalry has shown that the conscious percept may not only evolve from a competition between eye channels but also from a competition between percepts based on inputs from both eyes (i.e., eye rivalry versus stimulus rivalry; Alais, O'Shea, Mesana-Alais, & Wilson, 2000; Lee & Blake, 1999; Logothetis, Leopold, & Scheinberg, 1996; Suzuki & Grabowecky, 2002). For example, two spatially identical patterns with opposite mixed colour settings that are separately shown to the two eyes may reveal mixed colour percepts according to either the left-eye pattern or the right-eye pattern, alternating with global one-colour percepts in which identically coloured parts of both patterns are visible (Kovács, Papathomas, Yang, & Fehér, 1996). Here, seeing one colour implies suppression of the other and vice versa, presumably modulated by binocular neurons located beyond the input layers (Logothetis & Schall, 1989; Sengpiel & Blakemore, 1994), with a major role for the primary visual cortex (Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001), and possibly mediated by recurrent signals as well (Lamme & Roelfsema, 2000). The above phenomena hold for cases in which colours are rivalling with each other. What if suppressed colours are not locally rivalling with each other but are scattered at different positions at the retinae? We show that in such cases a renewed activation of colour may cancel suppression of a patch of the same colour at non-corresponding retinal locations in the ipsi-lateral (IL) eye or in the contra-lateral (CL) eye. This colour-specific intra- and interocular activation might also play a role in stimulus rivalry or intra- and interocular grouping (Kovács et al., 1996), and, with that, also underlie colour-based Gestalt formations.

2. Experiment

We presented very similar images to both eyes (see Fig. 1). The images were composed of identical grids with four homogeneously coloured patches superimposed on the grid in a diamond-like configuration, with two coloured patches in each eye. In the first stage of each trial, these patches were perceptually suppressed by the simultaneous presentation of corresponding bright

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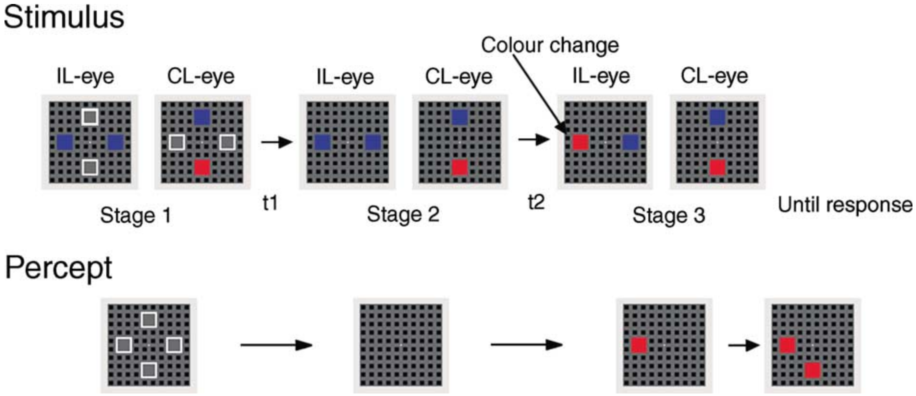

Fig. 1. Stimuli and experimental procedure. The upper row shows an example of a stimulus; the lower row shows a typical corresponding percept (see text for further explanation).

square outlines in the CL-eye (cf. Levelt, 1965). At this stage, the actual percept generally evolved into a colourless percept of four square outlines, superimposed on the grid. When, at *t1*, these suppressors were removed generally only the grid was perceived. That is, in both eyes the coloured patches remained invisible. At *t2*, the colour of one of the suppressed patches (the *trigger patch*, hereafter) was switched in the IL-eye (from red to blue or vice versa), which then caused the prompt visibility of that specific patch.

We investigated whether the renewed activation of a specific colour due to a physical colour change of one single patch affected the other—still suppressed—patches, in the IL-eye and in the CL-eye. The observers indicated which coloured patch was the *second* visible patch, i.e., the first patch visible after the trigger patch became visible. If the observers could not make a unique choice because the patches appeared (quasi-) simultaneously, or if not all coloured patches were initially suppressed then these trials were marked ‘invalid’. Given the global configuration of four patches (two patches in each eye), and given the two possible colours, all possible stimuli were shown to each observer.

