Sound Affects the Discrimination of Low Light Intensities in the Rabbit Visual Cortex

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Visual evoked potentials (VEP) recorded from the visual cortex of conscious rabbits in chronic experiments were used to study the effects of sound (2000 Hz, 70 dB, 40 msec) on the discrimination of low light intensities ($0.3–1$ cd/m^2). Sounds were delivered with different time delays before and after replacement of one light intensity by another (range -750 to $+150$ msec). The sound itself did not induce any response. A total of 42 experiments on three rabbits showed that sound had a significant modulatory effect on the discrimination of low light intensities in the range of sound-light intervals from -300 to $+50$ msec. Sound had the strongest effect going from high light intensities (1 cd/m^2) to low (0.3 cd/m^2). Analysis of the phases of visual evoked potentials showed that sound had a significant influence on the light response at intervals of -300, -100, -60, -40, -20, 0, $+20$, and $+50$ msec. During the P2 phase (120–150 msec from the moment of light stimulus substitution), sound had its greatest influence on substitution of low light intensities both in terms of the number of time intervals (seven) at which the effect of sound was significant ($p < 0.05$) and in terms of the extent of the effect of sound on the light response. The effects of sound in the P2 phase were almost exclusively facilitatory – by 19–36% compared with responses to light, while the N1 (80–110 msec) and N2 (180–250 msec) phases included 2–3 intervals with significant sound effects, the extent of facilitation of the response to light varying over the range 8–12%. It is suggested that the action of sound on the light response over time is mediated in the visual cortex with some delay due to passage of the sound signal through the auditory cortex, parietal cortex, and superior colliculi.

Keywords: visual evoked potentials, rabbit, primary visual cortex, intermodal interaction, multisensory integration, modulatory effect of sound on light responses over time.

The modulatory action of sound on the reactions of individual primary visual cortex cells in animals and the overall responses of neurons (evoked potentials) have been described in a significant number of reports [Polyanskii et al., 2011; Benjamins et al., 2008; Fujisaki and Nishida, 2010; Jaekl and Harris, 2007; Kauser and Logothetis, 2007; Liu et al., 2007; Molholm et al., 2002; Shams and Kim, 2010].

Sound and visual stimuli have been demonstrated to interact and undergo integration in humans. Thus, subjects studied by Romei et al. [2009] experienced two flashes when presented with a single flash accompanied by two clicks.

In our earlier reports [Polyanskii et al., 2011; Sokolov et al., 2003], we investigated the effects of sounds not simply on light responses, but also on the substitution of lights of different intensities. In other words, the effects of sound on the ability of the visual cortex to discriminate intensities was studied. Our results and those of other investigators showed that sound mainly enhances light responses. This increase is seen mainly at low light stimulus intensities. The main effect of modulation occurs in the early interval (80–200 msec from the start of stimulation) of the response to light [Kauser and Logothetis, 2007; Liu et al., 2007; Shams and Kim, 2010]. Our experiments [Polyanskii et al., 2011] provide evidence that exposure to sound significantly increases the spatial distance representing stimuli of the lowest light

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intensities (0.28–6 cd/m^2). These results suggest that sound, used along with light, improves the discrimination of low light intensities.

All the studies cited above demonstrated the effects of sound on the light response using synchronous stimulation with light and sound. At the same time, sounds in nature are generally not coincident with the actions of light – they are heard before the light or after the light. How does sound modulate the response to light in this situation?

Almost paradoxically, studies of this type have been performed almost exclusively in humans in noninvasive psychophysiological experiments; experimental results have been based on the subjective responses of the participants.

In the studies reported by Benjamins et al. [2008] and Fujisaki [2010], sound and light stimuli were presented rhythmically with different time delays. Subjects reported where they located the signal (for example, a light) – within one modality or between different modalities. Clear responses were obtained only at frequencies of lower than 4 Hz. At frequencies of 4 Hz above, subjects were unable to comply with the instruction, as the modalities evidently fused to form a single percept. Thus, the "time window" for active interaction of light and sound was 250 msec.

Similar results were obtained in other studies: 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]. Some authors have presented data giving a different view of the "time windows" for the interaction and integration of modalities: from –21 to +150 msec [Stone et al., 2001], 50–125 msec [Jaekl and Harris, 2007 and 2009], and, finally, 370–410 msec (Liu et al., 2007].

