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One More Evidence Against the Classical Conditioned Hypotheses of McCollough Effect

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ABSTRACT. The goal of the experiments carried out was to find out whether the McCollough effect (MCE) is a classical example the conditioned case or it has different explanation. Ten test subjects of different age with normal color vision participated in two series of researches. We tried to find out whether the use of a conditioned stimulus (in this case – sound) will have an impact on elaboration of the McCollough type after-effect. The addition of sounds with different tone frequencies to stimuli used in classical McCollough adaptation procedure did not impact on elaboration of McColough effect. In the following experiment orientation was excluded. We tried to produce a conditioned reflex only by color and sound pairing. A red rectangle paired with 700 Hz tone as well as a green rectangle paired with 300 Hz tone were presented to the test subject. After the adaptation procedure the subjects did not perceive illusive colors on white rectangular test stimuli accompanied with sounds (300 and 700 Hz frequencies). This fact indicates that the temporary connection between auditory and vision areas was not established in such cases. We suppose that explanation of MCE as a classical conditioned reflex maybe is not true.

Key words: McCollough effect; colour perception; conditional reflex

In 1965 Cheleste McCollough [1] showed that if an observer was presented black-and colored gratings of opposite orientation and additional colors (e.g. black-red vertical and black-green horizontal gratings) in turns, after a certain period an observer perceives white stripes of black-white gratings as colored. There exist too many hypotheses for explanation of MCE. Cheleste McCollough originally proposed that "The effect results from the color adaptation of neurons in the visual cortex that code for local orientation — neurons fitting this description were found in area V1"[1].

According to the group of authors, McColough type color after-effects occur with the participation of neurons that simultaneously encode information about orientation and color. The MCE indicates that color- and orientation-coding mechanisms interact at some point during visual processing; but the question remains as to whether this interaction occurs at an early or later stage in the cortical visual pathways.

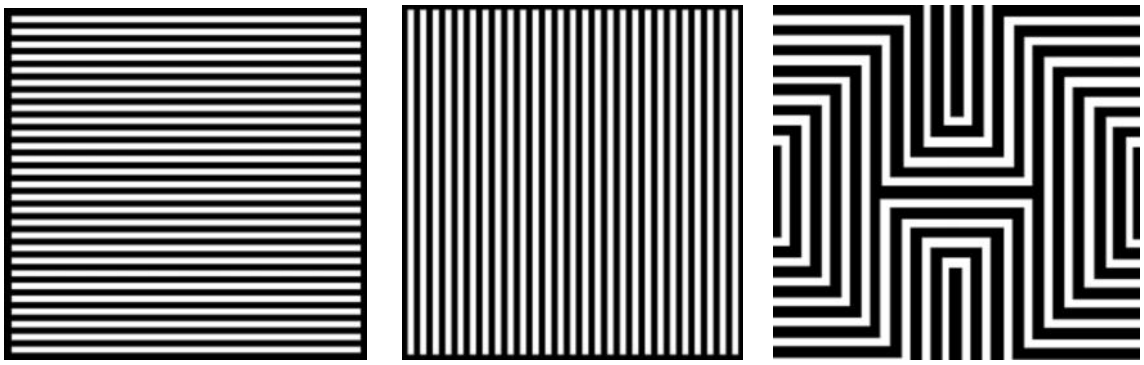
Neuropsychological and perceptual tests demonstrated that the patient, which has a profound impairment in a form perception and is even unable to discriminate between 90° differences in the orientation of grating stimuli. He is also unable to use orientation information to control his reaching or grasping. Nevertheless, this patient with a damage in the extrastriate cortex can name and discriminate different colors reliably, including those used to induce the MCE. After adaptation with red-and-green gratings, he appropriately reported the orientation-contingent after-effect colors, even though he continued to be unable to discriminate the orientations of the test patterns [2].

In some cases the McCollough effect was discussed as possible manifestation of associative learning of orientation and color in early visual areas. Some authors via decoded fMRI neurofeedback termed ''DecNef'' [3], tested whether associative learning of orientation and color can be created in early visual areas.

One fMRI (functional magnetic resonance imaging) study found BOLD (blood-oxygen-level dependent**)** activity changes in multiple areas and concluded that the McCollough effect is created through top-down processing from a high cognitive area [4]. Another fMRI study found that the left anterior portion of the color-selective area in the ventral occipital cortex, presumably V4 alpha, was significantly activated in association with the McCollough effect [5]. Second, in the McCollough effect, the induced color is complementary to the exposed color. This indicates that in contrast to the associative learning in the present study, the McCollough effect is not due to a simple form of association but rather reflects the complexity of the underlying neural mechanism, including adaptation processes [6]. Some studies suggest that the McCollough effect is not due to associative learning [7].