2.1. Observers

Three observers participated in the experiment: RL (first author), PS, and MP. All were experienced observers in psychophysical experiments and were members of the NICI perception division at the University of Nijmegen. The observers were acquainted with the successive stages within each trial as, preceding the experiment, presentation durations were optimized per observer (see below). However, observers PS and MP were unfamiliar with the full details of the experiment.

2.2. Apparatus

The experiment was run on a PC-Pentium-III configuration with a 19-inch 100 Hz monitor. The stimuli were viewed dichoptically by way of a standard double-mirror arrangement. The viewing distance (i.e., the length of the optical path) was 114 cm. The width of the square grid subtended 2.51° and the width of the square patches subtended 24 min of arc. The CIE(x, y)-chromaticity values of the red and blue patch colours were (0.63, 0.34) and (0.16, 0.08), respectively (monitor calibration and measurement of colour values were done with the aid of ‘Colorshop 2.6/monitor optimizer’, X-Rite inc.). The luminances (L) of the various stimulus parts were as follows. Red: 13.86 cd/m^2; blue: 8.85 cd/m^2; grey (grid): 11.53 cd/m^2; black (grid): 0.32 cd/m^2; white (square outlines): 99.8 cd/m^2. The contrast values $(L_{\max} - L_{\min})/(L_{\max} + L_{\min})$ of the red patches, the blue patches, and the square outlines were 0.09, 0.13, and 0.79, respectively.

2.3. Procedure

Before a trial started, only the two grids were shown (one to each eye). As soon as the participant pressed a key, the coloured patches and the square outlines appeared (stage 1). At *t1* the square outlines abruptly disappeared (stage 2) and at *t2* the colour of one patch (the trigger patch) was switched into a different colour (the *trigger colour* hereafter; stage 3). By convention, the trigger patch is situated in the IL-eye. Periods *t1* and *t2* were optimized per observer such that, generally, suppression of all coloured patches occurred in stage 1 and only the grid was perceived in stage 2 (2000 and 100 ms, respectively, for observers RL and MP, and 5000 and 500 ms for observer PS). Stage 2 was included in the experiment to make possible that the observers could check whether all coloured patches remained invisible after removal of the square outlines. In stage 3, responses on the second visible patch were to be given with the arrow indexed keys on the numerical part of a standard keyboard. The observers were instructed to press the key of which the arrow pointed to the position of the second visible patch (top, bottom, left, right); an alternative button on that part of the keyboard (more in particular, the key in between the arrow-keys) was pressed when a trial was considered non-valid. The observers were instructed to perform the task as accurately as possible.

There were basically six different stimulus categories (see Table 1 for an example of each category). In each stimulus there were four coloured patches, each of a specific colour (red or blue) which were suppressed in stages 1 and 2, followed by a switch of the colour of one of the suppressed patches. The six categories were based on the number of patches in the IL-eye and in the CL-eye that were of the trigger colour; in the IL-eye the non-trigger patch could, or could not, be of the trigger colour (see columns Table 1), and in the CL-eye the number of patches that were of the trigger colour could be 0, 1, or 2 (see rows Table 1). All possible trials were constructed. The trigger patch could be in each of the four patch locations (left, right, top, or bottom) and presentations to the left and right eye were balanced for both colour settings (red–blue). So far, this would reveal $4 \times 2 \times 2 = 16$ different trials per cell. Notice, however, that for the cases in which there were two different colours in the CL-eye also the colour and patch location in the CL-eye could be balanced, which revealed 32 trials in the cells with $\mathrm{CL} = 1$. To obtain an equal number of presentations per cell, the stimuli with $\mathrm{CL} = 0$ and $\mathrm{CL} = 2$ were presented twice, revealing $6 \times 32 = 192$ trials. Finally, there were three different positional configurations of the patches (top/down-left/right, top/left-bottom/right, and top/right-bottom/left). To further balance the number of orthogonal and diagonal configurations the first one was presented twice, revealing a total of $4 \times 192 = 768$ stimuli.

