

Asynchronous processing in vision: Color leads motion

Derek H. Arnold^{*†}, Colin W.G. Clifford[†] and Peter Wenderoth^{*}

It has been demonstrated that subjects do not report changes in color and direction of motion as being co-incident when they occur synchronously. Instead, for the changes to be reported as being synchronous, changes in direction of motion must precede changes in color. To explain this observation, some researchers have suggested that the neural processing of color and motion is asynchronous. This interpretation has been criticized on the basis that processing time may not correlate directly and invariantly with perceived time of occurrence. Here we examine this possibility by making use of the color-contingent motion aftereffect. By correlating color states disproportionately with two directions of motion, we produced and measured color-contingent motion aftereffects as a function of the range of physical correlations. The aftereffects observed are consistent with the perceptual correlation between color and motion being different from the physical correlation. These findings demonstrate asynchronous processing for different stimulus attributes, with color being processed more quickly than motion. This suggests that the time course of perceptual experience correlates directly with that of neural activity.

Addresses: ^{*}Department of Psychology and [†]Macquarie Centre for Cognitive Science, Macquarie University, Sydney, New South Wales 2109, Australia.

Correspondence: Derek Arnold
E-mail: derek@vision.psy.mq.edu.au

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Results and discussion

It is now generally accepted that within the visual cortex there are distinct, spatially separated, and relatively independent anatomical structures that are specialized for processing different stimulus attributes [1, 2]. However, we do not know how activity within these different structures can be brought together to form a unified visual experience. This mystery is commonly referred to as the “binding problem.”

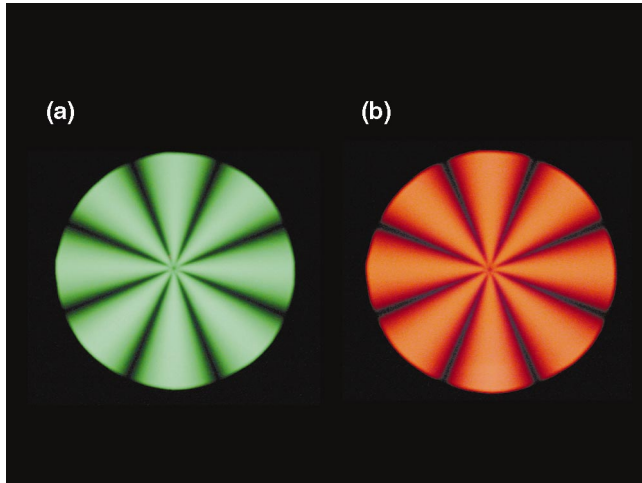
The possibility that specialized processing structures feed into a central executive that then forms the neural correlate of visual consciousness has been largely dismissed. There is simply no anatomical evidence for the existence of a visual area that receives projections from all other specialized visual areas [3, 4]. In contrast, current theories focus on how the activity of separate cortical structures might be brought into temporal coherence with one another [5], the assumption being that synchronous activity across multiple cortical areas is a necessary precursor for a unified and conscious visual experience to occur [6].

A contrasting perspective to theories of this kind is that activity within individual specialized cortical areas might actually be consciously experienced without any necessary interaction with other specialized areas [7–10]. The activity of one cortical area might produce our conscious experience of color while that of another could produce our conscious experience of motion [10]. This view differs from other theories of visual consciousness in that it supposes that the process of perceptual binding does not cause conscious visual experiences but that it merely integrates the activity of multiple cortical areas where neural activity is already consciously experienced [8, 9].

Perhaps the strongest evidence that the normal human brain contains multiple and relatively independent sites where activity is consciously experienced is derived from experiments that purport to demonstrate an asynchrony of visual consciousness [7, 10]. In these experiments, subjects were required to report which of two possible states of stimulus attribute X coexisted with which of two possible states of stimulus attribute Y. For instance, the subject might be presented with a stimulus that changes color from red to green and changes direction from moving upward to downward. When the change in color is perfectly in phase with the change in direction, a phasic relationship of 0°, upward motion might always be physically paired with the color red and downward motion with the color green. When changes in color and motion are perfectly out of phase, a phasic relationship of 180°, this situation would be reversed. At phasic relationships of 90° and 270°, both upward and downward motion would be equally paired with red and green. By testing multiple phasic relationships, it is possible to plot the percentage of times that a subject reports the color red (or green) as being coexistent with the direction up (or down) across a range of phasic relationships.