The point of view of Thompson, P. and Latchford, G. also is interesting. They exploited color constancy, the tendency for objects to appear constant in hue despite large changes in the spectral composition of the illuminant, to examine whether the colors observed on the McCollough effect test gratings are determined by the wavelength composition of the adaptation patterns or by their perceived color. The key to this approach can be illustrated by Edwin Land's elegant demonstrations of color constancy using Mondrian displays. By embedding the adapting grating that is used to induce the McCollough effect within Mondrian we show that the effect depends upon the wavelength of light coming from the grating, rather than the perceived color [8].

According to the opinions of some authors, the McCollough effect is a classical example of conditioned case [9-13]. In this model the lined grid in inspection is seen as the conditioned stimulus (CS) and the paired color as the unconditioned stimulus (UCS)[14]. According to a conditioning analysis of the orientation-contingent color after-effect (McCollough effect, MCE), orientation stimulus (grids) become associated with color. Contrary interpretation reports that simple forms cannot be used to elicit illusory color and that the MCE is not degraded by decreasing the grid-color correlation. The present results indicate: (a) form stimuli can contingently elicit color after-effects; (b) even a non-patterned stimulus the lightness of a frame surrounding colored area can contingently elicit color after-effects; (c) this frame lightness-contingent after-effect, like the MCE, persists for at least 24 hr; (d) the frame lightness-contingent after-effect can be used to demonstrate that correlational manipulations affect the MCE, as they affect other types of conditional responses [15]. Following an induction procedure in which a colored grid is alternated with a square of complementary color, subjects report color after-effects on both - the grid orientation present during induction and the orthogonal non-induced grid orientation. The after-effect reported on the induced grid orientation is called the McCollough effect (MCE). The after-effect reported on the non-induced grid orientation is called the indirect MCE. There is evidence that the MCE



A. B. C.

Fig. The test stimuli for McColough effect. During the adaptation procedure the white stripes of A and B gratings were colored in red (R-255, G-0, B-0) and green (G- 255, R-0, B-0) colors.

represents an instance of Pavlovian conditioning. The present results support conditioning interpretation of the indirect MCE and are inconsistent with interpretations of the indirect MCE that attribute the phenomenon to special orthogonal coding mechanisms within the visual system [16].

Finally, it can be said that despite a lot of hypotheses [17-21], there is no common well-grounded consideration on neurophysiological mechanisms of elaboration the McCollough effect. Among other hypotheses, neither conditioned reflex hypothesis is completely clear. Our experiments aim to elucidate namely this issue. We tried to find out whether the use of a conditioned excitatory (in this case – sound) will have an impact on producing the McCollough type aftereffect.

Materials and Methods

The experiments were carried out on the test subjects with normal color vision, age range – 17-65. In total 10 test subjects participated. Color Vision of participants was estimated by **Ishihara's tests for Color Blindness** .

The first stage of the experiment was elaboration of the "classical" McCollough effect: black-green gratings of vertical orientation and black-red gratings of horizontal orientation (Fig. 1) were presented, but the effect was produced by adding a sound stimulus; presentation of adaptation stimuli was followed by an audio signal; different sound tone corresponded to different orientation. Particularly, while presenting black-red horizontal grating, the test subject was provided with 300 Hz tone frequency; in case of black-green vertical orientation – 700 Hz. Sequential presentation of these gratings was performed during 4 seconds, with a dark interval of 2 seconds.

After the 30 presentations of each orientation of gratings (what needs 10 min), to participants the combined test stimulus with black-white vertical and horizontal gratings was presented. If the participant saw white stripes of gratings respectively greenish and reddish it means that McCollough effect is produced.

After 10 minute adaptation, the combined test stimulus consisted of black-white grating was presented to the test subject (Fig. 1). If the test subject confirmed that he/she saw tinted white stripes of the stimulus, we provided him/her with 300 and 700 Hz tones in turns. Each time we asked the test subject to estimate whether he/she could notice any changes in phantom colors. The same task was given to the test subject while presenting black-white vertical and horizontal gratings separately.

In the next series of the experiment orientation was excluded. We tried to produce a conditioned reflex only by color and sound pairing. A red rectangle paired with 700 Hz tone as well as a green rectangle paired with 300 Hz tone was presented to the test subject. Quantitative and time parameters of the adaptation procedure were the same as in the first series.