Thus, the results of different experiments clearly differ from each other. This is probably linked with the experimental methodologies and the properties of the stimuli used.

The aim of the present work was to identify the time difference between a sound and a light (before and after light) at which the sound significantly alters the response to the light for lights of low intensities. In other words, to identify the "time window" in which sound has significant influences on responses to light.

This report presents analysis of objective measures of brain operation – evoked potentials in the visual cortex in rabbits whose amplitudes are compared for responses to low-intensity light stimuli and complex sound-and-light stimuli in which the sound was presented with different intervals before and after substitution of one light intensity for another.

Methods

Experiments were performed on three European rabbits (*Oryctolagus cuniculus*) aged 2–3 years and weighing 3–3.5 kg. Rabbits underwent preliminary surgery under Nembutal (40 mg/kg) anesthesia along with local anesthesia (2% novocaine). After skin incision and clearing of the skull of periosteum, 3–4 openings were drilled over each hemisphere (coordinates AP = –10, L = 7). Openings were drilled through the bone to within 0.2–0.4 mm of the meninges.

Steel electrodes of diameter 1 mm were inserted into the holes. The indifferent electrodes were attached to the nasal bone. Electrodes were attached to the skull surface with acrylic glue.

Before experiments, rabbits were placed on a wooden bench with the head firmly fixed with bandages. In this state, rabbits can remain calm in the experiment for several hours, the eyes not making any significant movements [Wyrwitz et al., 2000]. In the experiments, the rabbits were in a screened, sound-proofed chamber 45 cm from a CRT monitor screen. Visual evoked potentials were recorded using a monopolar method from the hemisphere opposite to the stimulated eye.

Potentials were passed to an amplifier constructed by Yu. B. Kuznetsov and then via an analog-to-digital converter (ADC) to a Pentium 4 computer controlled by the experimenter and used to processing the experimental data. Two monitors were used, one located in the chamber with the rabbit and used for stimulus presentation and the other used for display neurophysiological data from the ADC. Brain macroactivity was recorded and analyzed using the Emerald Spike program by B. V. Chernyshev for online processing of incoming data. Visual stimuli consisted of instantaneous substitutions of diffuse light stimuli of intensity 0.3 and 1 cd/m^2 for each other, with both increases and decreases in intensity. The light stimulus presentation scheme was: 0.3 cd/m^2 → 1 cd/m^2 → 0.3 cd/m^2 → 1 cd/m^2 → …. A total of 30 presentations at each intensity were delivered using this scheme. The duration of presentation of each light stimulus was 2.5 ± 0.5 sec. Each of the two intensities used was accompanied by a sound of frequency 2000 Hz, loudness 70 dB, and duration 40 msec. Sounds with these parameters were shown by analysis of VEP not to produce any response in the visual cortex. The sound source (a loudspeaker) was positioned at the same distance as the monitor screen. Fifteen variants of the difference between the moment of sound stimulus delivery relative to the moment of light stimulus substitution were used. Ten variants in which the sound preceded the light (–750, –500, –300, –200, –150, –100, –80, –60, –40, and –20 msec) were used, along with synchronous presentation of the sound and light (0 msec), and four variants in which the sound was delayed with respect to the light (+20, +50, +100, and +150 msec). Stimuli with different delays were presented in pseudorandom order, each stimulus 30 times. For controls, each complex stimulus presentation was preceded by recording of responses to light stimuli, as the functional state of the rabbit could change during the experiment.

