LIGHT-SOUND INTERACTION IN THE NEURONS OF THE RABBIT'S VISUAL CORTEX

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Abstract. One hundred cells of the visual cortex were studied using flashes, clicks and light-sound combinations with different delays. Forty nine neurons changed the total number of spikes to click stimulation. Twenty eight cells responded to clicks with specific response pattern. In 23 cells the initial discharge occurred at 60–70 msec after the onset of clicks. In 39 cells the responses to light-sound combinations differed from the responses to flashes. While 16 cells decreased their responses, the addition of sound increased firing in 23 cells. The specific modification of the light-evoked responses under acoustic stimulation were classified into three main categories: 22 cells generated new response patterns, 18 cells showed a re-distribution of peaks in the PTS histogram and three cells demonstrated a desynchronization of the spike discharge. The study of the heteromodal recovery cycle revealed that the majority of the cells increased their firing during 0–100 msec and decreased firing during 200–300 msec of the response time scale. The critical delays between light and sound, resulting in the modification of the response for the majority of the cells, were within 100 msec in both directions.

INTRODUCTION

Neurons located in the visual projection area of the cortex respond not only to light, but also to stimuli of other modalities, and in particular to acoustic stimuli (1, 10–14, 26). Jung (6) and Jung et al. (7) demonstrated the convergence of specific retinal and nonspecific thalamic afferents on single neurons of the visual cortex. Similarly, Vinogradova and
Lindsley (27) found that neurons of the visual cortex responded to sounds with short-latency, nonhabituating spike discharges. Jung et al. (7) also presented evidence showing short-latency, specific spike discharges evoked in neurons of the visual cortex by visual, acoustic and vestibular stimuli, which emphasized the role of specific multisensory convergence at the cortical level. Skrebitsky and Bomstein (24), Sokolov et al. (25) have demonstrated the modification of light-evoked responses by simultaneously presenting acoustic stimulation. Such acoustically mediated changes of light-evoked responses, characterized by habituation under repeated presentation of the auditory stimuli, might be regarded as a non-specific effect from the acoustic stimulation. The influence of the sound on the light-evoked spike discharge might be also very specific. Thus, a neuron of the visual cortex unresponsive to both light and sound showed a specific, nonhabituating response to light-sound combinations (19).

The following questions arise with respect to the light-sound interaction upon the neurons of the visual cortex:

1. What types of sound-evoked spike discharges are characteristic of the neurons of the visual cortex?
2. How does the light-evoked response relate to the sound-evoked response in the same neuron?
3. What are the effects from simultaneous presentation of both light and sound?
4. How is a response to light effected when the sound either precedes or follows the light with different delays?

The present study was directed mainly toward the clarification of the specific and nonspecific effects related to the light-sound interaction. The role of the time interval between light and sound in the production of this interaction was examined. The heteromodal recovery cycle (i.e., the recovery of the light-evoked response after sound, and to sound after light) was used to assess the organization of the neuronal nets responsible for the light-sound interaction.

METHODS

The experiments were performed on 29 adult unanesthetized chinchilla rabbits. Several days before initial experimentation, the scalp and the periosteum of each subject were removed under local anesthesia. On the day of the experiment the animal was loosely fixed in an extended position with its limbs tied to a frame and the head placed in a special wooden, nontraumatic head-holder. A cranial opening (diameter \( \varnothing \) 5 mm) was made unilaterally above the striate or peristriate cortex (see 22). The opening was covered with agar-agar to reduce pulsations.
Each animal was placed in a sound-proof cage. Single-unit activity was recorded by means of electro-polished tungsten microelectrodes using a microdrive apparatus. A special contact lens was used to prevent the eyelid closure. The eyes were atropinized in order to stabilize the pupils.

Three types of stimuli were used for each neuron in the experiment:

1. Visual: A brief (50 msec) flash from a xenon tube (0.136 joules) was led through a plastic fiberoptics light guide to the eye contralateral to the hemisphere under investigation. 30–40 flashes were given with 3–5 sec intervals.

2. Auditory: 0.3 joule clicks of short duration (1 msec) were presented with 3–5 sec intervals through the loudspeaker placed 30 cm above the animal’s head. The number of clicks was 30–40.

3. Combinations of light and sound coinciding in time were presented at 3–5 sec intervals. The heteromodal recovery cycle was studied for 15, 30, 50, 100, 200, 400 and 1,000 msec light-sound and sound-light delays using 10–30 presentation of pairs for each respective delay.

The unit activity was amplified, taped and off-line fed into Nokia-4,000 digital analyser for compiling post-stimulus-time (PST) histograms and numerical data printing. The calculations of the number of spikes during 0–100, 0–200, 0–400, 0–1,000 and 0–2,000 msec of the response time scale were used for constructing the heteromodal recovery cycles.

A range of 1 to 4 experiments was carried out on each rabbit, and in all experiments, recording was typically from one to three cells. Different cells in one rabbit were studied with 1–1.5 hr intervals, sufficient for the recovery of the background activity as well as the dishabitation of the evoked responses. However, the effect from chronic habituation was not eliminated. After each experiment the rabbit was returned to its home cage.

