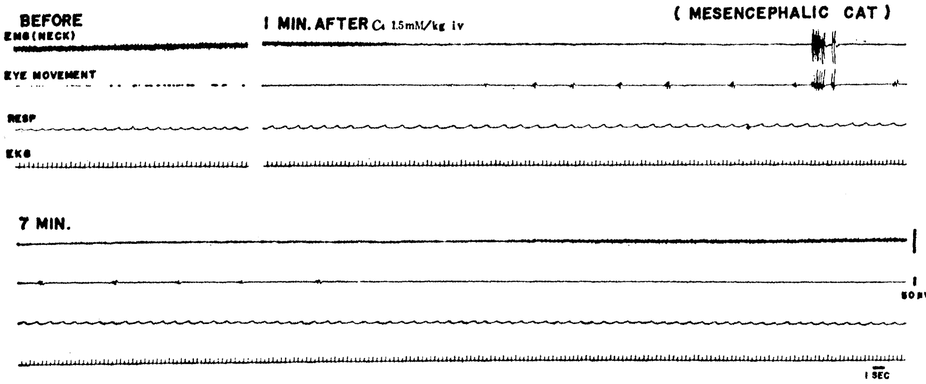

Fig. 2. The paradoxical phase of sleep in the mesencephalic cat. The control state is at top left, and the state after 1 minute is at top right. The state after 7 minutes is at the bottom. The activity shown by the EMG disappears and eye movements appear after 1 minute.

state to the slow-wave and spindle-burst pattern for 1 to 2 minutes, and the paradoxical phase followed for several to 10 minutes. In untreated cats, the spontaneous paradoxical phase occurred repeatedly for 6 to 10 minutes at intervals of 2 to 2.5 hours.

When the concentration of sodium butyrate was between 0.5 mM/kg and 1 mM/kg, the paradoxical phase of sleep was not observed, and the slow-wave phase continued for less than 15 minutes. If a more concentrated solution (4 to 5 mM/kg) was administered, appearance of the paradoxical phase of sleep was delayed, appearing for a short time of 0.5 to 2 minutes after a prolonged period of slow-wave sleep for 40 to 60 minutes.

Similar changes in the paradoxical phase of sleep were also induced by sodium butyrate in the mesencephalic cat, while the mesencephalic cats not injected with sodium butyrate showed no sign of the paradoxical phase. As illustrated in Fig. 2, 1.5 to 3 minutes after administration the neck-muscle activity disappeared for 4 to 15 minutes and returned to the control amount.

At this time, irregularity of the heart rate and respiratory movements, and jerky movements of the eyes and facial muscles characteristic of the paradoxical phase of sleep in the intact cat, were observed. These facts indicate that the paradoxical phase is induced in the mesencephalic cat by the butyrate. If the butyrate (1.5 mM/kg) was administered at intervals of 40 to 50 minutes to the same cat, the paradoxical phase was always produced for 4 to 15 minutes, with a delay of 1.5 to 2 minutes. Even after seven or eight injections no sign of desensitization was noticed. Compared with the intact state, the time at which the activity of the neck muscle disappeared in the EMG or at which other signs appeared was relatively constant within a narrow range (1.5 to 2 minutes).

If a small amount of sodium butyrate (0.15 mM kg^{-1} min^{-1}) was given continuously for 20 to 30 minutes in the mesencephalic cat, the duration of this phase could be prolonged for 40 to 70 minutes. The application of saline as a control solution (1 to 3 ml/kg) under the same experimental conditions could not induce the paradoxical phase of sleep in the intact or the mesencephalic cats.

The concentrations of sodium butyrate and related compounds which could reproducibly induce the paradoxical phase of sleep in the cat by intravenous application were as follows; sodium n-butyrate (1 to 3 mM/kg), sodium isobutyrate (1 to 3 mM/kg), sodium isovalerate (1 to 2 mM/kg), sodium n-caproate (0.3 to 0.5 mM/kg), sodium γ-hydroxybutyrate (1 to 1.5 mM/kg), sodium γ-butyrolactone (0.5 to 1 mM/kg), sodium α-hydroxyisobutyrate (1 to 1.5 mM/kg). Sodium propionate (1 to 2 mM/kg), sodium acetoacetate (1 mM/kg), and β-hydroxybutyrate (1 to 1.5 mM/kg) were not effective in producing the paradoxical phase of sleep.

From polygraphic observations in the intact and mesencephalic cat, it is concluded that sodium butyrate and related compounds are capable of inducing the paradoxical phase of sleep after a state of appropriate duration characterized by slow waves and spindle-shaped bursts. The manner in which the paradoxical phase of sleep is produced by these substances is not resolved.