Each rabbit was used in 20–25 experiments. After removal of artifacts, the amplitudes of the different phases of recorded EP were determined: N1 (80–110 msec), P2 (120–150 msec), and N2 (180–250 msec) in response to "pure" light and light in complex with a sound with different sound anticipation and delay intervals. The P1 phase was not considered because our previous study [1] did not identify any
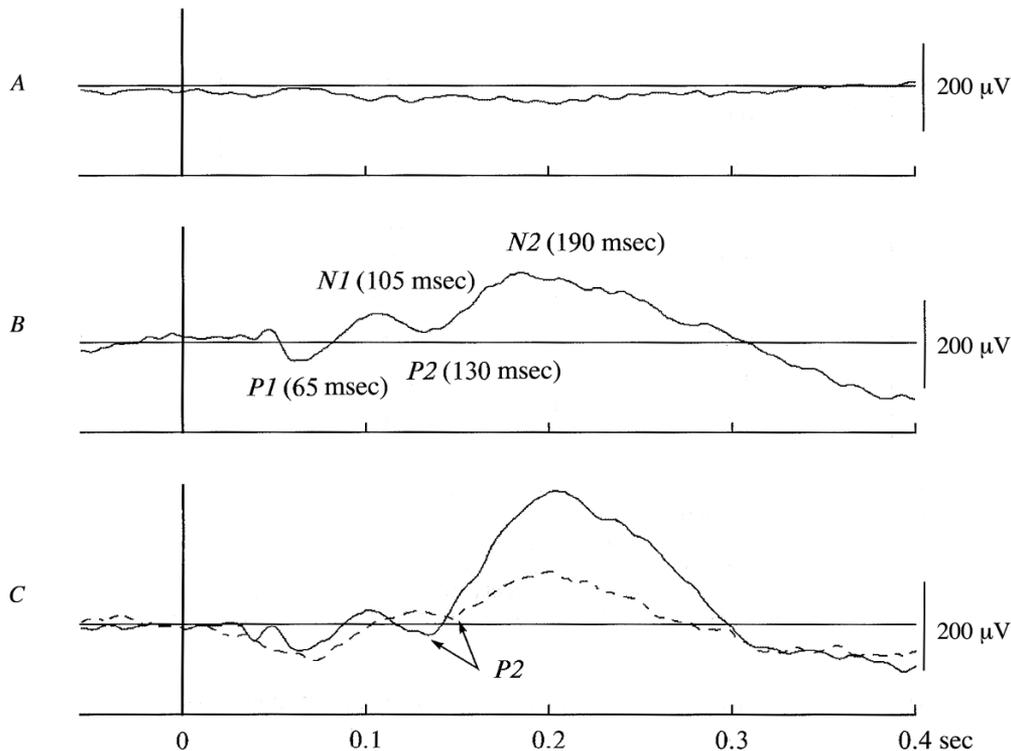
Fig. 1. Original traces of EP from a rabbit. The vertical line shows the moment of light stimulus substitution. *A*) Example of a visual cortex EP in response to presentation of a sound (2000 Hz, 70 dB, 40 msec); *B*) example of a response to light stimulus substitution from 0.3 to 1 cd/m^2. The main phases of EP are identified, along with their latencies, msec; *C*) comparison of EP in responses to light stimulus substitution from 0.3 to 1 cd/m^2 (dotted line) and in response to substitution of the same stimuli with synchronous addition of the sound (continuous line). Sound delivery coincided with the moment of stimulus substitution.

significant changes in amplitude on addition of the sound to the light stimulus. Amplitudes were measured peak-to-peak. Statistical analysis of the results (using Statistica, Statsoft to run the Wilcoxon T test) were based on comparison of sets of responses to light before a particular complex and responses to complex of light with sound for each of the sound delay intervals used. Sets of amplitudes of substitutions of 0.3 by 1 cd/m^2 (direct substitution), 1 by 0.3 cd/m^2 (reverse substitution) and mean values for direct and reverse substitutions were compared separately. Differences between sets were regarded as significant at $p < 0.05$. Ratios of the amplitudes of responses to complexes to the amplitudes of the corresponding responses to light were also assessed.

The effects of different factors on the amplitudes of VEP phases in response to light stimuli and complexes of light with sounds were studied by factor analysis of variance (run on Statistica, Statsoft; Fisher's F test). The effects of two factors were analyzed. The first factor was the time shift of the sound relative to the moment of light stimulus substitution (a total of 15 intervals, from –750 to +150 msec). The second factor was the intensity of the light stimulus delivered (0.3 or 1 cd/m^2). Separate analyses were run for each VEP phase (N1, P2, and N2). Factor effects on amplitude were regarded as significant at $p < 0.05$.

Experiments were performed in compliance with the positions of the Ethics Commission of Lomonosov Moscow State University in relation to studies using experimental animals and with observation of the humanitarian principles laid out in the directives of the European Community (86/609/EC) and approved by the Medical Ethics Committee.

Results

Figure 1, *A* shows the response of the visual cortex of rabbit No. 1 to sound (2000 Hz, 70 dB, 40 msec). The response to sound was not discriminated from baseline, and this was also characteristic of other responses. Despite the absence of responses, modulatory actions of sound on responses to light were apparent.