If two stimulus attributes are perceived at the same time, we would expect the distribution of the reported co-existence of different stimulus attributes in tasks like that

Figure 1

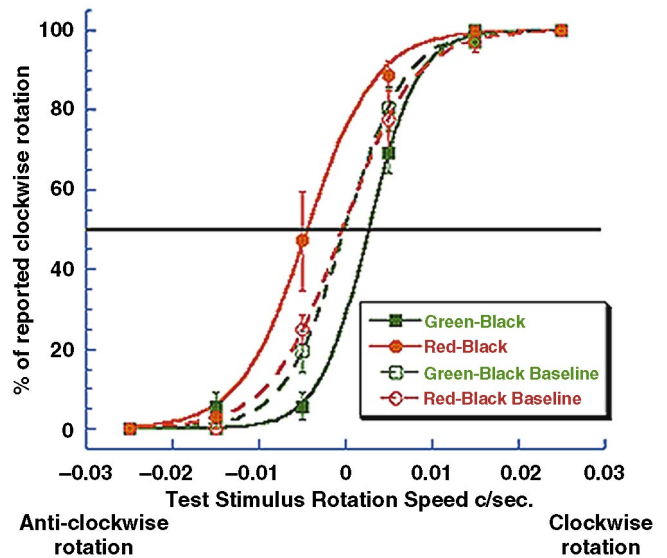


Depiction of the stimuli used. All stimuli had a diameter of 14° , a contrast of 0.6, and a spatial frequency of 8 c/360°. The central fixation point had a diameter of 0.2° . The peak luminance of the red luminance-modulated stimulus was 25.4 cd/m^2 . The peak luminance of the green luminance-modulated stimulus was made isoluminant with the red for each subject by the use of the minimum motion technique of Anstis and Cavanagh [26]. The chromaticity coordinates (CIE 1931) for the red and green stimuli were ($x = 0.61, y = 0.34$) and ($x = 0.28, y = 0.595$), respectively. Test stimuli were presented for 500 ms, during which time they rotated either clockwise or anticlockwise at speeds ranging from 0.005 to 0.025 cycles/s for D.A. and C.C. and from 0.01 to 0.05 cycles/s for the naïve subjects. The stimuli were displayed on a 19 inch Sony Trinitron Multiscan 400PS monitor with a refresh rate of 100 Hz and were driven by a VSG 2/3 (Cambridge Research Systems). The stimuli were viewed binocularly in darkened conditions from 57 cm while the head was placed in a head rest. All subjects had normal or corrected-to-normal visual acuity and color vision.

described above to be centered upon a phasic relationship of 0° . However, when experiments of this kind were performed, it was found that the distributions of reported co-existence were not so centered. Instead, the distributions were displaced so as to be consistent with color being perceived approximately 60–80 ms before motion [7, 10]. This was described as an asynchrony of visual consciousness [7–10]. It was argued that this asynchrony arose because different stimulus attributes are processed asynchronously [8, 9].

The possibility of a processing asynchrony is controversial. An asynchrony of this form appears to contradict the available physiological evidence that suggests that, if anything, motion should be processed more quickly than color [11, 12]. Reaction time data also appear to be inconsistent with a large perceptual asynchrony of the form described above, and this finding suggests instead that processing times for changes in color and motion can either be effectively equivalent [13] or differ only slightly [14]. It has also been argued that neural processing time may not

