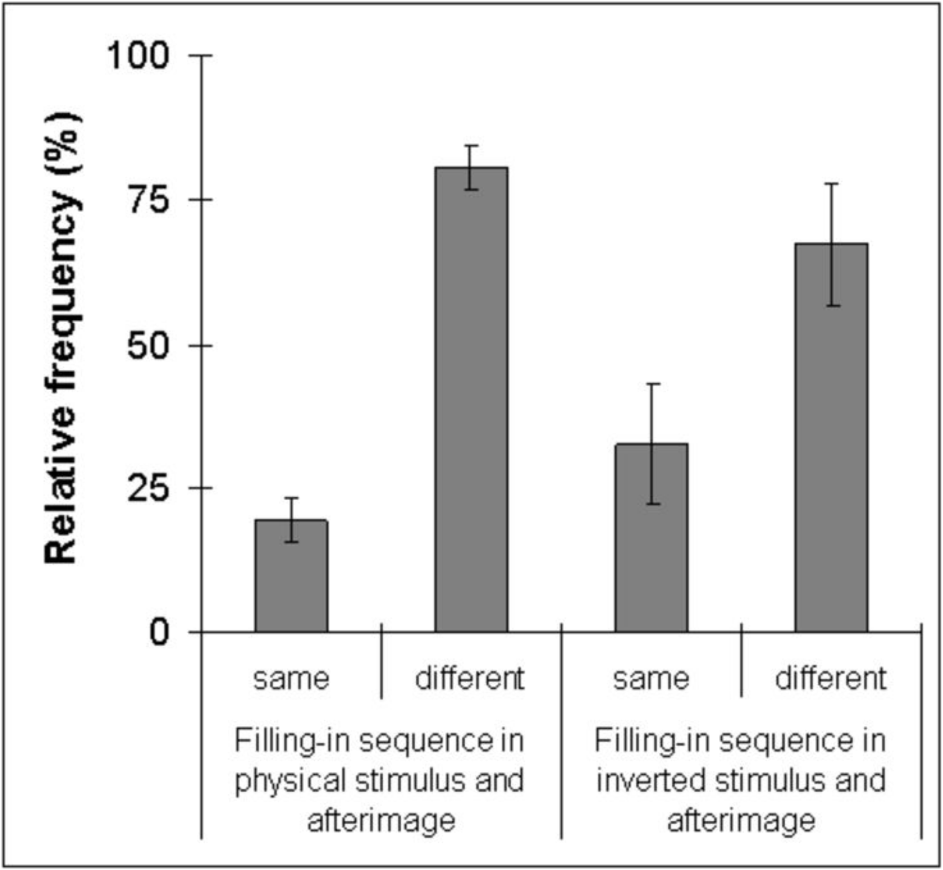
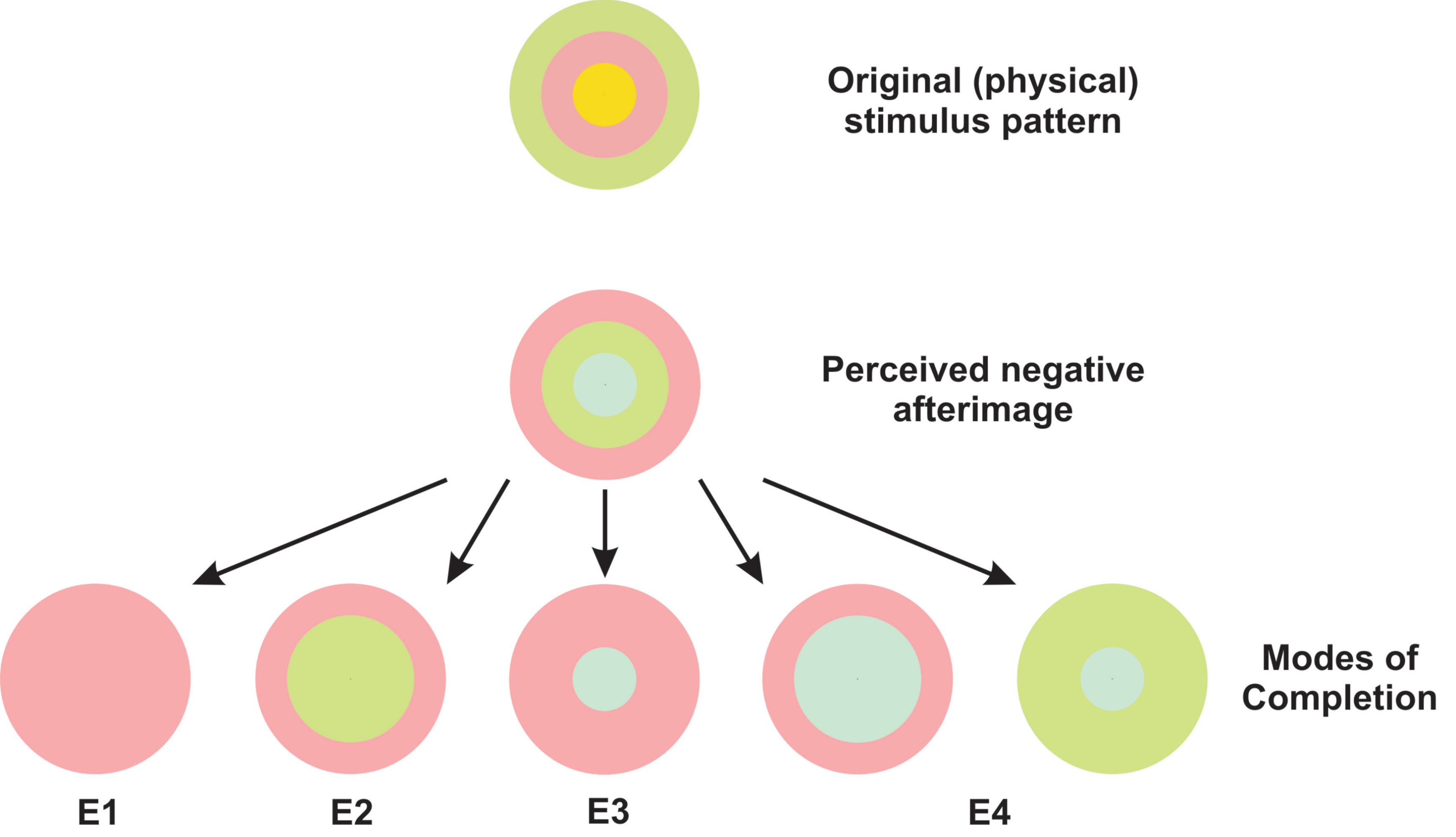