Figure 1, *B* shows an original evoked potential trace of the response to substitutions of light intensity with identification of the main phases of the response and their time parameters. The N1 (150 msec), P2 (130 msec), and N2 (190 msec) phases are clearly apparent.

Figure 1, *C* shows the evoked potential response, averaged from original traces for 30 presentations, to substitution of lights of low intensity (0.3 for 1 cd/m^2) in rabbit No. 2 (dotted line). On synchronous addition of the sound to the action of the light (the sound shift interval was 0), the marked increase in the amplitude of the P2 wave as com-

TABLE 1. Effects of Sound on the Amplitude of the N1 Phase of the Response to Light with Different Sound Delay Intervals with Respect to the Light

Sound delay, msec	0.3 by 1 cd/m^2	1 by 0.3 cd/m^2	Mean for both substitutions
−750	0.91	0.93	0.93
−500	0.97	0.99	0.98
−300	0.96	1.07	1.01
−200	1.00	1.00	1.00
−150	1.06	1.09	1.08
−100	**0.90**	0.96	0.92
−80	1.00	0.91	0.97
−60	0.96	1.07	1.01
−40	1.11	1.12	**1.12**
−20	1.03	0.89	0.97
0	0.99	0.92	0.96
+20	0.90	0.94	0.92
+50	1.07	1.00	1.03
+100	0.95	0.97	0.95
+150	1.03	1.02	1.04

Note. The first column shows the sound delay intervals from the moment of light stimulus substitution, msec. The second column shows the ratio of the mean amplitude of this wave of the response to the light + sound complex to the corresponding amplitude of the response to light for each of the intervals on substitution of light at 0.3 cd/m^2 by light at 1 cd/m^2. The third column is as the second but for substitution of light at 1 cd/m^2 by light at 0.3 cd/m^2. The fourth column is the same but for the mean for both substitutions. Numbers in bold show significant changes in responses to light on addition of sound ($p < 0.05$).

TABLE 2. Effects of Sound on the Amplitude of the P2 Phase of the Response to Light with Different Sound Delay Intervals with Respect to the Light

Sound delay, msec	0.3 by 1 cd/m^2	1 by 0.3 cd/m^2	Mean for both substitutions
−750	1.16	1.07	1.07
−500	0.87	0.92	0.90
−300	1.06	**1.19**	1.07
−200	0.98	0.98	0.95
−150	0.91	0.94	0.94
−100	0.93	1.00	0.86
−80	1.21	0.95	1.04
−60	0.99	**1.32**	1.11
−40	0.82	1.16	1.00
−20	1.24	**1.35**	**1.30**
0	**1.27**	0.99	1.09
+20	0.95	**1.23**	1.04
+50	**0.81**	1.07	1.00
+100	0.87	1.04	0.91
+150	1.08	1.06	1.05

Note. For further details see Table 1.

pared with the response to light, from 18 to 59 μV, is clearly visible (continuous line).

The modulatory action of the sound on substitution of light intensities with synchronous delivery of sound and light has been described in detail in our previous studies [Polyanskii et al., 2011; Sokolov, 2003].

We then continued to analysis of the modulatory effect of sound on light responses with different delays between the moment of sound delivery relative to the moment of light stimulus substitution.

The results obtained from analysis of responses are shown in Tables 1, 2, and 3.

The data in Table 1, which are ratios of phase N1 amplitudes on delivery of light + sound to the amplitudes of responses to light, show that this phase had little relationship with the effects of sound on light responses over time. Only at –40 msec (for the mean amplitudes of the direct and reverse substitutions) was there a significant increase in the response to the complex compared with the response to

TABLE 3. Effects of Sound on the Amplitude of the N2 Phase of the Response to Light with Different Sound Delay Intervals with Respect to the Light

Sound delay, msec	0.3 by 1 cd/m^2	1 by 0.3 cd/m^2	Mean for both substitutions
−750	1.03	1.09	1.06
−500	1.04	0.95	1.01
−300	0.98	1.00	1.00
−200	1.00	1.03	1.04
−150	1.02	0.96	1.02
−100	**1.09**	0.99	1.05
−80	1.07	1.01	1.04
−60	1.01	0.94	0.98
−40	0.99	1.01	1.00
−20	0.97	1.07	1.01
0	1.03	**0.87**	0.98
+20	0.97	**1.12**	1.05
+50	1.00	1.04	1.02
+100	0.96	0.93	0.95
+150	0.96	1.14	1.02

Note. For further details see Table 1.

sound. With an interval of −100 msec, there was even a significant reduction in the response to the complex.