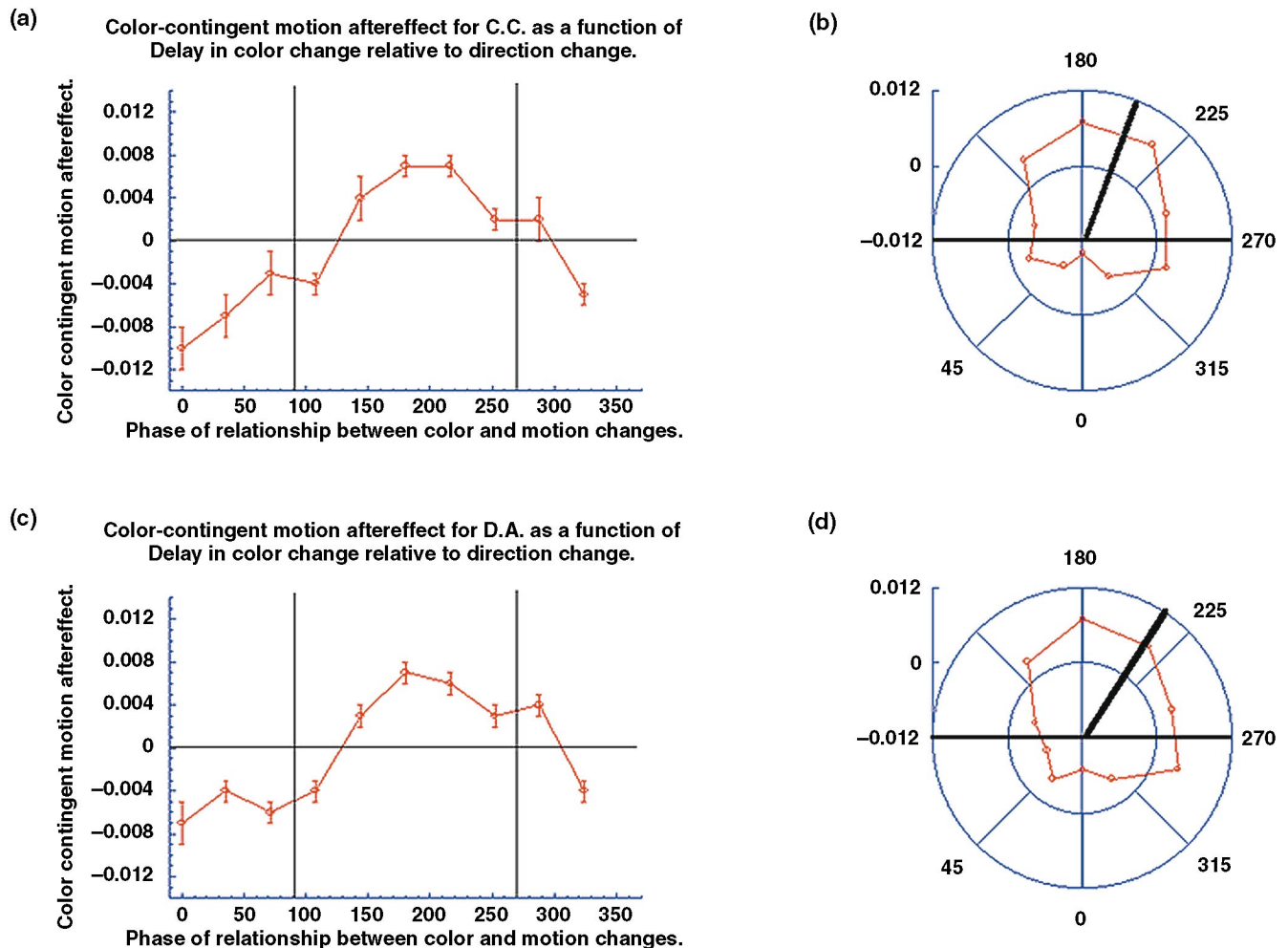
Figure 2



Sigmoid curves fitted to data for D.A. We obtained this data during six trial runs without adaptation and within six trial runs that followed adaptation to a phasic relationship of 108° . The individual data points within each curve represent the average response from 36 discrete trials. Curves derived following adaptation are continuous, while curves derived without adaptation are broken. The points of subjective stationarity are given by the intersection of the relevant fitted curve with the horizontal 50% line. The curves derived following adaptation are shifted relative to those derived without adaptation. After adaptation, the curve derived with the red-black test stimulus is shifted to the left, and the curve derived with the green-black test stimulus is shifted to the right. This is indicative of contingent adaptation.

correlate directly and invariantly with the perceived time of occurrence. Simultaneous neural activity might be consciously experienced as being representative of events that have occurred at different times [15, 16]. As data of the form described above is derived from analysis of subjective reports, it is unclear if the evident asynchrony is the direct result of asynchronous neural activity or the indirect result of synchronous neural activity that is subsequently subjected to further interpretative analysis.