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Köllner Effect and Suppression of the View of an Eye

Abstract. *Köllner's discovery of binasal hemianopia as an early stage in binocular color rivalry is extended to the study of the subsequent suppression of the color seen by an eye. The Köllner effect is one of the five two-color configurations that occur initially, and through which total suppression develops by the visible expansion of one of the colors. However, suppression sometimes occurs without a two-color phase.*

When corresponding areas of the two retinas of a subject are exposed to different colors there may be binocular color mixture. When this does not occur, there is binocular color rivalry, characterized by the alternation of suppression of the view of the left and the right eye. The popular theory is that the brain employs suppression "as a psychic means of escape from conflict" (*1*). It is not known how "the brain" accomplishes suppression, nor how suppression of the view of one eye occurs during binocular color rivalry.

Köllner first reported that the colors

Table 1. Frequency of occurrence of each kind of suppression of the color presented to one eye.

Subject	Type of spatial incursion: Köllner effect	Reverse Köllner effect	Frame	Stripe	Layer	Other: One color dissolves	No complete suppression
1	10	3	0	1	6	4	0
2	11	2	1	5	1	4	0
3	10	4	1	0	4	5	0
4	3	16	5	0	0	0	0
5	10	6	2	3	1	2	0
6	5	5	9	4	0	0	1
7	9	9	0	0	5	1	0
8	4	9	3	1	4	1	2
9	15	0	0	0	2	7	0
10	13	2	1	1	3	2	2
11	5	14	0	1	2	2	0
12	1	4	3	0	0	11	5
Total	96	74	25	16	28	39	10
Percentage	33.3	25.7	8.7	5.6	9.7	13.5	3.5

presented to both eyes are both partly visible at first—that is, early suppression is incomplete. He found that before the view of one eye becomes suppressed something like binasal hemianopia happens: one sees a split field with the left-eye color appearing to the left of the right-eye color. This sensation is the Köllner effect (*2*). We now know that it depends in part on the size of the retinal areas stimulated. For areas subtending as little as 1° and 2° of visual angle, the reverse Köllner effect is more common: the left-eye color appears to the right of the right-eye color (*3*). To complicate matters, there are three other two-color configurations that are sometimes reported when exposure duration is short (a tenth of a second). They are frames (one color appears surrounding a central area of the other color), stripes (one color appears in a vertical stripe between two stripes of the other color), and layers (one color appears in a horizontal band above a band of the other color). A surprising fact is that only these five two-color configurations have appeared often in our studies.

These two-color configurations are related to the subsequent full suppression of the color shown to one eye. Some subjects in a pilot study sketched with colored crayons the "stages" that occurred when the color square was presented continuously for a few seconds. Their sketches indicated that often the two-color configurations remain visible until full suppression of one color occurs, and that the color that comes to occupy all the perceptual space often does so by visibly expanding from its location in the early two-color configuration. I have investigated the extent to which the first full suppression of one color develops through a visible spatial incursion of one color into the area formerly occupied by the other color, and the relative frequency at which such expansion occurs through each of the five two-color configurations.

Twelve college students viewed a red square with one eye and a green square with the corresponding area of the other eye in the apparatus used for previous studies (*3*, *4*). The duration of exposure was 3 seconds. There were six trials with each of four squares differing in size; they subtended from 2°12′ to 6°08′ of visual angle, and the order of presentation was counterbalanced. After each observation period the subject reported the initial appearance of the colored square, and the changes in the colored square ending with the appearance of the full area in only one color (in cases in which the initial report was of only one color, which occurred for about half the trials, the first full suppression of interest was the suppression of that color as the other color became dominant). The experimenter coded the reports with respect to whether the change that occurred was a spatial incursion of one color and, if so, whether the incursion was an expansion of a color from a location typical of one of the two-color configurations (*5*). For example, a color might expand through the Köllner effect (with the left-eye color expanding from left to right), the reverse Köllner effect (with the left-eye color expanding from right to left), frames (with one color expanding from all the borders into the center), stripes (with one color expanding from the left and the right border into the center), or layers (with one color expanding from the upper or the lower border).

Table 1 shows the frequency of occurrence of each type of development of suppression of one color. There was no significant difference between stimulus sizes; data from all trails are pooled. For over 80 percent of the trials suppression occurred through an apparent incursion of one color so that it took over the "former territory" of the other color. Most types of development of suppression were reported by most subjects, indicating that the discovery of a visual syndrome in which only one type of two-color configuration occurs might prove of special interest. Apparently such a discovery has been made: patients with strabismus and anomalous retinal correspondence have been reported to see a color rivalry target as conforming to the Köllner effect for patients with exotropia, and conforming to the reverse Köllner effect for patients with esotropia (*6*).

For the subjects in the present study, on some trials one color was reported to dissolve uniformly, allowing the other color to be seen. But the color to be dominant usually expanded through one of the five two-color configurations. This appears to be the relevance of the Köllner effect, first reported 50 years ago, to the more general problem of visual suppression. The mechanisms that underlie the two-color configurations and that determine the flow of color within them remain unknown.

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