On substitution of light stimuli of 1 cd/m^2 by 0.3 cd/m^2, sound had no significant influences over time.

A different pattern was seen for the P2 phase (120–150 msec from substitution of intensities) (Table 2). Changes here were seen in different variants of light delivery (0.3 by 1 cd/m^2, 1 by 0.3 cd/m^2, and the mean of the response magnitudes for these substitutions). Thus, on substitution of intensities from 0.3 to 1 cd/m^2, significant increases in responses to light were seen on synchronous delivery of the sound + light, while at a delay of +50 msec there was a significant reduction in the response to light as a result of the sound (0.81).

Most of the significant results were obtained on substitution of light intensities of 1 for 0.3 cd/m^2. Here, sound induced a significant increase in the response (at −300, −60, −20, and +20 msec). An increase in the response was also seen for the mean value for both substitutions (0.3 by 1 cd/m^2 and 1 by 0.3 cd/m^2) with an interval of −20 msec.

Analysis of the N2 phase (180–250 msec) showed a significant increase in the response at −100 msec (substitution of 0.3 by 1 cd/m^2) and +20 msec (1 by 0.3 cd/m^2). Synchronous delivery of the sound and light (interval 0 msec) produced a small but significant decrease in the response.

All VEP phases studied showed significant effects for both factors on amplitude – both the factor consisting of the interval between the sound and the moment of light stimulus substitution and the factor consisting of the intensity of the light stimulus (F test, $p < 0.002$).

Thus, analysis of the data presented in Tables 1–3 showed that the largest number of significant effects of the sound on the light response was seen for the P2 phase (seven cases), which is clearly greater than for the N1 and N2 phases (three cases each). In addition, the ratio of the re-

sponse to the complex to the response to the light for the P2 phase was greater (from 1.19 to 1.35 – Table 2) than for the N1 phase (1.12) and N2 phase (1.09, 1.12).

Figure 2 shows histograms of the ratios of the averaged (for all responses) amplitudes of responses to the complex to the amplitudes (averaged for the same experiments) of responses to light for all the three phases of evoked potentials. This shows that the P2 phase differed markedly (Fig. 2, *B*) in terms of the large increase in amplitude and significant increases in responses to the light + sound complex at intervals of −300, −60, −20, 0, and +20 msec, as compared with the N1 (Fig. 2, *A*) and N2 (Fig. 2, *C*) phases.

The plots corresponding to Tables 1–2 (Fig. 2) show mean responses (15–42 experiments). In this case, increases in responses to light for the P2 phase were by 19–35%, compared with 11% and 8–12% for the N1 and N2 phases, respectively. This does not mean that the upper limit of the ratio of the response to the light + sound complex to the response to light had reached its maximum. Increases in responses in individual traces, especially for the P2 phase, could reach values of 2.0, 2.52, and even 3.66.