RESULTS

A total number of 100 neurons of the visual cortex were studied using the described program. For 44 units the heteromodal recovery cycles were evaluated.

I. Background activity

The average background firing rate for 100 neurons of the visual cortex was $6.49 \pm 0.67$ spike/sec. The limits of the background firing rate modifications were 0–40 spike/sec. 29 units had firing rates below
2 spike/sec, while 43 cells showed firing rates between 3 and 8 spike/sec. The continuous monitoring of the spike shape on the oscilloscope eliminated the possibility that the observed firing rate changes were related to cellular irritation by the tip of the microelectrode.

II. Light-evoked responses

Two main types of the light-evoked response patterns could be distinguished.

A type I response was composed of a primary discharge between 20–30 msec followed by decrease of spike activity between 100–300 msec, hyperactivity during 300–600 msec and delayed firing decrease lasting up to 1,500 msec (Fig. 1b). This evoked response might be represented by a sequence of increase (i) and decrease (d) phases as the i-d-i response pattern. In some cases this response might be complicated due to the

![PST-histograms](image)

Fig. 1. PST-histograms for sound (a) light (b) and the light-sound combination (c) in the neuron of the visual cortex (unit 447). Abscissa, response time in msec; ordinate, average number of spikes per bin. Time interval (bin width) is 20 msec. Ten trials contributed to each average response. The second vertical bar indicates the moment of the stimulus presentation. The background firing is shown on the left from the second bar, while the evoked spike discharge is represented on the right. The neuron is acoustically non-responsive. The light-sound combination produced a new response pattern differing from the light-evoked response by an additional discharge during the pause of the light-evoked response and pause, instead of the secondary discharge.
split of the primary discharge into several components, formation of an additional pause during the secondary discharge and appearance of a tertiary discharge around 800 msec (Fig. 2b).

Fig. 2. PST-histograms for sound (a), light (b) and light-sound combination (c) (unit 518). For designations see Fig. 1. The neuron responded to sound with a short latency spike discharge, followed by firing at the background level. The light elicited an initial multipeak discharge followed by a short pause, a secondary discharge and a longer lasting second pause. The light-sound combination resulted in a new response pattern differing from both the sound and light-evoked responses. The difference are reflected in the shortening of the secondary discharge latency, formation of the tertiary spike discharge and the elimination of the longer lasting second pause.

A type II response was characterized by an initial long-lasting firing decrease (60–250 msec), followed by a slightly patterned discharge in the interval 250–400 msec (Fig. 3b). In some cases this discharge might be followed by secondary pause in firing. The type II response of the light-evoked discharge might be represented by a d-i-d sequence.

Each neuron in the population was characterized by the particular time on the response scale when the discharge was maximal. The distribution of the neurons, with respect to the time of maximal discharge on the response scale, revealed two populations of cells that showed either short or long latency peaks of the discharge (Fig. 4). Seventy two per cent of the neurons demonstrated a type I response, and 28% showed a type II response. The majority of the neurons did not change their responses during repeated presentations of light stimuli. However, in some cases, a stabilization, facilitation or partial habituation of the responses were observed.
Fig. 3. PST-histograms for sound (a), light (b) and light-sound combination (c) (unit 312). The response to sound is characterized by an initial discharge at 60 msec after stimulus presentation. The response to light consisted of an initial pause followed by a discharge of long duration. The response to the light-sound combination differed from both the sound- and light-evoked responses by a peak of firing arising at 100 msec instead of the primary pause observed in the light-evoked response. The late, long lasting discharge, characteristic for the light-evoked response, was reduced. For designations see Fig. 1.

Fig. 4. Distribution of the neurons that depended upon the maximal spike discharges to light on the response time scale. Abscissa, response time in msec; ordinate, number of units demonstrating maximal spike discharge during an appropriate interval. The majority of neurons have a maximal discharge in the intervals of 30–60 msec and 180–200 msec.
III. Sound-evoked responses

The spike discharges in the neurons of the visual cortex were less pronounced to clicks than to flashes. Only 28 neurons demonstrated stable responses to sound. The sound-evoked responses might be classified into three main types: Firing increase type (i), numbering 16 neurons; firing decrease type (d), of which 4 neurons were observed; decrease-increase type (d-i), a single neuron sound; and increase-decrease-increase type (i-d-i), numbering 7 neurons.

A clear distinction of the firing increase–firing decrease phases in the click-evoked discharges was observed in 8 cells only. Thirty five neurons did not demonstrate any response to click stimuli, and such a neuron is shown in Fig. 1a. The i-d-i response pattern to clicks presented in Fig. 2a, consisted of an initial peak at 20 msec followed by short pause of firing, which in turn was followed by secondary spike discharge of 60–100 msec. The neuron having a spike discharge lasting from 60 msec to 200 msec is shown in Fig. 3a.

