How Sound Modulates Responses to Light with Different Time Intervals between Stimuli of Different Modalities

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Extracellular recording of 34 neurons in the primary visual cortex of three conscious rabbits was performed in chronic experimental studies addressing the effects of sound (2000 Hz, 70 dB, 40 msec) on the discrimination of weak light intensities (0.3-1 cd/m²). Sound was delivered with different time intervals before and after substitution of one light intensity by another (using a total of 15 intervals in the range -750 to +150 msec). Factor analysis of variance (ANOVA) showed that the time interval between the sound and the light had statistically significant influences on neuron responses. Sound itself provoked no response. Neuron reactions consisted of responses to increases (on responses) and decreases (off responses) in light intensity. The most marked effect of sound was seen in the initial phase of the response (40-100 msec from the moment at which intensities were substituted). For every interval, neurons demonstrated both increases and decreases in reactions to complexes as compared with their responses to light. Wilcoxon's T test was used to assess differences in sets of responses to light and to complexes. For the on responses of the whole group of neurons, the absolute values of responses to sound + light complexes were significantly (p < 0.05) different from responses to light (increased reactions) at intervals of -150, -40, and 0 msec. Two groups of neurons were identified, for which the effects of sound on responses to light were markedly different. Neurons of group 1 (n = 16) showed significant positive influences of light on *on* responses over a wide range of intervals (-150, -40, -20, 0, +20, +100 msec), along with a larger increase in the number of spikes due to sound (by 18-28%) as compared with responses to light. Neurons of group 2 (n = 18) had no significant intervals, i.e., at which reactions to complexes were not significantly different from responses to light. None of the study groups of neurons showed intervals with significant decreases in responses to complexes, though there was a tendency for reactions to complexes to shift towards weakening of responses at intervals of -750 and -80 msec for group 1 (p < 0.07) and at intervals of -500 and +20 sec for group 2 (p < 0.1). On responses were found to be more strongly affected by sound than off responses. The effects of sound on the second phases of responses to light (120-160 msec and later, n = 23) were also studied. Sound had markedly weaker effects on the second phase than the first. For the whole group of neurons with late phases, sound had significant influences on on responses with an interval of 0 msec and on off responses with intervals of +100 and +150 msec. Our study demonstrated similarity in the time intervals for modulation of reactions to light by sound in experiments on animals and psychophysical studies in humans. These data provide for more detailed studies of the integration of light and sound when used simultaneously.

Keywords: primary visual cortex neurons, interaction of light and sound, multisensory integration, asynchrony of the onset of stimulus actions.

The integration of responses to sound and light in the higher parts of the visual system in animals and humans has been demonstrated in many investigations [Polyanskii et al., 2011, 2014; Sokolov, 2003; Molholm et al., 2002; Kauser and Logothetis, 2007; Liu et al., 2007; Jaekl and Harris, 2007; Benjamins et al., 2008; Romei et al., 2009; Fujisaki and Nishida, 2010; Shams and Kim, 2010; Jaekl et al., 2014], the effects sound on responses to light in most cases consisting of increases in reactions. The authors of [Jaekl et al., 2014] take

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the term "increase" in relation to responses to light due to sound in a broad sense: this and the more precise perception of a visual event, with decreases in the latent period of the visual response, decreases in the detection threshold, etc.

In our early experiments [Polyanskii et al., 2011] we demonstrated that sound widened the area of the sensory space representing stimuli with very low light intensities $(0.28-6 \text{ cd/m}^2)$. It was suggested that sound does not simply increase responses to light, but improves the discrimination of low intensities.

Many studies addressing intersensory interactions use synchronous delivery of sound and light, though sound and light are rarely synchronized in nature. Sound can arise before or after light, and the modalities can interact at some interstimulus intervals, fusing into a single percept.

There are a number of classical studies [Benjamins et al., 2008; Fujisaki and Nishida, 2010]. In these studies, subjects were presented with sound and light rhythmically. The subject had to indicate whether the signals delivered belonged to the same modality or were of different modalities. At frequencies of 4 Hz and above, subjects were unable to solve this task, as the modalities combined to form a complex. Thus, the "time window" for active intermodal interaction was 250 msec or less.