2.4. Results and discussion

The results showed both intra- and interocular colour activation (see Fig. 2). Analyses were done on all valid trials (which formed about 84% of all trials, with the non-valid trials spread homogeneously across the relevant conditions, see caption Fig. 2) for each observer separately. In the following, the *visibility* of patches is related to the frequency of seeing these patches as the second visible patch, after colour change and appearance of the trigger patch. In Fig. 2, this visibility is expressed by the percentage of valid trials in which the second visible patch was located in the IL-eye (Fig. 2, upper panel) or in the CL-eye (Fig. 2, lower panel). There was a significant influence of colour on the visibility of the other patch in the IL-eye (see Fig. 2, upper panel): if this patch was of the trigger colour, it was more often the second visible patch than if it was not of the trigger colour (conversely, the visibility of a patch in the CL-eye was lower); for all three observers: $p < 0.0005$ (RL: $\chi^2(1) = 12.95$; PS: $\chi^2(1) = 29.06$; MP: $\chi^2(1) = 36.52$). Most noteworthy, the visibility of patches in the CL-eye depended on the colour correspondence between the trigger patch in the IL-eye and the colour of the patches in the CL-eye (see Fig. 2, lower panel). In general, there was an increase in the visibility of a patch in the CL-eye when one of the patches was of the trigger colour compared to stimuli in which both patches were of the non-trigger colour; $p < 0.005$, $p < 0.005$, and $p < 0.0005$, for observers RL, PS, and MP, respectively (RL: $\chi^2(1) = 8.25$; PS: $\chi^2(1) = 8.68$; MP: $\chi^2(1) = 25.45$). More specifically, the patch of the trigger colour had a higher visibility than the other patch in the CL-eye; $p < 0.005$, $p < 0.005$, and $p < 0.0005$, for observers RL, PS, and MP, respectively (RL: $\chi^2(1) = 10.3$; PS: $\chi^2(1) = 9.02$; MP: $\chi^2(1) = 19.02$). Additionally, there was no significant further increase for those stimuli in which both patches were of the trigger colour (RL: $\chi^2(1) = 1.65$; PS: $\chi^2(1) = 0.01$; MP: $\chi^2(1) = 0.33$).

The pattern of results reveals a near 50–50 probability for the visibility of a patch in either the IL-eye or the CL-eye if there is no colour correspondence between the trigger patch and all other patches, increased with an

Table 1
Examples of the six basic stimulus categories (see text)

# Patches in CL-eye of trigger colour		Non-trigger patch in IL-eye			
		Non-trigger colour		Trigger colour	
		IL	CL	IL	CL
0	Stage 1, 2	RR	RR	RB	RR
	Stage 3	**B**R	RR	**B**B	RR
1	Stage 1, 2	RR	BR	RB	BR
	Stage 3	**B**R	BR	**B**B	BR
2	Stage 1, 2	RR	BB	RB	BB
	Stage 3	**B**R	BB	**B**B	BB

IL: ipsi lateral; CL: contra lateral; R: red; B: blue. By definition the trigger patch was located in the IL-eye. For each stimulus category, a possible initial setting is shown (stages 1 and 2). In stage 3, the colour of one of the suppressed patches (the target patch) was changed into the target colour (indicated in bold font).