The evaluation of the total number of spikes generated by clicks during the response time of 1,000 msec showed that 51 neurons were unresponsive, 25 neurons were activated and 24 showed a decrease of firing. The identification of the response type was based on a 30% modification in the number of generated spikes as the criterion. In 37 cells the responses to sounds habituated either completely or partially. Twenty eight neurons with patterned stable responses to acoustic stimulation, lacking any habituation, were regarded as the neurons of the visual cortex specifically responsive to sound.

A further classification of the sound-responsive cells was found on the basis of location of the spike discharge maximum on the response time scale (Fig. 5). The maxima of spike discharges were located in the range of 50–100 msec, mainly between 60–70 msec. The latency of the response, measured according to the position of the first spike, was 10–15 msec. The broad range of the response latencies (10–300 msec) and different resistances of the discharges, with respect to repeated acoustical stimulation, demonstrated two different populations of the neurons of the visual cortex: Sound-specific and sound-nonspecific. The sound-nonspecific responses were mainly diffuse, non-patterned and habituating. The sound specific responses were patterned, habituating and stabilized under repeated stimulation.

The specific response to light and sound in a given neuron might be different and even opposite. Accordingly, the firing increase to sound (Fig. 3a) might parallel the decrease of firing to light (Fig. 3b). In 7 neu-
Fig. 5. Distribution of the neurons that depended upon the maximal spike discharges to sound on the response time scale. Abscissa response time in msec, while the number of units demonstrating maximal spike discharge during an appropriate interval is plotted along the ordinate. The majority of neurons demonstrated the maximal discharge in the interval of 50–120 msec.

Irons the responses to both light and sound were characterized by firing decrease, in 32 neurons by firing increase, while in 33 neurons the responses to light and sound were opposite to each other.

IV. Responses evoked by coincidence in time of light and sound

Specific and nonspecific influences, from the sound-evoked upon the light-evoked responses, were found when light and sound coincided in time. The nonspecific modification of the light-evoked response by the addition of sound might be either decreasing or increasing. In both cases after 10–15 presentations of the light-sound combination the spike discharge became undistinguishable from the response evoked by light alone. The specific effect of the sound on the light-evoked response was characterized by its stable modification. Under repeated presentations of the light-sound combination, the specific spike discharge remained unchanged.

The formal differentiation of the sound-modifiable and sound-unmodifiable light-evoked responses was based on the calculation of the number of spikes generated separately for sound, light and light-sound stimuli during each 100 msec on the response time scale.

The light-sound combination produced an effect which cannot be explained as the linear summation of the light- and sound-evoked responses. The magnitude of the effect of acoustic stimulation on the light-evoked response was estimated by a difference in the total number of spikes generated during 1,000 msec for light and the light-sound combination. If the difference of generated spikes was greater than 30%/s, the neuron was regarded as having a sound-modifiable light response. The neurons,
with respect to the light-sound evoked responses, were divided into three main categories, having (i) unmodifiable light responses, (ii) decreased light responses and (iii) activated light responses.

Among 56 neurons responding to light with an increase of firing rate, 16 units were characterized by a decrease of firing rate through the light-sound combination with the 30% criterion. Among 44 units responding to light with a decrease of firing, 23 neurons were activated by the light-sound combination above the same criterion. In 61 units the responses were unmodified as evaluated.

The following effects of the sound on the light-evoked response were found in this experiment:

1. The lack of an effect

The neuron 413 (Fig. 6), having no response to sound (a) presented alone, responded with the i-d-i pattern to light stimulation (b). The spike discharge evoked by the light-sound combination (c) did not differ from the spike discharge evoked by the light alone. Thirty eight such unmodifiable neurons were found.

![Fig. 6. PST-histograms for sound (a), light (b) and light-sound combination (c) (unit 413). The neuron responded to sound with a slight decrease of firing at 300–400 msec. The responses to light and light-sound combination did not differ from each other. For designation see Fig. 1.](image)

2. The nonspecific effect

The sound given alone resulted in either a diffused response or produced no response. The sound still may influence the light-evoked response by increasing or decreasing the number of generated spikes. When the light-sound combinations were repeatedly presented, this nonspecific effect diminished and disappeared after 10–30 trials, and the spike
The discharge evoked by light-sound combination became indistinguishable from the light-evoked response. In the neuron of Fig. 7, responding to sound alone (a) with a marked decrease of firing, a combination of the sound + light (c) resulted in an increase of amplitude over the i-d-i response pattern evoked by the light alone (b). The response to the light-sound combination was profoundly augmented with respect to the light-evoked response during 1–10 trials only (c). However, during the following 11–20 trials (d), the activation produced by sound in the light-evoked response disappeared, and the light-sound combination evoked spike discharges similar to the light-evoked response. Only 6 units were identified as having pronounced nonspecific modifications.