Similar results were also obtained from studies reported by other psychophysiologists: less than 250 msec [Lewald et al., 2001; Lewald and Guski, 2004] and less than 200 msec [Molholm et al., 2002; van Wassenhove et al., 2007]. At the same time, some authors have identified different "time windows" for integration of modalities: from -21 to +150 msec [Stone et al., 2001], 50-125 msec [Jaekl-Harris, 2007, 2009], and 370-410 msec [Liu et al., 2007].

In our pervious study [Polyanskii et al., 2014], visual event-related potentials recorded from the primary visual cortex in conscious rabbits were used to investigate the effects of sound on the discrimination of low light intensities $(0.3-1 \text{ cd/m}^2)$. Sound was delivered with different time delays before and after the moment at which stimuli with different light intensities were substituted (15 intervals in the rage -750 to +150 msec). Sound alone produced no response. Sound was found to exert a significant modulatory action on the discrimination of low light intensities in the range of time displacements of the sound relative to the light from -300 to +50 msec. Sound was found to have the strongest effect when the light intensity increased. The P2 phase (120-150 msec from the moment of light stimulus substitution) was the most strongly affected by sound. In most cases, the action of sound on the P2 phase was facilitatory (by 19-36% compared with the response to light).

The aims of the present work were:

1) to identify the intervals separating sound from light at which the sound significantly altered the responses of rabbit primary visual cortex neurons to light of low intensity;

2) to compare data obtained by the event-related potentials method in previous studies [Polyanskii et al., 2014] with data from individual neurons in identical experimental conditions.

Methods

Experiments were performed on three European rabbits (Orictolagus cuniculus) aged 1.5-2 years and weighing 3-3.5 kg. Rabbits initially underwent surgery under Nembutal anesthesia (40 mg/kg) and local anesthesia (2% novocaine solution). After skin incision and clearing of the skull of periosteum, a round hole 5 mm in diameter was made over the primary visual cortex of one of the hemispheres (coordinates AP = -10, L = 7). A mixture of wax and Vaseline was poured into the opening to prevent the brain from pulsating. A Plexiglas shaft was positioned over the hole by attaching it to bone with acrylic glue, to be used in the experiment for fitting a mechanical micromanipulator. The indifferent electrodes were implanted into the nasal bone. The recording electrodes were made of tungsten wire 100 µm in diameter. Electrode tips were sharpened to $1-2 \mu m$ in KNO₂ solution, after which the electrodes were coated in viniflex lacquer. Electrode impedance was $0.5-1 \text{ M}\Omega$.

In experiments, a rabbit was placed on a wooden bench and the head was fixed rigidly with screws. The rabbit could remain in this state for several hours without the eyes making significant movements [Wyrwitz et al., 2000]. The rabbit was then placed in a soundproofed, screened chamber at a distance of 50 cm from the screen of a cathode ray tube monitor.

In the experiments, a micromanipulator was attached to the shaft and neuron activity was recorded from the hemisphere opposite the stimulated eye. Neuron activity was passed to a cathode repeater constructed by Yu. B. Kuznetsov and then to the Pentium-4 computer used for controlling the experiment and processing the results. Two monitors were used, one in the chamber for stimulus presentation and the other for display of neurophysiological data. Inline data processing and analysis of neuron activity were performed in the program Emerald Spike by B. V. Chernyshev. The studies reported here used the same set of stimuli and delivery program as the previous investigation using the event-related potentials method [Polyanskii et al., 2014].

Visual stimulation consisted of substitution of diffuse white stimuli of intensities 0.3 and 1 cd/m² for each other, generating both increases and decreases in intensity. Presentation duration for each light stimulus was 2.5 ± 0.5 sec. Each of the two intensities used was accompanied by delivery of a sound of frequency 2000 Hz, loudness 70 dB, and duration 40 msec. Analysis of neuron responses showed that sound with these parameters produced no responses in the visual cortex. The sound source (a loudspeaker) was located at the same distance as the monitor screen. A total of 15 intervals between the moments at which sound was delivered and light stimuli were substituted (-750, -500, -300,-200, -150, -100, -80, -60, -40, -20, 0, +20, +50, +100,and +150 msec). Series of stimulus presentations with different intervals were delivered in pseudorandom order, with

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30 presentations per series. Controls before each series with sound were obtained by recording responses to substitution of the same light stimuliwithout delivery of sound. The experimental program was completed on 34 neurons.