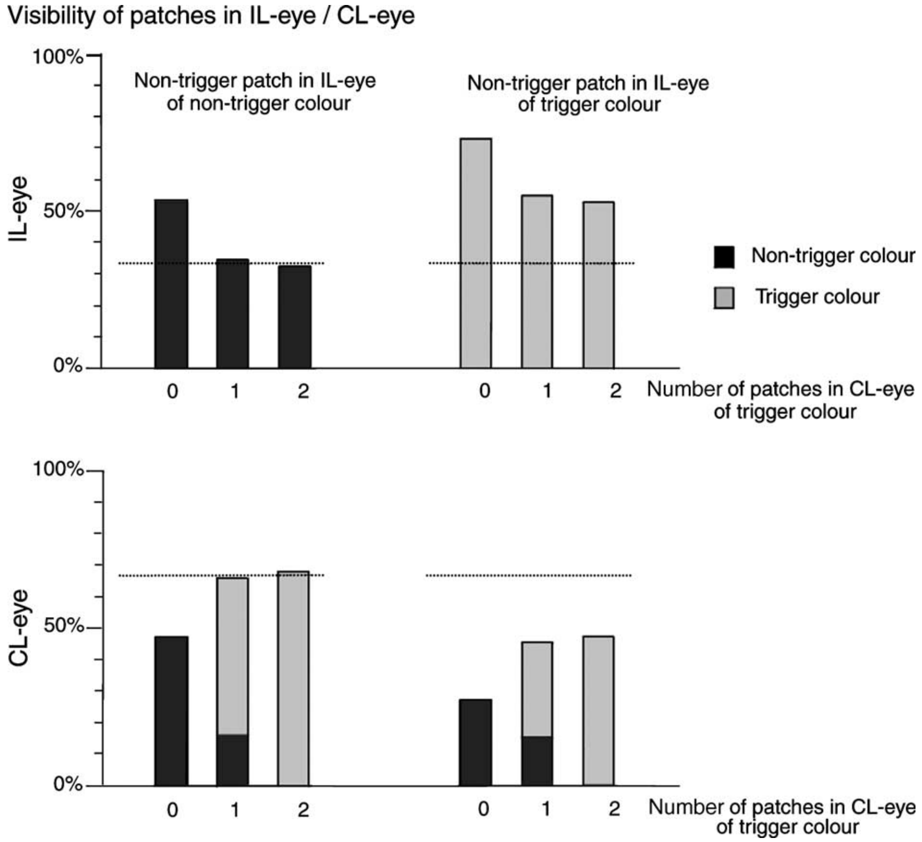

Fig. 2. The overall data for the three observers (RL, MP, PS). The dependent variable at the y-axis is the 'visibility' of a patch in the IL-eye (upper panel) or in the CL-eye (lower pannel). This visibility is expressed by the percentage of valid trials in which the second visible patch, i.e., the first patch visible after appearance of the trigger patch in the IL-eye, was located in the IL-eye (upper panel) or in the CL-eye (lower panel). The visibility is plotted as a function of the number of patches in the CL-eye that were of the trigger colour. In both the upper panel and the lower panel, the left graph shows the percentages when the colour of the other patch in the IL-eye (the non-trigger patch) was different from the trigger colour (the non-trigger colour), and the right graph shows the percentages when that patch was of the trigger colour. For each of the bars, the maximum value (100%) is based on the total number of valid trials for that specific combined IL–CL condition (the proportion of non-valid trials for each of these conditions were, from left to right, 0.16, 0.16, 0.16, 0.16, 0.16, 0.18, with no significant differences). The dashed lines indicate the expected visibilities if the patches would appear entirely at random (33.3% for the patch in the IL-eye and 66.7% for a patch in the CL-eye). Note that, for both the two left graphs and the two right graphs, the percentages indicating the visibility in the IL-eye and the percentages indicating the visbility in the CL-eye sum up to 100%.