![Fig. 7. PST-histograms for sound (a), light (b) and two sets of light-sound combination (c, d) (unit 437). The sound resulted in a decrease of firing around 300 msec along the response time scale. The light resulted in the i-d-i response pattern. PST-histogram for 1–10 presentations of the light-sound combination (c) demonstrated the intensification of the light-evoked response without any modification of its pattern. PST-histograms for 11–20 presentations of the light-sound combination (d) were not distinguished from the light-evoked response. For designations see Fig. 1.](image)

3. The stable changes of the magnitude of the spike discharge without modification of its response pattern

In some stable nonhabituating neurons the increase or decrease of the light-evoked response under the influence of simultaneously presented sound occurred without any change in the shape of the light-evoked response. The depression of the light-evoked response with the addition of acoustic stimulation, when the shape of the spike discharge for light remained unchanged, is shown in Fig. 8A. The sound given alone (a) resulted in no response at all. However, the light-evoked response was considerably diminished under the light-sound combination (c). The
Fig. 8.A: PST-histograms for sound (a), light (b) and light-sound combination (c) (unit 449). The neuron is unresponsive to sound. The response patterns to light and light-sound combination are similar, with differences only in regard to the total number of generated spikes. For designations see Fig. 1.

B: The dependence of the number of generated spikes on the number of presented stimuli. Each point represents a block of 10 presentations of light-sound combinations (open circles). The blocks of 10 flashes (crosses) were used to test stability of the light-evoked response during the experiment (unit 449). Abscissa, the number of light-sound combinations; the ordinate, the number of spikes generated during 1,000 msec of the response time. The curve representing the number of spikes generated by light-sound combinations remains below the curve representing the number of spikes generated by flashes alone. The sound results in a non-habituating depression of the light-evoked response.

Stability of this sound-evoked depression in the light-evoked response was tested during 400 presentations of light-sound combinations. After each 60 trials, 10 flashes were given alone for evaluation of the light responsiveness in the tested neuron. Figure 8B shows constant decreasing effect of the sound on the light-evoked response. The curve representing the number of spikes evoked by the light-sound combination remained generally lower than the curve representing the number of spikes evoked by the light alone. Similar stable effects might be of an activating type when sound results in a nonhabituating increase of spike generation for the light-evoked responses. From 100 units studied, 5 de-
monstrated a stable decrease, and 8 showed a stable activation of the light-evoked response without any change of the shape of the response evoked by the light-sound combination.

4. Specific modifications in the light-evoked response

In 43 of the 100 units studied, the effect of sound on the light-evoked response could be characterized as a specific modification in the shape of the spike discharge persisting under repeated stimulation. Three main types of the modifications of the light-evoked response pattern were identified:

A. A new response pattern. In this case the response to the light-sound combination was totally different from the light-evoked response, due to the appearance of new peaks and elimination of some peaks present in the light-evoked response. The new response patterns to the light-sound combination were observed in 22 units, however, only 9 neurons were sound-responsive. This finding means that in 13 neurons, which were unresponsive to sound, the shape of the light-evoked responses was modified under the influence of acoustical stimulation. The change in the shape of the spike discharge might be combined with an increase or a decrease in the total number of spikes generated by light + sound. In 8 units the modification of the shape of the response was accompanied by a reduction in the total number of generated spikes and, in 5 units, by an augmentation of the response.

The most frequent response pattern modification involved the initiation of firing in the light-sound response during the pauses recorded in the light-evoked response. This effect was demonstrated in neuron 447 of Fig. 1. The neuron was unresponsive to sound (a). The flash (b) resulted in the spike discharge having a peak with a latency of 80 msec, followed by firing decrease at 100–320 msec. The light-sound combination (c) resulted in a response pattern markedly different from the light-evoked response. The maximal peak on the light-sound PST-histogram occurred at 40 msec. During the pause in firing, there appeared a new secondary discharge with a peak at 240 msec. The secondary spike discharge of light-evoked response was replaced by a secondary decrease in the response evoked by the light-sound combination.

The neuron 518 (Fig. 2) responded to sound (a) with a short latency (20 msec) spike discharge, followed, after a brief decrease in firing, by a secondary discharge. The flash (b) generated three discharges at 40, 80 and 180 msec interrupted by pauses. The time period of 400–850 msec on the response time scale was characterized by an elimination of spikes. The light-sound combination (c) resulted in a new response pattern, differing from both the sound-evoked response and the light-evoked res-
response. Two maxima of spike discharges at 70 and 150 msec occurred during the pauses of the light-evoked response. The secondary pause in the response pattern, evoked by light-sound combination at 200 msec, interfered with the tertiary discharge of the light-evoked response. The response to the light-sound combination was characterized by a late discharge reaching a maximum at 400 msec, which coincided with the late pause in the light-evoked response.

The neuron 312 shown in Fig. 3 displayed a similar effect. The light-sound combination (c) elicited a new response pattern, different from either the sound-evoked or the light-evoked response patterns. The acoustic stimulation (a) gave rise to an initial spike discharge at 60 msec on the response time scale. The response to the light-sound combination (c) was chiefly characterized by the spike discharge at 100 msec preceded, and followed by, pauses in firing.