If a processing asynchrony exists, it should be possible to demonstrate it without recourse to a subjective report regarding time of occurrence. A possible mechanism that might be utilized is that which mediates contingent after-effects. An aftereffect arises after extended exposure to a given stimulus attribute. An example is that after looking at a given direction of motion, a subsequently viewed stationary object can appear to move in the opposite direction. These aftereffects can be made to be contingent upon another stimulus attribute. Clockwise rotation can be paired with the color green, and anticlockwise rotation with the color red. Subsequently viewed stationary green objects can then appear to rotate anticlockwise, while stationary red objects will appear to rotate clockwise [17].

Figure 3

Average color-contingent motion aftereffects for subjects C.C. (Figure 3a) and D.A. (Figure 3c) as a function of the phasic relationship between color and motion. In Figures 3a,c, horizontal lines indicate the point at which no contingent aftereffect is evident. The vertical lines indicate points within the phasic relationship at which clockwise and anticlockwise rotations are equally correlated with the green and red color states. We fitted the distribution of contingent aftereffects to polar plots in Figure 3b for C.C. and in Figure 3d for D.A. to provide a nonparametric analysis of the data. These polar plots are unusual in that data points within the inner circles represent negative contingent aftereffects, the middle circles represent points where no contingent aftereffects are evident, and all data points within the outer circles represent positive contingent aftereffects. The bold horizontal line indicates points where the physical correlation between color states and direction of motion was equivalent. If changes in color and

direction of motion are processed in synchrony, all data points below these lines should be located within the inner circle, and all data points above should be located within the outer circle. This is not the case. The centroids of the distributions are indicated by bold black lines and are rotated clockwise by 20.8° for subject C.C. (Figure 3b) and by 32.6° for D.A. (Figure 3d). This is indicative of processing advantages for color of 57.8 ms for C.C. and 90.6 ms for D.A. The centroids were fitted according to the equation

$$\phi_c = \tan^{-1} \left(\frac{\sum_{i=1}^N M_i \sin \phi_i}{\sum_{i=1}^N M_i \cos \phi_i} \right) \text{ where } \phi_1 = 0^\circ; \phi_2 = 36^\circ \dots; \phi_N = 324^\circ$$

$M_i = \text{signed magnitude of CAE}$

$\phi_c = \text{phase of centroid}$

While the neural mechanisms that mediate contingent aftereffects are not fully understood, the available evidence suggests that they are located relatively early within the visual processing system, possibly within V1 [18–22]. Although a recent imaging study has demonstrated that perception of a color-contingent aftereffect is correlated with activity within the extrastriate cortex, the authors of

the study note that it is probable that the activity observed “reflects only color vision” rather than activity that is causally related to the aftereffect [23]. Certainly, the fact that the perceived hue of orientation-contingent color aftereffects is dependent upon the physical wavelength of the adapting stimulus and not upon its perceived color [24] suggests that contingent aftereffects are mediated at

a point prior to any neural correlate of visual consciousness. As this is the case, if an apparent asynchrony can be demonstrated within the context of a contingent aftereffect it would provide strong evidence for the asynchronous processing of different stimulus attributes. If color is processed approximately 80 ms more quickly than motion, as suggested by Moutoussis and Zeki [7, 10], the physical correlation between the two stimulus attributes should differ systematically from their perceptual contingency.

We tested this prediction by measuring color-contingent motion aftereffects as a function of the phasic relationship between color state and direction of motion. The test stimuli used are depicted in Figure 1. Within a run of trials, an individual trial would consist of one of these two stimuli rotating very slowly in a clockwise or anticlockwise direction, after which subjects were required to complete a forced-choice direction discrimination task wherein they indicated their response by pressing one of two response levers. Six speeds were sampled six times for both color states within every run. Each trial run therefore consisted of 36 trials for each color state and 72 trials overall. We analyzed the results of each run to provide estimates of the speed of rotation that subjects perceived to be stationary (hereafter referred to as the point of subjective stationarity) for both the green-black and red-black stimuli.

We determined baseline estimates of the point of subjective stationarity by fitting sigmoid curves to data obtained during runs in which only test stimuli were presented. Subsequent runs were preceded by a 5 min adaptation period. During this period, subjects viewed a stimulus that oscillated between rotating clockwise and anticlockwise at 0.78 cycles/s, and between being green-black and red-black. The period of the oscillations in both color and motion was 1 s. After the adaptation period the subject completed the first trial. Each trial was then followed by a further 4 s top-up adaptation period. Only one phasic relationship was used within any run. Each top-up adaptation period commenced at a random point within the stimulus sequence to ensure that any evident aftereffects could not be attributed to a systematic point of offset for the adapting stimulus.