Raster and poststimulus histograms were plotted by counting the numbers of spikes in the first (40–110 msec) and second (120–160 msec and later) phases of neuron responses to complex light + sound stimuli.

Statistical processing of results (in Statistica, Statsoft; Wilcoxon's T test) compared sets of responses to light before sound + light complexes with response to light + sound complexes for each of the sound delay intervals tested. Sets of spike counts in the corresponding phases of responses to substitution of 0.3 by 1 cd/m² (*on* responses) and 1 by 0.3 cd/m² (*off* responses) and mean values for *on* responses and *off* responses were compared separately. The ratios of the numbers of spikes in responses to complexes to the numbers in the corresponding responses to light were also determined.

The effects of the interval by which sound was displaced relative to light on neuron responses were studied by analysis of variance (ANOVA). Factor effects were taken as significant at p < 0.05.

Experiments were performed in compliance with the views of the Ethics Committee of Lomonosov Moscow State University regarding work with experimental animals and with the humanitarian principles laid out in the directives of the European Community (86/609/EC) and were approved by the Medical Ethics Committee.

Results

At the beginning of the study, multifactorial analysis of variance (ANOVA) was performed on the data obtained. Group variables were the interval factor, i.e., the time interval between the sound and light stimuli. The analysis showed that the interval between the sound and light stimuli had significant influences on neuron responses.

Figure 1 shows an *on* response from neuron No. 30 in the rabbit visual cortex to substitution of weak light intensities without sound (*B*) and complexed with sound (*C*). The sound was delivered with different time shifts relative to the moment at which the lights were substituted. Sound alone with these parameters (2000 Hz, 70 dB, 40 msec) did not induce any response (*A*). Figure 1 shows that with an interval of -150 msec, sound induced facilitation of the response in the first phase of the neuron response (40–100 msec)as compared with the response to light (+60%). The same was seen at -100 msec (+27%), -40 msec (+10%), +20 msec (+17%), and +100 msec (+18%).

Other neurons showed facilitation of activity on addition of sound to light with other intervals too.

Overall data on the effects of sound on the *on* responses of the whole group of neurons studied (n = 34) are shown in Fig. 2. Data for the whole group of cells are shown with black columns. "Distant" intervals (from -750 to -300 msec) produced virtually no enhancement of responses to light.

On processing of absolute data, these intervals did not sow significant influences of sound (Wilcoxon, p > 0.05). Further along the scale of intervals, sound had increasing positive effects, reaching values of 1.07, 1.15, and 1.10 at intervals of -150, -40, and 0 msec, respectively. These intervals were significant (p < 0.05) on assessment of the effects of sound on the light response.

Analysis of the effects of the interval between the sound and light stimuli suggested that in the overall set of neurons, the delay interval of the sound from the light could be to a significant extent evened out. We then sought to identify that group of neurons where this factor was stronger and occurred with a larger number of significant intervals.

Further analysis of the data identified two groups of neurons. The criterion for dividing them into groups was the number of intervals where increases in responses to complex stimuli were by more than 10% compared with the response to light. The number of such neurons for neurons of group 1 was 8 or more. The remaining neurons belonged to group 2. The mean increases in the groups were significantly different (Wilcoxon, p < 0.05).

Figure 2 clearly shows that neurons of group 1 (white columns) showed the largest increases in *on* responses to light on addition of sound (-150 msec: 18%; -40 msec: 28%; -20 msec: 10%; 0 msec: 21%; +20 msec: 15%; +100 msec: 20%). There were more significant intervals than in the overall group (Wilcoxon, p < 0.05), i.e., -150, -40, -20, 0, +20, and +100 msec.

At the same time, group 2 (gray columns) showed markedly less increase in *on* responses to light on addition of sound (compared with both group 1 and the overall group of neurons). There were no significant intervals in group 2, i.e., responses to the complex were not significantly different from responses to light. For all groups of neurons studied, negative significant intervals were not seen, though there was a tendency for responses to complexes to shift towards weakening of responses at intervals of -750 and -80 msec for group 1 (p < 0.07) and intervals of -500 and +20 msec for group 2 (p < 0.1). It should also be noted that starting from the interval -200 msec, neuron responses on addition of sound were dominated by facilitation. This applied particularly to group 1 and the overall set.