A specific type of modification of the response shape involved a contrast effect, which consisted in the separation of single peaks and pauses from the diffuse response to light due to simultaneously presented sound. The neuron 548 (Fig. 9) responded to the click (a) with a slight firing decrease around 300–600 msec and late activation having a maximum at 800 msec. The light-evoked response (b) included the initial firing decrease followed by a diffuse firing increase with maxima at 200–300 and 600 msec. The light-sound combination (c) reproduced the main features of the light-evoked response, contrasting both peaks and pauses of spike discharge, which resulted in the separation of three main maxima at 80, 200 and 300 msec.

![Fig. 9. PST-histograms for sound (a), light (b) and light-sound combination (c) (unit 548). The neuron was slightly inhibited by acoustic stimulation, and the inhibition was followed by excitation at 800 msec. The flash resulted in an initial reduction of firing followed by a lasting activation. The effect of the light-sound combination might be characterized as the contrasting of both peaks and pauses of spike discharge. This sound induced effect might be called contrasting modification of the light response. For designations see Fig. 1.](image-url)
B. Re-distribution of the peaks in the spike discharge. The re-distribution of the peaks in the spike discharge might be identified when the response pattern evoked by light-sound combination remains similar to the light-evoked response. However, the contribution of different peaks was modified. The neuron 407 (Fig. 10) responded to sound (a) with a slight initial discharge followed by a decrease in firing lasting from 200 msec to 800 msec. The response to light (b) contained peaks at 280, 440, 780 and 850 msec. The light-sound combination (c) resulted in an augmentation of the discharges generated at 40 and 120 msec. Simultaneously, the spike discharge at 280 msec of the light-evoked response was diminished. The discharges at 440 and 820 msec were enlarged with respect to the light-evoked response. In the 18 neurons, constituting the group of cells with the re-distribution of peaks in the light-evoked response due to the addition of acoustic stimulation, 3 units were characterized by a decrease of the total number of spikes, while another 3 units revealed increase of firing. Only 6 units were unresponsive to sound.

C. Desynchronization of the spike discharge. The main characteristic of the desynchronization in the spike discharge was the decrease in differences between the peaks and pauses in the light-evoked spike discharge due to the addition of sound. The desynchronization of the spike discharge might be accompanied by augmentation of the total number of generated spikes or by its reduction. This group of neurons consisted of 3 cells, and only 1 cell was responsive to sound. In the 2 other units, that were not responsive to sound, the acoustic stimulus affected the light-evoked response. The firing of the neuron 504 (Fig. 11) was reduced...
Fig. 11. PST-histograms for sound (a), light (b) and light-sound combination (c) (unit 504). The click initiated a short latency pause in firing lasting up to 350 msec. The flash produced a powerful initial spike discharge followed by a decrease in firing, interrupted by several peaks of spikes discharges. The light-sound combination resulted in a reduction of the light-evoked discharge up to the level of background firing. For designations see Fig. 1.

by sound stimulation (a) during 0–300 msec. The flash (b) resulted in the multipeak spike discharge with a latency of 40 msec. The light-sound combination (c) resulted in the elimination of peaks in such a way that the spikes appeared spread over the entire time response scale.

V. The contribution of different intervals on the response scale in modification of the light-evoked response due to the addition of sound

For each neuron a part of the response to light underwent maximal modification by the addition of sound. In the majority of the neurons the maximal change in direction to the increase of firing level was evident during the first 100 msec. The number of cells demonstrating such modification decreased the total number of spikes with an increase of the epoch of analysis up to 700 msec. The number of cells with augmentation of spike generation increased when the epoch of analysis was prolonged up to 1,000 msec.

The maximal reduction of firing in the majority of cells was within 200–300 msec. The prolongation of the epoch of analysis resulted in a decrease in the number of cells having such changes in the response to light. Similar effects were observed when different criteria were used for evaluating the response modification. Figure 12 shows that the main contribution to the modification of the light-evoked response involved discharge of the components with latencies shorter than 400 msec.
Fig. 12. The distribution of the neurons that depended upon the epoch of the analysis in which the responses to light-sound combinations demonstrated maximal depression or activation in regard to the light-evoked responses. Abscissa, the epoch of analysis in msec; ordinate, the number of neurons demonstrating maximal or minimal spike discharge in the given interval. The upper portion shows activation, and the lower portion indicates depression of spike discharge. Different shadows on the histogram represent various criteria for the accepted modification: More than 500%, 200–500%, 100–200%, 50–100%, and less than 50%. The majority of the neurons showed increases in responses during the interval 0–100 msec and decreases during the interval 200–300 msec.

VI. The relationship between the sound-evoked response and the modifications in the light-evoked response due to the addition of sound

The question arises concerning the relationship between the sound-evoked response and the type of modification in the light-evoked response by the light-sound combination. The neurons with the specific response to sound were compared with other types of neurons in regard to the modification of the light-evoked response during the presentation of light-sound combinations.