Ten phasic relationships were used for adaptation. At a phasic relationship of 0° , clockwise rotation was always green-black and anticlockwise was always red-black. At a phasic relationship of 180° , this situation was reversed. The range of phasic relationships that subjects experienced ranged from 0° to 324° in steps of 36° (which corresponds to steps of 100 ms). We determined points of subjective stationarity by fitting sigmoid curves to data obtained after contingent adaptation to each phasic relationship. Figure 2 shows the average fitted curves for

Table 1**Color-contingent MAE: Period = 1000 ms, Phase = 108° .**

	Avg. baselines	Avg. test	Avg. effects
J.N.	0.00030	-0.00215	-0.00245
J.M.	0.00098	-0.00418	-0.00515
J.L.	-0.00048	-0.00223	-0.00175
K.C.	-0.00013	0.00240	0.00253
V.L.	0.00260	-0.00313	-0.00573
G.L.	-0.00075	-0.00773	-0.00698
R.P.	0.00380	-0.00373	-0.00753
Avg. effect			-0.00386
Std. error			0.00134

subject D.A. for runs completed without adaptation and following adaptation to a phasic relationship of 108° .

The average effect of contingent adaptation was calculated as being half the difference between the points of subjective stationarity calculated for the red-black and green-black stimuli following adaptation less half the difference between the points of subjective stationarity in the absence of adaptation. These aftereffects are plotted as a function of the phasic relationship in Figure 3a,b for C.C. and in 3c,d for D.A. Each data point within Figure 3 was calculated from data obtained in 8 runs for C.C. and within 12 runs for D.A., which means that each point was calculated from 576 psychophysical judgements for C.C. and 864 for D.A. If the two stimulus attributes are processed synchronously, we would expect the distribution to be centered upon a phasic relationship of 0° . However the centroid of the distribution is rotated clockwise by 20.8° for subject C.C. (Figure 3b) and by 32.6° for D.A. (Figure 3d). As the period of time represented by 360° is 1 s, the degree of rotation is indicative of processing advantages for color of 57.8 ms for C.C. and of 90.6 ms for D.A.

The evident processing asynchrony is emphasized by consideration of the contingent aftereffects observed at phasic relationships of 108° and 288° . At a phasic relationship of 108° , changes in color lagged behind those in direction of motion by 300 ms. Clockwise rotation was therefore physically paired with the red-black color state for 300 ms and with the green-black color state for only 200 ms. Yet the contingent aftereffects observed are consistent with clockwise rotation being perceptually correlated more highly with the green-black color state. The reverse situation is also true for both subjects at a phasic relationship of 288° .

To test the robustness of these findings, seven naïve subjects were tested with the same test and adaptation stimuli. Baseline estimates of the point of subjective stationarity were derived from trial runs without adaptation and were compared to the corresponding points determined after contingent adaptation to a phasic relationship of 108° . These data are shown in Table 1. Six of the seven

subjects experienced average contingent aftereffects that were in the same direction as those observed for subjects D.A. and C.C. after adaptation to the same phasic relationship. This indicates that, on average, the naïve subject data are also incompatible with the simultaneous processing of color and motion ($t_0 = -2.88$; $p < 0.05$).

These findings provide strong evidence for asynchronous processing of color and motion. They show that, under the present experimental conditions, when motion in a given direction persists for 500 ms and color changes lag changes in direction by 300 ms, the second color state is perceptually contingent with the initial direction of motion. The similarity between our data and earlier findings regarding the asynchrony of visual consciousness [7, 8] strongly suggests that the asynchrony of visual consciousness is a direct consequence of asynchronous neural processing.

The magnitude of the processing lag suggested by this data is surprising. The measurement of onset latencies within low-level cortical structures, while indicative of systematic differences between color and motion, does not suggest a discrepancy of this magnitude [25] or form [11, 12]. Of course, such measurements were not conducted during concurrent exposure to both color and motion, and so it is unclear if the onset latencies observed are actually incompatible with our psychophysical data or if the stimulus conditions that we have used might actually alter the response properties of low-level cortical structures. Also unresolved is the apparent task dependence of the asynchrony [15]. A continuing point of interest is therefore to determine if the evident processing asynchrony occurs as a result of particular task requirements and stimulus conditions or if the asynchrony represents a general principle of visual processing.