Thus, we divided neuron responses on the basis of modulation of *on* responses to light by sound. The next step was to analyze *off* responses. Figure 3 shows increases in *off* responses to light at different sound delay intervals in the overall group of neurons and also in groups 1 and 2. In the overall group (black columns), only three intervals were significant (p < 0.05): -40, +20, and +150 msec. These intervals also showed the greatest increases in responses on addition of sound (7, 8, and 8%, respectively). In group 1 (white columns), significant intervals (p < 0.05) were -150, -40, and +50 msec. It was of note that increases in responses to the complex in *off* responses were smaller than those in *on* reactions. The *on* group was significantly different from

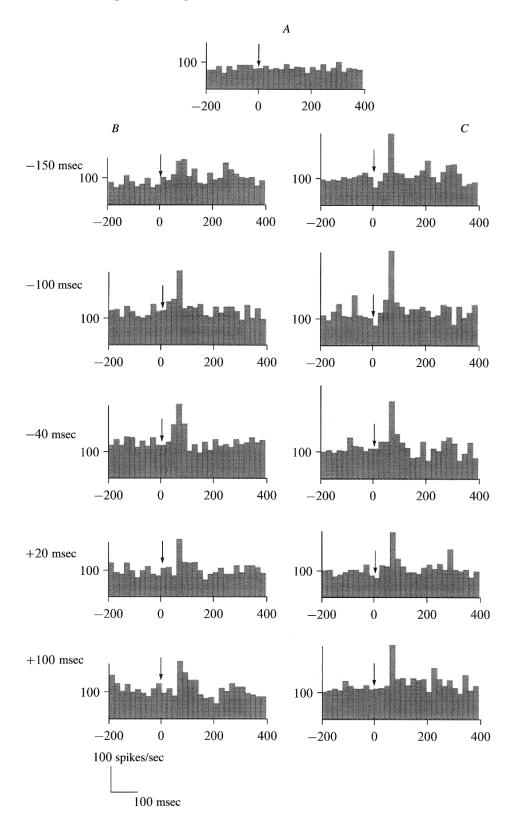


Fig. 1. Poststimulus histograms of *on* responses of neuron No. 30. *A*) Responses to presentation of sound; *B*) responses to presentation of light; *C*) responses to presentation of sound + light complexes. Intervals between the beginning of exposure to sound and the moment of light substitution are shown at left, msec. Horizontal axes show time, msec. Vertical axes show neuron discharge frequency, spikes/sec. the arrow shows the moment of light stimulus substitution. Bin width = 20 msec.

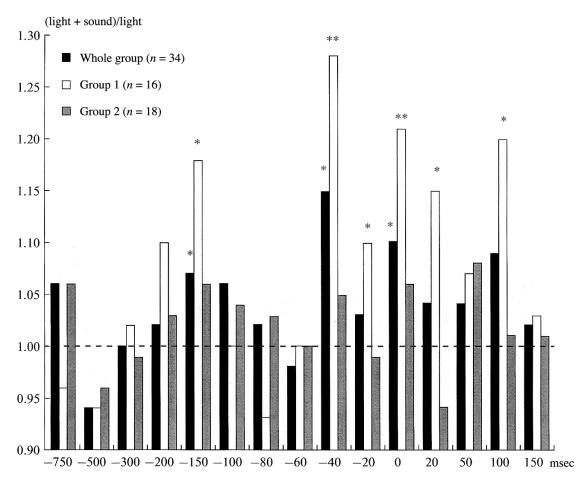


Fig. 2. Ratios of *on* responses to light + sound complexes to *on* responses to light for the whole group of neurons (black columns), group 1 neurons (white columns), and group 2 neurons (gray columns). Numbers on the horizontal axis show intervals between the onset of sound action and the moment of light substitution, msec; the vertical axis shows the ratios of group mean responses to light + sound complexes to responses to light. *Significant increase, p < 0.05; **significant increase, p < 0.001.

the *off* group in terms of the extent of facilitation of responses by sound (p < 0.04).