There was no difference between the neurons specifically responsive to sound and the other types of neurons with respect to modifications in
the light-evoked responses due to the addition of sound. Thus, 41% of the sound-specific neurons and 37% of the remaining neurons modified their responses to flashes during presentation of the light-sound combinations. The distribution of sound-specifically responsive neurons, sound-unresponsive neurons and sound nonspecifically responsive neurons were very similar and independent from the response type to sound (Fig. 13).

Fig. 13. The distribution of the sound specific responsiveness (A), nonspecifically responsive to sound (B), and neurons nonresponsive to sound (C), depending upon the time intervals when the responses to light-sound combinations demonstrated maximal depression or activation with respect to the light-evoked responses. Abscissa, time in msec; ordinate the number of neurons demonstrating maximal or minimal spike discharge in the given interval. The upper panel shows activation, while the lower indicates depression. The histograms are independent of the neuronal response types to sound.

There was no difference between the sound-responsive cells and sound-unresponsive cells with respect to the sound induced modifications of the light-evoked responses. The main conclusion is that the effect of the sound on the light-evoked response in light-sound combination was independent from the response type to sound only. The response pattern evoked by the light-sound combination cannot be deduced from the algebraic summation of the responses to light and sound given separately.

**VII. Heteromodal recovery cycle**

The generation of the specific, nonhabituating response pattern to the light-sound combination differed from both the responses evoked by light and sound given separately, as well as the calculated algebraic sum of their discharges. The interaction in auditory and visual pathways might be studied by means of the recovery cycle in a manner similar to the recovery cycle for the visual system. The homomodal recovery cycle characterized the time interval required for the re-establishment of the initial response pattern after stimulation of the same modality. The specific measure of the homomodal recovery cycle consisted of the critical
Fig. 14. A: PST-histograms for sound, light and light-sound combination with different delays (unit 331). The left column from top to bottom indicates background activity (a), sound alone (b), and sound-light combinations with different delays: 0(c), 15(d), 30(e), 50(f), 75(g), 100(h), 200(i), 400(k), 680(l) msec. The right column from top to bottom shows background activity (a'), light alone (b'), and light-sound combinations with different delays: 0(c'), 15(d'), 30(e'), 50(f'), 75(g'), 100(h'), 200(i'), 400(k'), 680(l') msec. Abscissa, response time in msec after onset of flash; ordinate: the number of spikes per bin. The bin width is 20 msec. Ten trials contributed to each average response. The neuron with low background firing generated the i-d-i response pattern to the flash and was unresponsive to sound. The initial short latency spike discharge for the flash was enhanced and sharpened if the sound preceded the light by 50–75 msec (f, g). However, this initial spike discharge was
interval between the two stimuli when the response to the second stimu-
lus was completely masked by the preceding stimulation. The complete
elimination of the response to the second stimulus might be due to the
fact that the second stimulus was acting on the same population of neu-
rons as the first stimulus. The homomodal recovery cycle characterized
the recovery of responsiveness of those neurons involved in action by
the preceding stimulation. Similar reasoning may be applied to the light-
sound interaction. That is, combinations of the light and sound presented
with different delays against each other might be used to evaluate the
heteromodal recovery cycle. The study of the light-evoked responses,
preceded or followed by sound with different delays, might demonstrate
several types of interactions:
1. The sound does not affect the light-evoked response and the light
does not affect the sound-evoked response, if the latter is present.

2. The sound that evokes no response modifies the light-evoked re-
sponse of the neuron. However, this possibility is precluded due to the
common pathways.

3. The sound and light, which evoke separately different responses,
modify their responses by a combination. If the total response is the
sum of the separate responses, one may assert that two independent
inputs are summated on the same neuron.

4. The response to the light-sound combination differs totally from
the sum of the responses and from responses to light and sound.

reduced if the sound preceded the light by 400–680 msec (k, l). The secondary
multipeak spike discharge evoked by the flash was completely depressed when the
sound preceded light by 0–30 msec (c, d, e) and partially eliminated if the sound
preceded the light by 100–400 msec (h, i, k). The initial component of the light-
evoked response was influenced by sound even following the light with 15–75 msec
delays (d'–g'), indicating a very short latency effect from the sound upon the visual
pathway. The depression of the secondary light-evoked spike discharge under the
acoustic stimulation was evident in the range of 0–200 msec delays. The sound
evoking no direct response in the neuron of the visual cortex resulted in the
powerful modifications of the light-evoked spike discharge.