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References

1. Felleman DJ, Van Essen DC: **Distributed hierarchical processing in the primate cerebral cortex.** *Cereb Cortex* 1991, **1**:1-47.
2. Livingstone MS, Hubel DH: **Segregation of form, color, movement, and depth: anatomy, physiology, and perception.** *Science* 1988, **240**:740-749.
3. Zeki S: **A vision of the brain.** Oxford: Blackwell; 1993.
4. Singer W: **Consciousness and the structure of neuronal representations.** *Phil Trans R Soc B* 1998, **353**:1829-1840.
5. von der Malsburg C, Schneider W: **A neural cocktail-party processor.** *Biol Cybern* 1986, **54**:29-40.
6. Crick F, Koch C: **Towards a neurobiological theory of consciousness.** *Sem in the Neurosciences* 1990, **2**:263-275.
7. Moutoussis K, Zeki S: **A direct demonstration of perceptual asynchrony in vision.** *Proc R Soc B* 1997, **264**:393-399.
8. Zeki S, Bartels A: **The asynchrony of consciousness.** *Proc R Soc B* 1998, **265**:1583-1585.
9. Bartels A, Zeki S: **The theory of multistage integration in the visual brain.** *Proc R Soc B* 1998, **265**:2327-2332.
10. Moutoussis K, Zeki S: **Functional segregation and temporal hierarchy of the visual perceptive systems.** *Proc R Soc B* 1997, **264**:1407-1414.
11. Schiller PH, Malpeli JG: **Composition of geniculostriate input to superior colliculus of the rhesus monkey.** *J Neurophysiology* 1978, **41**:788-797.
12. Munk MHJ, Nowak LG, et al.: **Visual latencies in cytochrome oxidase bands of macaque area V2.** *Proc Natl Acad Sci USA* 1995, **12**:371-384.
13. Nishida S, Johnston A: **Dissociation of perceived temporal synchrony and response latency for changes in colour and motion.** *Invest Ophthalmol Vis Sci* 2000, **41**:S712.
14. Barbur JL, Wolf J, Lennie P: **Visual processing levels revealed by response latencies to changes in different visual attributes.** *Proc R Soc Lond B* 1998, **265**:2321-2325.
15. Nishida S, Johnston A: **Perceptual delay for rapid direction alternations: a new account in terms of the dichotomy of first-order and second-order temporal changes.** *Perception* 2000, **29** (suppl): 27c.
16. Dennett DC, Kinsbourne M: **Time and the observer: the where and when of consciousness in the brain.** *Behav Brain Sci* 1992, **15**:183-247.
17. Favreau OE, Emerson VF, Corballis MC: **Motion perception: a color-contingent aftereffect.** *Science* 1972, **176**:78-79.
18. McCollough C: **Color adaptation of edge-detectors in the human visual system.** *Science* 1964, **149**:1115-1116.
19. Humphrey GH, Goodale MA: **Probing unconscious visual processing with the McCollough effect.** *Consciousness Cogn* 1998, **7**:494-519.
20. Murch GM: **Classical conditioning of the McCollough effect: temporal parameters.** *Vision Res* 1976, **16**:615-619.
21. Potts MJ, Harris JP: **Dichoptic induction of movement aftereffects contingent on color and on orientation.** *Perception & Psychophysics* 1979, **26**:25-31.
22. Mayhew JEW, Anstis SM: **Movement aftereffects contingent on color, intensity and pattern.** *Percept Psychophys* 1972, **12**:77-85.
23. Humphrey GK, James TW, et al.: **Perception of the McCollough effect correlates with activity in extrastriate cortex: a functional magnetic resonance imaging study.** *Psychol Science* 1999, **10**:444-448.
24. Thompson P, Latchford G: **Colour-contingent after-effects are really wavelength-contingent.** *Nature* 1986, **320**:525-526.
25. Schmolesky MT, Wang Y, et al.: **Signal timing across the Macaque visual system.** *J Neurophysiology* 1998, **32**:3272-3278.
26. Anstis SM, Cavanagh P: **A minimum motion technique for judging equiluminance.** In *Color Vision: Physiology and Psychophysics*. Edited by Mollon J and Sharpe RT. London: Academic Press; 1983: 155-166.