We then analyzed the mean responses of neurons ((on + off)/2) to light on addition of sound for the same groups of neurons (Fig. 4). Here, although the extent of increases in responses on addition of sound was relatively small, significant intervals were detected. In the overall group, these intervals were -150, -40, +20, +100, and +150 msec. Intervals in group 1 were -150, -40, 0, +20, and +100 msec. The only intervals in group 2 were +50 and +150 msec.

It was characteristic that analysis of mean values for *on* and *off* responses revealed not only "universal" intervals, of -150, -40, and 0 msec, but also the later intervals of +20 and +150 msec.

Finally, the actions of sound on the second phases of the responses of the test neurons (120–160 msec and more from the moment of light stimulus substitution) were analyzed. Data for *on* reactions show that increases in responses to light on addition of sound in the initial phase were significantly greater than those in the later phases (p < 0.05).

at the same time, the later phases of *on* responses also had the significant interval 0 msec. The *off* responses of the first and second phases were not significantly different for the overall group. Sound had a significant effect on the second phase at intervals of +100 and +150 msec.

Comparison of the first and second phases of averaged neuron responses ((on + off)/2) did not identify any statistically significant differences between them in terms of increases in responses to light in response to sound. At the same time, the early phase of the response showed five significant intervals for the sound delay: -150, -40, +20, +100, and +150 msec, while no intervals were seen in the group of late response phases.

Thus, the second phase of the response to the complex had fewer significant intervals than the first phase, and these were among the longer intervals: 0, +100, and +150 msec.

Discussion

Thus, assessment of the results obtained in this study by analysis of variance (ANOVA) and processing of the data using the nonparametric Wilcoxon test showed that the

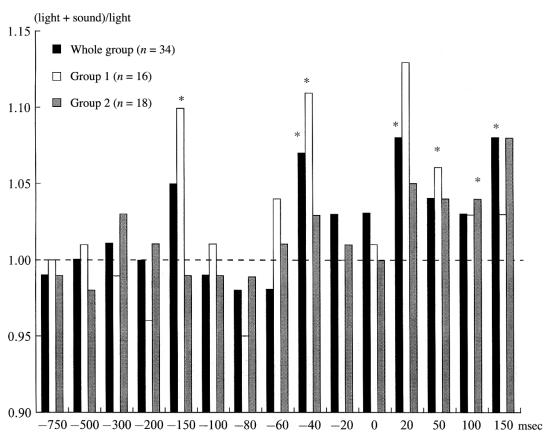


Fig. 3. Ratios of off responses to light + sound complexes to off responses to light. For further details see caption to Fig. 2.

time interval between the sound and the light had significant influences on the interaction and integration of these modalities in rabbit visual cortex neurons.

In our study, the effects of sound on light responses using different time shifts between the sound and the light were mainly positive, strengthening the response. This is consistent with data from studies of intersensory interactions and the integration of modalities [Polyanskii et al., 2011, 2014; Molholm et al., 2002; Kauser and Logothetis, 2007; Ziu et al., 2007; Benjamins et al., 2008; Jaekl and Harris, 2007; Shams and Kim, 2010; Fujisaki and Nishida, 2010; Jaekl et al., 2014]. Increases were seen mainly at low light intensities, as used in the present studies.

We will now discuss the intervals themselves and the time window in which light and sound interact, as well as complexes perceived as single percepts. It should be noted that data of this type have been obtained almost exclusively in psychophysical experiments. Rhythmic sound and light stimuli with different frequencies were used and subjects had to discriminate the modalities. The time window was assessed as 250 msec [Benjamins et al., 2008; Fujisaki and Nishida, 2010]. Similar results have also been reported by other authors [Lewald et al., 2001; Lewald and Guski, 2004; van Wassenhove et al., 2007].

Overall, our data are similar to the results noted above from psychophysical experiments and to our previous results obtained by recording responses to sound and light using visual event-related potentials [Polyanskii et al., 2014].