B: A graph illustrating the modification of the light-evoked response due to the
presentation of sound, preceding or following the flash. Abscissa, intervals between
the sound and light (on the left) and between the light and sound (on the right)
in msec; ordinate, the average number of spikes generated by 10 presentation of
the light-sound and sound-light combinations for 0–100 (crosses), 0–200 (dots), 0–400
(open circles) and 0–1,000 msec (triangles) epochs of analysis. The summation of the
generated spikes for 100 msec indicated the activation of the initial component of
the light-evoked spike discharge, when the sound preceded the light. The epoch
of the analysis for 0–1,000 msec showed the depression of the late components of
the light-evoked spike discharge if the light was preceded or followed by the sound.
Let us consider the heteromodal recovery cycle (Fig. 14A) when the sound given alone (b) produced a slightly diffused reduction of firing, and light presented alone (b') resulted in the i-d-i response pattern. The initial and late components of the light-evoked response were changed differently under simultaneous presentation of light and sound. More specifically, the initial component of the light-evoked response was intensified. Similarly, the primary discharge was also intensified if the sound preceded the light by less than 75 msec (d-g) or followed the light by 15 msec (c', d'). Conversely, secondary spike discharge of the light-evoked response was depressed by the addition of sound, and this depression was very similar to the phenomena related to the homomodal recovery cycle. The recovery of the secondary light-evoked discharge occurred with the increase of the delay between the light and sound up to 400-680 msec (k', l'). The duration of the influence of sound on the light-evoked response might be deduced from this experiment when sound is given prior to light. The depression of the secondary light-evoked discharge was present up to 680 msec (l).

The calculation of the total number of spikes during 0–100 msec and 0–400 msec after light stimulation, under different time delays of the acoustic stimulation, made it possible to construct the graph representing the recovery cycle for the light-sound interaction (Fig. 14B). The heteromodal recovery cycle was studied in 44 neurons. Twenty two cells were not affected by sound at any light-sound and sound-light intervals, while 21 cells demonstrated the phasic modification of the light-evoked response. In one cell there was a tonic effect of the sound on the light-evoked response.

For representing the results obtained on the total population of cells modifying the responses to light under acoustic stimulation, the number of spikes was calculated during 0–100, 0–400, 0–1,000 msec by different time delays of the light-sound and sound-light sequence. The percentage of cells modifying their responses during a given interval was evaluated as a function of light-sound and sound-light delays (Fig. 15). The majority of the cells decreased or increased their responses during 0–150 msec between sound and light presentations under the light-sound combination while the majority of the units modified their responses during 0–100 msec period. For the majority of the cells, response modification with an increase of firing was present in the sound-light sequence: For 0–100 msec interval at 30 msec delay, for 0–400 at 15 msec delay, and for 0–1,000 msec at 50 msec delay. In the light-sound sequence, a similar modification was present in a majority of cells for 0–100 msec at 0 msec delay, for 0–400 msec at 15 msec delay and for 0–1,000 msec at 100 msec delay.
The modification, with reduction of firing in sound-light sequence, occurred in a majority of cells for 0–100 msec at 50 msec delay, for 0–400 msec at 50 msec delay and for 0–1,000 msec at 50 msec delay. In the light-sound sequence such modification was seen in the majority of cells for 0–100 msec at 50 msec delay, for 0–400 msec at 50 msec delay and for 0–1,000 msec at 100 msec delay. Thus, for the majority of the cells, the light-sound interaction occurred primarily if the delays for light and sound were 100 msec in both directions.

DISCUSSION

Types of sound-evoked responses

Two main types of the sound-evoked responses were demonstrated in the neurons of the visual cortex: Short latency, nonhabituating phasic responses and long latency, habituating tonic responses. The short latency (15 msec) spike discharge for sound, which was evoked in the neurons of the visual cortex specifically responsive to flashes, might be characterized as a specific response also. This finding indicates that some auditory signals are transmitted to the visual cortex via specific projections in-
dependent from the non-specific pathway. This assertion, concerning the specific input from the auditory pathway into the visual cortex, is reinforced by the fact that the sound-evoked discharge was characterized by a high stability during repeated sound stimulation. Also, the specific reduction of firing evoked by sound was characterized by similar features. Specifically, the tonic responses to sound might be habituated during repeated presentations of acoustic stimuli, which seems to be dependent on the transmission of impulses via non-specific system. No correlation of the type of the light-evoked response and the type of the sound-evoked response was found.

Responses to light-sound combination coinciding in time

The algebraic summation of the light-evoked response and the sound-evoked response on the same neuron of the visual cortex was present for non-specific sound-evoked response only. However, the main effect of the acoustic stimulation on the light-evoked response might be characterized as the generation of a new response pattern, which cannot be deduced from the shapes of the separate responses to light and sound. In some cases the sound producing no response at all still modified the light-evoked response. The effect of the sound on the light-evoked response may differ with respect to different peaks of the PST histogram. The activation of the initial components might parallel the depression of the late components. The stable depression of the late components of the light-evoked response during acoustic stimulation shows a stability of some non-specific structures. The habituating, non-specific effect is only a subset of a class of non-specific responses.