Relative frequency (%)
100
75
50
25
0
same
different
same
different
Filling-in sequence in physical stimulus and afterimage
Filling-in sequence in inverted stimulus and afterimage


Original (physical)
stimulus pattern
Perceived negative
afterimage
Modes of
Completion
E1
E2
E3
E4

An illusion induced by an illusion – perceptual filling-in of coloured negative afterimages

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Visual filling-in relates to a perceptual phenomenon in which a stimulus pattern apparently undergoes dynamic changes assuming an attribute such as colour, texture, or brightness from the surround. This perceptual completion effect has up to now been shown only for real images. Here, we present filling-in in *negative afterimages,* a phenomenon not yet reported. Using coloured disk-ring patterns for stimuli, we demonstrate that afterimage filling-in arises independently, and is not simply a replica of filling-in observed in real images. Such filling-in does not occur when the afterimage is elicited dichoptically, suggesting its emergence within the monocular visual pathway. In this way, our findings indicate that filling-in under certain conditions may derive from an active neural mechanism located at low levels of the visual pathway.

The study of visual illusions delivers insights into the operating mode of the visual system. For instance, with prolonged fixation of a coloured disk-ring pattern, the disk assumes the colour of the ring (filling-in) or, less frequently, the ring assumes the colour of the disk (filling-out). If one turns the gaze subsequently to these spreading effects and views a white background, a negative afterimage of the original stimulus is perceived initially. For example, the formerly red ring looks greenish, and the formerly green disk appears reddish. Yet, soon thereafter one of the two colours in the afterimage will give way to the other, producing filling-in (i.e., all greenish) or filling-out (i.e., all reddish) in the afterimage as happened in the real image during adaptation. The question arises whether these filling-in effects in the afterimage follow the same rules as those observed in the real image or whether they arise independently.