Our experiments showed (Figs. 1–4) that the significant intervals between the sound and the light at which sound produced marked increases in responses to light were in the range from –150 to +150 msec. These values are close to the results of a recent study in humans [Senkowski et al., 2013]. Experiments using an audiovisual task evaluated the effects of light on the γ rhythm (30–80 Hz) on addition of sound. Intersensory interactions were seen at the greatest level of synchronicity of the light and sound stimuli. In addition, the interaction had an effect in the occipital areas when sound led the light by 75–125 msec. Data on the significant influences of the effect of sound were obtained in a study addressing the early phase of the neuronal response to light, which is consistent with results from studies addressing intermodal interactions of sound and light [Jaekl et al., 2014].

The number of significant intervals at which sound exerted an effect was greater in *on* responses to light, when the stimulus intensity of 0.3 cd/m² was substituted with one of 1 cd/m² (Figs. 1, 2), though this applied less to the whole group of neurons (n = 34), for which intervals of -150, -40,

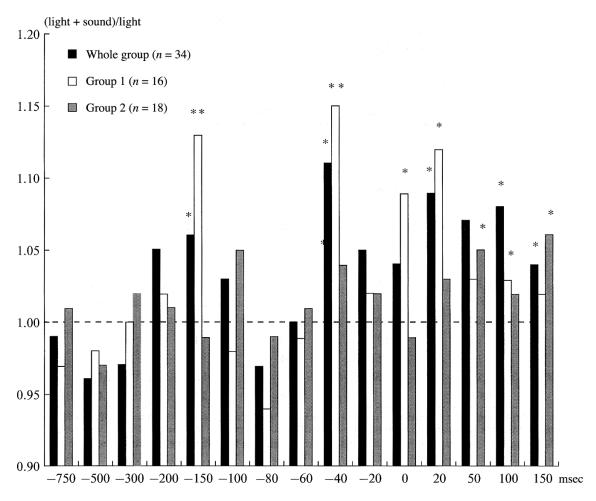


Fig. 4. Ratios of averaged (on + off)/2 responses to light + sound complexes to averaged responses to light. For further details see caption to Fig. 2.

Interval, msec -	on responses		off responses		(on + off)/2	
	Phase 1	Phase 2	Phase 1	Phase 2	Phase 1	Phase 2
-750	1	1	0.99	0.93	0.99	0.95
500	0.94	0.98	1	0.96	0.96	1
-300	1	1	1.01	1.04	0.97	1.01
-200	1.1	1.06	1	1.04	1.05	1.07
-150	1.07	1	1.05	1.06	1.05	1.01
-100	1.06	0.98	0.99	0.97	1.03	0.94
-80	1.02	1	0.98	1.03	0.97	1.06
-60	0.98	1.01	0.98	1.09	1	1.02
-40	1.15	1.06	1.07	1.15	1.12	1.12
-20	1.03	1	1.02	1.06	1.05	1.03
0	1.08	1.15	1.03	1.07	1.04	1.12
20	1.13	1.01	1.08	1.05	1.09	1.01
50	1.1	0.96	1.04	1.05	1.07	1.01
100	1.1	1.05	1.03	1.23	1.08	1.07
150	1.02	1	1.08	1.09	1.04	1.08

TABLE 1. Ratios of Mean Values for the First (n = 34) and Second (n = 19) Phases of Neuron Responses for *on* Responses, *off* Responses, and Average *on* and *off* Responses

Notes. Values are mean ratios of discharge frequencies in responses to complex stimuli to discharge frequencies in responses to light. Numbers in bold are statistically significant increases in responses to complex stimuli compared with responses to light.

and 0 msec were significant, than to group 1 (16 cells), where there were six significant intervals: -150, -40, -20, 0, +20, and +100 msec. This group included neurons with the greatest increases in responses on addition of sound. Group 2, consisting of 18 cells (Fig. 2), had no significant intervals. These groups were statistically significantly different (Wilcoxon, p < 0.04). It can be suggested that neurons of group 1 play a greater role in the processes of intersensory integration, while group 2 neurons have other functions.

Analyzing the work of authors studying intersensory interactions led us to the conclusion that most evaluated the effects of sound only on activation by light (*on* responses). Our studies also assessed the effects of sound on *off* responses when the intensity of the visual stimulus decreased (from 1 to 0.3 cd/m^2). Here, the influence of sound was significantly weaker than in the case of *on* responses (Figs. 2 and 3) and significant intervals were in the later part of the range (from -40 to +150 msec).