Non-linear effects by the light-sound interaction

A new response pattern to the light-sound combination cannot be predicted from the responses to each single stimulus, which indicates that the non-linear process occurred in the neuronal nets during such an interaction. The re-arrangement of the synaptic inputs to the neurons of the visual cortex, demonstrated by the modification of the PST histogram, might depend on the change in the population of the interneurons participating in the transmission of impulses within each sensory system. The heteromodal recovery cycle demonstrated that the response to light is different from the response to sound if the order of light-sound presentation is changed, which means that the sound and light signals do not pass the same route. Accordingly, the modifications in the light-evoked pattern by sound stimulation resulted from the collateral interaction.

The light-sound combination might be related to the single neuron of the visual cortex in terms of a specific stimulus that differed from
both the light and acoustic stimuli. It should be noted that sensory integration of visual and auditory signals in humans is also unequal to their algebraic summation (2). Similar results of auditory-visual interaction were demonstrated in behavioral experiments in rats (15), and in human psychological experiments (8).

**Time-dependence of the light-sound interaction**

The interaction resulting in a new effect on the neuron of the visual cortex occurred during short intervals lasting about 100 msec. Specifically, this effect relates to the initial component of the light-evoked response pattern. The late components might be influenced during 600–700 msec, depending on the duration of the response. Both modifications are stable.

**Possible biological significance of the light-sound interaction**

The study of the heteromodal recovery cycle indicates that no common neurons are involved in sensory interactions. The remaining possibility for the interactions is the modification of the neuronal pool responsible for each discharge due to collaterals coming from other modality. The sound influenced the different components of the light-evoked response in a different manner, and this effect of the sound upon the light-evoked response differed from the non-specific, habituating influence.

The non-specific effects might represent the participation of the orienting reflex in the facilitation of the initial stage of visual information processing, and the depression of the events that follow might possibly be related to reflexes which should be eliminated during the orienting activity (23).

Stable specific responses of the neurons of the visual cortex to sounds, which apparently depend on specific auditory input, were found in 28% of cells. 37% of cells have non-specific responses to sounds and 34% of cells were sound-unresponsive. The term “specific response” of the cell of the visual cortex to sound should not be misleading. Morrell (17), Fishman and Michael (3) demonstrated responses to sound in the neurons of the cat’s visual cortex, which were specifically responsive to the position of the sound source in space. The receptive field for sound in such neurons coincided with the receptive field for light stimuli.

A similar interaction was demonstrated in the visual system of the cat with respect to the vestibular and otolithic stimulations (4-6). From this point of view, the specific light-sound interaction in the single neuron of the visual cortex possibly represents the neuronal mechanism for the constancy of space perception where visual, vestibular and auditory
system interact. The elicitation of a specific response pattern to the combination of light and sound, differing from both the response to light and sound separately, was described by Murata et al. (18). Morrell (16) emphasized that 10% of the neurons in the visual cortex of the cat respond to light-sound combinations, with a discharge pattern differing from the discharges to each single component. The specific response pattern to the light-sound combination is another form of the non-visual specificity of the neurons of the visual cortex. The most interesting is a neuron, unresponsive to either light or to sound alone, but generating the spike discharge to light-sound combinations (20, 21). Such neurons as multimodal pattern detectors resembles the gnostic units hypothesized by Kornorski (9).

**SUMMARY**

1. One hundred neurons of the rabbit's visual cortex were studied under light flashes, sound clicks and light-sound combinations. The heteromodal recovery cycle was studied for 42 neurons using lights and sounds given with different delays.

2. Forty nine neurons demonstrated 30% or more change of the firing rate to sound with respect to the background activity. Twenty four neurons were activated and 25 decreased firing from acoustic stimulation. In 37 neurons such non-specific modifications were rapidly habituated.

3. Twenty eight neurons were characterized by specific response patterns to acoustic stimulation, unchanged during repeated presentations. Twenty three cells were excited at 60–70 msec after the onset of sound. Five cells responded with the initial pause of firing. Some neurons were characterized by 10–20 msec latency both for responses with increased and decreased firing. The total number of spikes with respect to the background firing was changed during the 0–1,000 msec interval in 12 neurons only: 4 cells were depressed, while 8 were activated.

4. In 39 neurons the responses to light-sound combinations differed from the light-evoked responses occurring during 0–1,000 msec. In 16 cells the responses to light-sound combinations were decreased, and in 23 cells responding increased. In 15 cells this sound dependent modification was unchanged during long-lasting presentations of the light-sound combination.

5. Twenty two cells demonstrated new shapes of response patterns to light-sound combinations, differing from the responses to single stimuli and from their algebraic summation. In 18 cells, the responses to light-sound combinations were characterized by the re-distribution of the
peaks of PST histogram. In three cells the desynchronization of the light-evoked response pattern occurred by presentation of the light-sound combination. The cells unresponsive to sound still may demonstrate the modification of the light-evoked response pattern by addition of sound.

6. The study of the heteromodal recovery cycle showed that the majority of the cells increased their responses during 0–100 msec and decreased their firing during 200–300 msec. The most effective range of the delays for light-sound and sound-light interactions is 100 msec for both light and sound in either direction.

REFERENCES


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