To answer this question, we used binocularly viewed stimulus patterns consisting of a coloured disk surrounded by *two* coloured rings, as shown in Fig. 1 (top). Using such stimulus patterns, Hamburger and colleagues[1] obtained 4 types of spreading effects, enabling us to compare filling-in and filling-out in real images with the effects observed in negative afterimages. Figure 1 (bottom) illustrates the 4 modes of spreading: In Effect 1 (E1), the colour of the outer ring fills in the inner ring and the enclosed disk, yielding a uniformly coloured percept. In Effect 2 (E2), the colour of the inner ring fills in the disk, while the colour of the outer ring remains unchanged. In Effect 3 (E3), the colour of the outer ring fills in the inner ring, while the colour of the disk remains unchanged. In Effect 4 (E4), colour spreading occurs in the opposite direction: from the disk onto the inner ring *or* from the inner ring onto the outer ring, i.e., filling-out (due to the infrequent occurrence of filling-out compared to filling-in, both filling-out modes were merged in Effect 4). Finally, Effect 0 (E0), not shown here, denotes that the initial percept of the stimulus remains unchanged (neither filling-in nor filling-out).

Our hypothesis was that there should be no difference as to the type and frequency of induced colour changes during adaptation to the physical stimulus (i.e., in the real image) and in the subsequent afterimage. However, this was not what we found. In fact, when we compared the spreading effects observed under the two conditions, they differed in 80.66 % of all observations (Fig. 2, second column). For example, during adaptation to the stimulus, both the inner ring and disk may have become entirely *filled in* by the colour of the outer ring (E1), while in the subsequent afterimage the colour of the disk may have spread outward from the disk onto the inner ring or from the inner ring onto the outer ring, i.e., *filling-out* (E4). Furthermore, filling-in or filling-out occasionally observed in the negative afterimage, when no completion effects occurred in the real image during the preceding adaptation period (E0).

A statistical analysis (Pearson correlation coefficient) between the two kinds of results revealed that there were no systematic correlations between the modes of colour filling perceived in the real image and in the subsequent afterimage (for the statistical analysis see caption Figure 2).

Since opponent colours are known to be differently strong inducers[1], we tested in a control experiment colour spreading in a stimulus whose colours were complementary to those in the original stimulus. Specifically, we used a green/red/yellow stimulus pattern (outer ring/inner ring/disk) instead of a red/green/blue stimulus, and, vice versa, a yellow/red/green pattern instead of a blue/green/red stimulus. This was done so that the colours of the afterimage would conform to the colours of the original stimulus. Yet, also for this condition we found a difference of 67.34 % between the type of colour spreading in the real image and in the subsequent afterimage (Fig. 2, fourth column). Furthermore, there were no systematic correlations between the filling-in of real stimuli and filling-in of afterimages having the same colours (cross-comparison).

These data suggest that filling-in (or filling-out) of the complementary colours in the negative afterimage do not follow the same rules as filling-in (or filling-out) in the real image. We therefore assume that afterimages are treated by the visual system as independent “stimuli” capable of eliciting perceptual filling-in effects of their own, suggesting that colour spreading in the afterimage arises independently of the real image.

A phenomenological effect apparently similar to ours was reported by Shimojo and colleagues[2]. After prolonged adaptation to a Varin figure[3], consisting of four white ‘pacmen’ in the corners, with four red wedges abutting the sides, they observed an illusory square in the complementary colour (green) to that of the four wedges filling the space between the four black pacmen. Shimojo et al. concluded that the complementary colour of the filled-in square was an afterimage of the red square induced by the four red wedges during adaptation, implying that filling-in occurred first, with the negative afterimage of the filled-in image occurring in second place. In contrast, we argue that afterimage filling-in in our experiment is prompted by the afterimage of the primary stimulus pattern, acting as an inducing stimulus.