The effects of sound on *on* and *off* responses to light for the whole group of cells (n = 34) were significantly different (Wilcoxon, p < 0.05). It may be that *off* responses "reveal" the effects of sound delivered after the light.

We also analyzed the effects of sound on averaged overall responses of cells ((on + off/2) to light. The data are shown in Fig. 4. Here, although the extent of the increase in the reaction to light was relatively small, there were quite a few significant intervals. For the overall group (n = 34), these intervals were -150, -40, +20, +100, and +150 msec. For group 1 the intervals were -150, -40, 0, +20, and +100 msec. For group 2 the only intervals were +50 and +150 msec.

We note that for almost all types of response (*on*, *off*, on + off)/2), three significant intervals were clearly apparent: -150, -40, and 0 msec. These may be the "reference" intervals for the interaction of modalities.

Our experiments also compared the sizes of intervals for the first and second phases of neuron responses to light (Table 1). There were fewer significant intervals for the second phase and these were displaced towards the end of the scale of intervals (for *on* responses: 0 msec; for *off* responses: +100 and +150 msec; for (*on* + *off*)/2 there were no such intervals). This leads to the conclusion that the interaction of sound and light in time was reflected in the late phases (120 msec and more from the beginning of the light stimulus), although only to a small extent. This is probably due to the operation of an information feedback loop from the primary visual cortex to higher cortical centers and back, the second phases reflecting either complete synchronicity of the sound and light in time or delivery of the sound after the light.

Finally, the results of our present studies (on cortical neurons) should be compared with our previous results (recording of visual event-related potentials).

The time window for the interaction of sound and light generally coincided (ERP data: from -300 to +50 msec; neuron responses: from -150 to +150 msec). Event-related potentials reflect the total synaptic activity of neurons. The

effects of sound on light in the ERP phases are therefore apparent with an interval of -300 msec, when synaptic activity from sound started to appear. Neurons respond when some certain threshold of synaptic activity is reached, leading to a decrease in the time window as compared with that seen in the ERP data.

We will now discuss which part of the response to light is influenced by sound. As noted previously, sound exerts its greatest effect on the early part of the response to light (40–100 msec).

These data are supported by other investigations of intersensory interaction. In the case of event-related potentials, reflecting synaptic activity, there is a shift in the peak of the response, by 40–80 msec.

Overall, the present study of individual neurons showed that active intersensory interaction between sound and light occurs in the rabbit visual cortex over the range of intervals from -150 to +150 msec. These experiments identified similarity in the time intervals for the sound modulation of responses to light in animal experiments and psychophysical experiments. These data provide a more detailed assessment of the integration of different modalities on perception.

Conclusions

1. Studies of the activity of individual neurons in the rabbit visual cortex showed that sound tones at a frequency of 2000 Hz, loudness 70 dB, and duration 40 msec, which alone did not evoke any response in the cortex, significantly increased the responses of neurons to substitution of two weak intensities for each other at intervals between the beginning of the sound and the moment at which light intensities were substituted over the range -150 to +150 msec.

2. the effects of sound on the light response were found to be most marked as an increase in the early phase of the neuron response (40–100 msec from the moment of light stimulus substitution).

3. The largest number of time intervals between the sound and the light at which significant increases in neuron responses occurred was seen for *on* responses to light. Significant intervals for the whole group of cells (n = 34) were -150, 40, and 0 msec.

4. The set of cells studied here could be divided into two groups. Significant intervals for group 1 (n = 16) were -150, -40, 0, +20, +50, and +100 msec. There were no significant intervals for group 2 (n = 18). Group 2 showed significantly smaller increases in responses to light on addition of sound and in terms of these parameters was significantly different from group 1. It can be suggested that the two groups of neuron perform different functions in intermodal interactions.

5. The effects of sound on *off* responses to light were weaker than those on *on* responses, while significant sound delay intervals were close to and after the moment of light stimulus substitution: -40, +20, +50, +100, and +150 msec.

6. It follows from our experimental results that sound also affected the second phase of neuron responses. Effects

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were significantly smaller in size than for the initial phase and mainly affected the later delay intervals from the light stimulus: 0, +100, and +150 msec.