Table

The Table presents the phantom colors what the participants saw instead of white stripes of gratings on combined stimulus

Subject	Age	Gender	Orientation	Phantom color
N.S.	33	female	H V	Greenish Reddish
E.D.	64	" - "	H V	 Reddish
L.G.	52	" – "	H V	 Reddish
I.K.	51	" – "	H V	 Reddish
N.M.	26	" – "	H V	Greenish Reddish
M.K.	65	" – "	H V	 Reddish
N.Z.	66	" – "	H V	 Reddish
S.U	35	" – "	H V	 Reddish
L.N.	27	" – "	H V	 Reddish
M.M.	38	" –"	H V	 Reddish

Results and Discussion

Every test subject, regardless age, developed the effect (Table 1). If we assume that the effect producing conditioned reflex theory is grounded, we have to expect that addition of a tone which has the function of a conditioned excitatory in this paradigm should cause a change in perception of phantom colors. As it is known from literature and is shown in the Table, it is not necessary for a test subject to see a color on both orientations. Quite often, a color is noticed in one orientation, in the other – the effect is significantly weaker or color is not seen at all. Exactly such cases are especially informative as it was anticipated that addition of a color could strengthen the effect; but as our experiment has shown, sound pairing does not affect perception of a phantom color. None of the test subjects felt any changes in color sensation.

The experiments of the second series did not reveal any connection between two different modality – color and sound either.

Hence, we can conclude that the results of these experiments can be considered as one more argument against the conditioned reflex hypothesis of producing effect.

They usually develop it by adding sound, i.e. on the combined test stimulus, they see white stripes of the vertical grating as pinkish and white stripes of the horizontal grating as greenish. While presenting the black-white vertical and horizontal gratings on the monitor in turns accompanied by 700 and 300 Hz sounds, all test subjects perceived white stripes of the vertical grating as pinkish and white stripes of the horizontal grating as greenish. When we changed the sound ratio, i.e. added 700 Hz sounds to the horizontal black-white grating and 300 Hz sounds to the vertical black-white grating, test subjects still perceive white stripes of the vertical black-white grating as pinkish and vice versa, white stripes of the horizontal grating as greenish. It became obvious that sounds of different strength did not give any reference to colors.

The similar results were received after the second experiment. While presenting a white rectangle accompanied by 700 and 300 Hz sounds, the sounds did not give any reference to colors and every test

subject perceived the presented rectangle as white. We can say that sounds of different strength paired with red and green colors did not give any reference to colors. During the adaptation process, every test subject fixed which type of sound was added to which color and grating orientation. After the adaptation was over, participants stated that despite they distinctly heard a low-pitched sound while watching red color and horizontal orientation and a high-pitched sound while watching green color and vertical orientation, they still perceived white stripes of the vertical grating of the test stimulus as pinkish and those of vertical grating as greenish. It seems that audio stimulus does not have any impact on producing the McColough effect; it neither impedes it nor makes stronger.

In the second series of the experiments, none of the test subjects perceived illusive colors on white rectangular test stimuli accompanied with sounds (300 and 700 Hz frequencies). This fact indicates that the temporary connection between auditory and vision areas was not established in this case.

ადამიანისა და ცხოველთა ფიზიოლოგია

კიდევ ერთი მტკიცებულება მაკ-კოლაფის ეფექტის პირობითრეფლექსური ჰიპოთეზის წინააღმდეგ

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ჩვენს მიერ ჩატარებული ექსპერიმენტების მიზანს წარმოადგენდა იმის დადგენა – არის თუ არა მაკ-კოლაფის ეფექტი კლასიკური პირობითრეფლექსური გამოვლინება, თუ მას სხვა ახსნა გააჩნია. სხვადასხვა ასაკის, ნორმალური ფერადი მხედველობის, 10 ცდისპირი მონაწილეობდა კვლევების ორ სერიაში. ჩვენ შევეცადეთ გაგვერკვია, ახდენს თუ არა ზემოქმედებას პირობითი გამღიზიანებელი (ამ შემთხვევაში ბგერა) მაკ-კოლაფის ეფექტის გამომუშავებაზე. კლასიკური მაკ-კოლაფის ეფექტის გამოსამუშავებელ სტიმულებზე - სხვადასხვა სიხშირის ბგერების დამატებამ ეფექტის გამომუშავებაზე არავითარი გავლენა არ მოახდინა. ექსპერიმენტის შემდეგ სერიაში საადაპტაციო სტიმულებზე ორიენტაცია გამოვრიცხეთ. ვეცადეთ გამოგვემუშავებინა პირობითი რეფლექსი ფერის და ბგერის შეუღლებით. ცდისპირებს წარედგინებოდათ წითელი მართკუთხედი შეუღლებული 700ჰც ბგერასთან, ხოლო მწვანე მართკუთხედი 300ჰც ბგერასთან. საადაპტაციო პროცედურის დამთავრების შემდეგ ცდისპირები სატესტო თეთრ მართკუთხედებზე, ბგერების თანხლებისას, ილუზორულ ფერებს ვერ ხედავდნენ. ეს ფაქტი მიუთითებს, რომ დროებითი კავშირი ბგერასა და ფერს შორის არ ჩამოყალიბდა. გამოვთქვამთ მოსაზრებას, რომ მაკ-კოლაფის ეფექტის კლასიკურ პირობით რეფლექსად განხილვა არ უნდა იყოს მართებული.