One fundamental question about filling-in is the presumptive site of origin within the visual system. In general it is commonly assumed that filling-in is of cortical origin since the properties of an active perceptual completion mechanism are assumed to be too complex for early visual areas[4,5]. However, up to now no common neural mechanism for filling-in has so far been found and it is conceivable that different types of perceptual completion such as filling-in of the blind-spot, of artificial scotomas and of stabilized images involve different mechanisms at different sites within the visual pathway.

Shimojo et al.[2] suggested that their observation was the result of cortical processing, since the filled-in square occupied an area outside the adapted regions of the red wedges on the retina. To find out whether our effect was cortical or precortical, we tested for colour spreading with a dichoptic stimulus. Using a mirror stereoscope, a green disk was presented to one eye and a red ring to the other, such that when perceptually combined they were concentric and in register. Under these conditions observers perceived colour spreading during stimulus adaptation, but never in the afterimage. These findings suggest that colour spreading in the negative afterimage originates at a precortical stage, i.e., prior to binocular fusion. On the other hand, filling-in due to Troxler's effect, has already been proposed earlier to originate at a lower level of the visual pathway[6,7].

Our findings support the assumption that filling-in in afterimages may originate at a precortical stage. Yet, while the retina can generate coloured afterimages, it is unclear whether retinal horizontal cells can mediate filling-in. On the other hand, color-selective center-surround neurons in the lateral geniculate nucleus (LGN) in conjunction with feedback connections from the visual cortex may give rise to such activity[8]. Top-down influences from cortical neurons, which themselves are capable of filling-in, directly to the rich interneuron circuits within the LGN have been demonstrated[9,10,11]. However, most studies on filling-in concentrate on cortical structures as origin of this illusory effect[12, 13]. Following our study, further neurophysiological investigations in primates or fMRI studies in humans might change this view and focus on the role of the LGN in coding for filling-in in coloured stimuli, especially since recent fMRI reports provide contradictory results for (the early visual cortex as) the origin of colour filling-in[5,13,14].

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Figures and figure captions:

Fig. 1: <u>Top:</u> Adaptation (*real/physical*) stimulus consisting of a disk surrounded by two rings. Stimuli were cut from cardboard and pasted on a white background. The disk and ring subtended 3.5 deg each while the outer ring subtended 7 deg. Observation distance was 65 cm. Four equiluminant colours were used, representing Munsell 5B7/8, 5G7/8, 5R7/8 and 5Y7/8. In the comparing condition the colours were combined as follows (disk | inner ring | outer ring): red/green/blue; control condition: green/red/yellow. In the dichoptic condition subjects were presented at the same time a red ring and a green disk separately to each eye, such that both were in register. Five observers with normal or corrected-to-normal vision participated. <u>Middle:</u> Corresponding negative *afterimage* as perceived following 30 seconds of binocular adaptation and viewing a white background. <u>Bottom</u>: Four modes of colour spreading as observed in the experiment in the afterimages and real images.

Fig.2: Frequencies (in percent) of same or different colour spreading effects for the real/physical image and for the afterimage. Five subjects took part in the experiment performing n = 30 trials for each condition. The bars indicate standard errors. The result of the T-test for the difference between the types of colour spreading were: for the physical stimulus and the subsequent afterimage: $t = 7.899$, $df = 4$, $p = .001$, and for the inverted stimulus and the subsequent afterimage: $t = 1.640$, $df = 4$; $p = .176$ (Due to the small sample in our experiment and a relatively large standard error the difference in the control condition was not statistically significant. However, there is a obvious descriptive difference between the types of filling-in in the inverted stimulus (column 3 and 4). We also performed a correlation analysis to test whether the single completion effects perceived in the afterimages correlated with the filling-in effects perceived in real images. The results of the correlation analysis (Pearson correlation coefficient) were: E0 $r=.236$, $p=.703$; E1 $r=.547$, $p=.340$; E2 $r=-.784$,

p=.116; E3 r=.379, p=.529; E4 r=-.241, p=.696. The results for the inverted stimulus and the subsequent afterimage were: E0 r=-.248, p=.687; E1 r=.809, p=.097; E2 r=.222, p=.720; E3 r=.117, p=.851; E4 r=1.00, p<.001. The last correlation refers to the reports of only one subject for both the real image and the afterimage.