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REFERENCES

- Polyanskii, V. V., Alymkulov, D. E., Evtikhin, D. V., and Chernyshev, B. V., "Sound improves the discrimination of weak light intensities in the rabbit visual cortex," *Zh. Vyssh. Nerv. Deyat.*, 61, No. 4, 1–11 (2011).
- Polyanskii, V. V., Alymkulov, D. E., Evtikhin, D. V., and Chernyshev, B. V., "Sound affect the discrimination of weak light intensities in the rabbit visual cortex," *Zh. Vyssh. Nerv. Deyat.*, 64, No. 5, 531–541 (2014).
- Sokolov, E. N., *Perception and the reflex. A New View*, Psychology Teaching Series, Moscow (2003).
- Benjamins, J. S., van der Smagt, M. J., and Verstraten, F. A., "Matching auditory and visual signals: is sensory modality just another feature?" *Perception*, 37, No. 6, 848–858 (2008).
- Fujisaki, W. and Nishida, S., "A common perceptual temporal limit of binding synchronous inputs across different sensory attributes and modalities," *Proc Biol. Sci.*, 277, No. 1692, 2281–2290 (2010).
- Jaekl, P. M. and Harris, L. R., "Auditory-visual temporal integration measured by shifts in perceived temporal location," *Neurosci. Lett.*, 417, No. 3, 219–224 (2007).
- Jaekl, P. M. and Harris, L. P., "Sounds can affect visual perception mediated primarily by the parvocellular pathway," *Vis. Neurosci.*, 26, No. 5–6, 477–486 (2009).
- Jaekl, P., Perez-Bellido, A., and Soto-Faraco, S., "On the "visual" in "audiovisual integration": a hypothesis concerning visual pathways," *Exp. Brain Res.*, 232, No. 60, 1631–1638 (2014).

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- Kauser, C. and Logothetis N. K., "Do early sensory cortices integrate cross-modal information?" *Brain Struct. Funct.*, **212**, No. 2, 121–132 (2007).
- Lewald, J., Ehrenstein, W. H., and Guski, R., "Spatio-temporal constraints for auditory-visual integration," *Behav. Brain Res.*, **121**, No. 1–2, 69–79 (2001).
- Lewald, J. and Guski, R., "Auditory-visual temporal integration as a function of distance: no compensation for sound-transmission time in human perception," *Neurosci. Lett.*, **357**, No. 2, 119–122 (2004).
- Liu, Q., Qiu, J., Chen, A., et al., "The effect of visual reliability on auditory-visual integration: an event-related potential study," *Neuroreport*, 18, No. 17, 1861–1865 (2007).
- Molholm, S., Ritter, W., Murray, M. M., et al., "Multisensory auditory-visual interactions during early sensory processing in humans: a high-density electric mapping study," *Brain Res. Cogn. Brain Res.*, 14, No. 1, 115–128 (2002).
- Romei, V., Murray, M. M., Cappe, C., and Thut, G., "Preperceptual and stimulus-selective enhancement of low-level human visual cortex excitability by sound," *Curr. Biol.*, **19**, No. 21, 1799–1805 (2009).
- Senkowski, D., Talsma, D., Grigutsch, M., et al., "Good times for multisensory integration: Effects of the precision of temporal synchrony as revealed by gamma-band oscillations," *Neuropsychologia*, 45, No. 3, 561–571 (2007).
- Shams, L. and Kim, R., "Crossmodal influences on visual perception," *Phys. Life Rev.*, 7, No. 3, 269–284 (2010).
- Stone, J. V., Hunkin, N. M., Porrill, J., et al., "When is now? Perception of simultaneity," *Proc. Biol. Sci.*, 268, No. 1462, 31–38 (2001).
- van Wassenhove, V, Grant, K. W., and Poeppel, D., "Temporal window of integration in auditory-visual speech perception," *Neuropsychologia*, 45, No. 3, 598–607 (2007).
- Wyrwitz, A. M., Chen, N., Li, L., et al., "fMRI of visual system activation in conscious rabbit," *Magn. Reson. Med.*, 44, No. 3, 474–478 (2000).