REFERENCES

1. *McCollough C.* (1965) Color adaptation of edge detectors in the human visual system. Science. **149**: 1115-1116.
2. *Humphrey, G.K., Goodale M.A., Corbetta M., et al.* (1995) The McCollough effect reveals orientation discrimination in a case of cortical blindness, Current Biology. issue **5**: 545–551.
3. *Amano K., Shibata K., Kawato M., et al.* (2016) Learning to Associate Orientation with Color in Early Visual Areas by Associative Decoded fMRI Neurofeedback. Current Biology. **26:** 1-6**.**
4. *Barnes J., Howard R.J., Senior C., et al*. (1999) The functional anatomy of the McCollough contingent colour after-effect. Neuroreport. **10**: 195–199.
5. *Morita T., Kochiyama T., Okada T., et al. (*2004) The neural substrates of conscious color perception demonstrated using fMRI. Neuroimage. **21**: 1665–1673.
6. *Skowbo D.* (1984) Are McCollough effects conditioned responses? Psychol. Bull. **96**: 215–226.
7. *Byth W., McMahon D., King D.J.* (2000) Cholinergic agents and the McCollough effect. Perception **29**: 461–480.
8. *Thompson P., Latchford G.* (1986) Color-contingent after-effects are really wavelength contingent. Nature. **320**(6062): 525-526.
9. *Leppman P.* (1973) Spatial frequency dependent chromatic after-effects. Nature. **242**: N 5397. 411-412.
10. *Murch G.*(1979) The role of test pattern background hue in the McCollough effect. Vision Res. **19**: 939-942.
11. *Shute C. C. D.* (1987) The McColough effect. Cambridge Univ. Press. 263-266.
12. *Skowbo D., Gentry T., Timney B., et al.*(1974) Influence of several kinds of visual stimulation on decay rate. Percept. Psychophys. **16**: 47-49.
13. *Skowbo D., Foster T.* (1983) Further evidence against the classical conditioning model of McColough effects. Percept. Psychophys. **34**: 552-554.
14. *Murch G.M,* (1976) Classical conditioning of the McCollough effect: Temporal parameters. Vision Research. **16**: Issue 6: 615-61.
15. *Siegel S., Allan L.G., Eissenberg T.* (1992) The associative basis of contingent color after-effects. J. Exp. Psychol. Gen. **121**(1): 79-94.
16. *Eissenberg T., Allan L.G., Siegel S., et al.* (1995) An associative interpretation of the indirect McColough effect. J. Exp. Psychol. Gen. **48**(3): 262-286.
17. *Durgin F.H.* (1996) Visual after-effect of texture density contingent on color of frame. J. Perception and Psychophysics. **58**: 207-223.
18. *Janelidze D., Roinishvili M., Pharkosadze C., et al*. (2008) Emergence of contingent achromatic after-effects are determined by differences in the stimuli luminance. Proc. Georgian Acad. Sci. Biol. Ser. A. **34,** 3-4: 257-265.
19. *Michael C.R.* (1978) Color vision mechanisms in monkey striate cortex: simple cells with dual opponent-color receptive fields. J. Neurophysiol. **41**: 1233–1241.
20. *Goodale M.A., Milner A.D., Jakobson L.S. et al..* (1991) A neurological dissociation between perceiving objects and grasping them. Nature. **349**: 154–155.
21. *Kezeli A., Janelidze D., Kezeli T., et al* (2015) What can tell us the McCollough effect about functioning of mechanisms of perception constancy?Proc. I.Beritashvili Center exp. Biomed. Nova Biomedical publ. NY. 63-74.

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