additional probability in case of colour correspondence—rather independently of the number of corresponding colour patches. One may also notice an overall, not colour-specific, 'same eye advantage' for the visibility of the single patch in the IL-eye as compared to the two patches in the CL-eye. This becomes clear when considering the condition in which the colour of the trigger patch differs from the colour of the other patches (both in the IL-eye and in the CL-eye). Here one would expect a visibility of 33.3% for the single patch in the IL-eye and 66.7% for the two patches in the CL-eye (if appearance would depend on an entirely random patch-based process—indicated by the dashed lines in Fig. 2). The actual visibility clearly deviates from this; $p < 0.0005$, $p < 0.005$, and $p < 0.05$, for observers RL, PS, and MP, respectively (RL: $\chi^2(1) = 13.85$; PS: $\chi^2(1) = 8.85$; MP: $\chi^2(1) = 5.40$). Nevertheless, there is no indication that the increase in visibility in case of colour correspondence with the trigger patch is eye dependent. Compare, for example, the cases in which there is just one patch with a corresponding colour, either in the IL-eye or in the CL-eye, with the condition in which there is no colour correspondence (for each of the subjects these increased visibilities do not significantly differ from each other; RL: $\chi^2(1) = 0.34$; PS: $\chi^2(1) = 0.07$; MP: $\chi^2(1) = 0.81$).

3. Control experiment

To control whether the higher probabilities for the visibility of patches of the trigger colour were simply due to an overall response-bias towards the first visible colour we performed an additional experiment using actual (physical) appearances of the same coloured patches in an experimental set-up with the same grids, again using dichoptic presentations. Now, each trial started with the appearance of one coloured patch (red or blue) in one eye. After a variable time interval (300, 500, or 700 ms) two other coloured patches appeared (one red, one blue), either both in the CL-eye or one in the IL-eye and one in the CL-eye, and either simultaneously or with a small time interval (10 or 20 ms). The first patch was always at the top location; the other two patches appeared at the left and right location. The same three observers responded to the second visible patch on a set of 480 trials in which all of the above factors were completely balanced and randomised. Again, when patches seemed to appear simultaneously or when no unique decision could be made this was indicated by pressing a different key. The results showed no effect of the colour of the first patch on the responses; the total percentage of choices for either a patch with the same colour or a patch with a different colour was 38.6% versus 38.0%, respectively (with a response indicating that no unique choice could be made in 23.4% of all cases). Also for each single observer the difference between the same-colour choice and the different-colour choice was not significant (RL: $\chi^2(1) = 0.00$; PS: $\chi^2(1) = 0.00$; MP: $\chi^2(1) = 0.05$). In addition, there was no effect of same versus different eye (considering stimuli in which the first patch and one of the subsequent patches were in one eye and the other subsequent patch was in the other eye): (RL: $\chi^2(1) = 0.03$; PS: $\chi^2(1) = 0.02$; MP: $\chi^2(1) = 0.40$).

4. Discussion

The results on the control experiment did not reveal an overall response-bias towards the patch with the same colour as the trigger patch, which strengthens the notion that the differences in the first experiment were based on the actual order of the visibility of the patches, caused by intra- and interocular colour-specific activations.

The finding of an overall increase in visibility of a same-colour patch in the CL-eye, independent of the number of same-colour patches, suggests a mediating role for binocular colour-specific feature maps (e.g., Treisman & Gormican, 1988). The fact that the increase in visibility apparently does not differentiate between the IL-eye and the CL-eye suggests that the colour-based activation, as measured by this paradigm, is as strong for the between eye similarities as for the within eye similarities. With that, the colour-specific activations appeared to be independent of the overall same-eye advantage. While the locus of the responsible neural substrates involved in the present colour-based activations plausibly lies in the primary visual areas, future research should clarify whether higher visual areas are also involved (cf., Lamme & Roelfsema, 2000).

In recent years, various studies have been performed in which grouping has been studied using binocular rivalry for a number of visual properties (e.g., colour: Kovács et al., 1996; motion: Alais & Blake, 1998; good continuation and common fate: Alais & Blake, 1999). The present method, in which suppressed elements are scattered at different non-corresponding positions at the retinae, provides an alternative way to study feature-based intra- and interocular activations and, with that, the mechanisms underlying perceptual grouping phenomena. In future investigations the present method could be used to investigate intra- and interocular activations, with varying designs (including those that would involve multiple suppressed elements in both eyes after activation by some trigger element), caused by different features and possibly conjunctions of features.

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