As illustration, Fig. 3 shows original responses to substitution of light intensities and complexes of light with sound for those intervals for which sound had significant influences (for the most significant P2 phase). The cases most indicative of the effects of sound on light responses were selected. The peak of the P2 phase was delayed from the moment of stimulus substitution by 120–150 msec. As at noted in the Methods section, P2 amplitude was calculated from the peak of the preceding wave to the peak of P2 itself. Comparison of P2 amplitudes in responses to light (dotted line) and responses to sound + light complexes (continuous line) shows that the increase in P2 amplitude on addition of sound with an interval of −300 msec was by 220%, compared with a 200% increase at −60 msec,
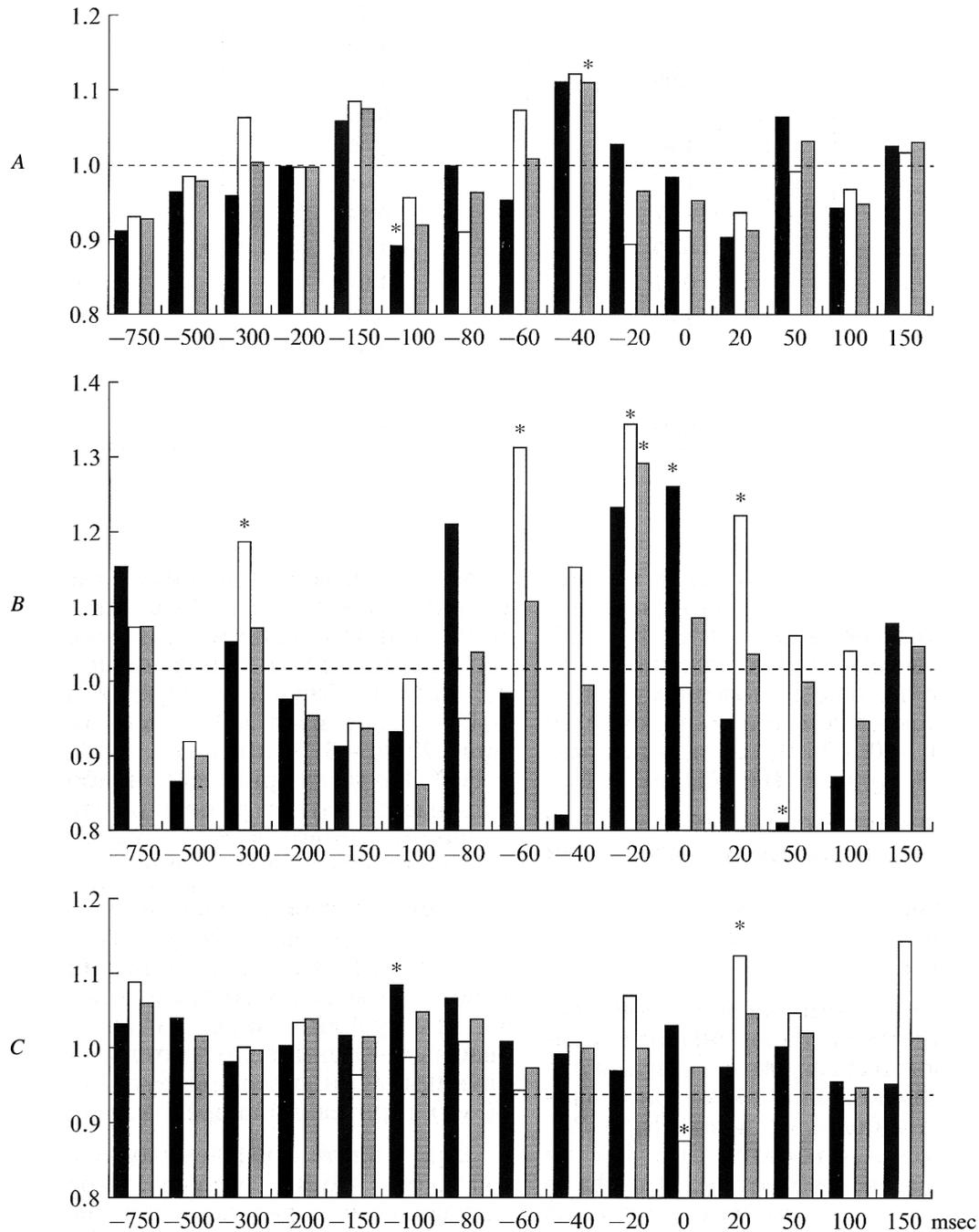
Fig. 2. Histograms showing the ratios of responses to light + sound complexes to responses to light with different sound delay intervals with respect to the light for different phases of the EP (*A* – phase N1; *B* – phase P2; *C* – phase N2). Black columns show substitution of light at 0.3 cd/m^2 by light at 1 cd/m^2; white columns show substitution of light at 1 cd/m^2 by light at 0.3 cd/m^2; gray columns show the mean for both substitutions. *Significant differences in responses to complex from responses to light for the sound delay interval indicated, $p < 0.05$. The vertical axis shows the ratio of the mean response to the complex to the mean response to light.

37% at –20 msec, 200% at 0 msec, and +20 msec. However, the most indicative cases from different experiments are shown here. Mean P2 amplitudes in responses to light and complexes are shown in the Tables, Fig. 2, and above in the text.

Discussion

Thus, we have studied the modulatory actions of sound on the responses of the visual cortex to substitution of low light intensities (0.3 and 1 cd/m^2) for each other with the sound presented with different time delays from the light.
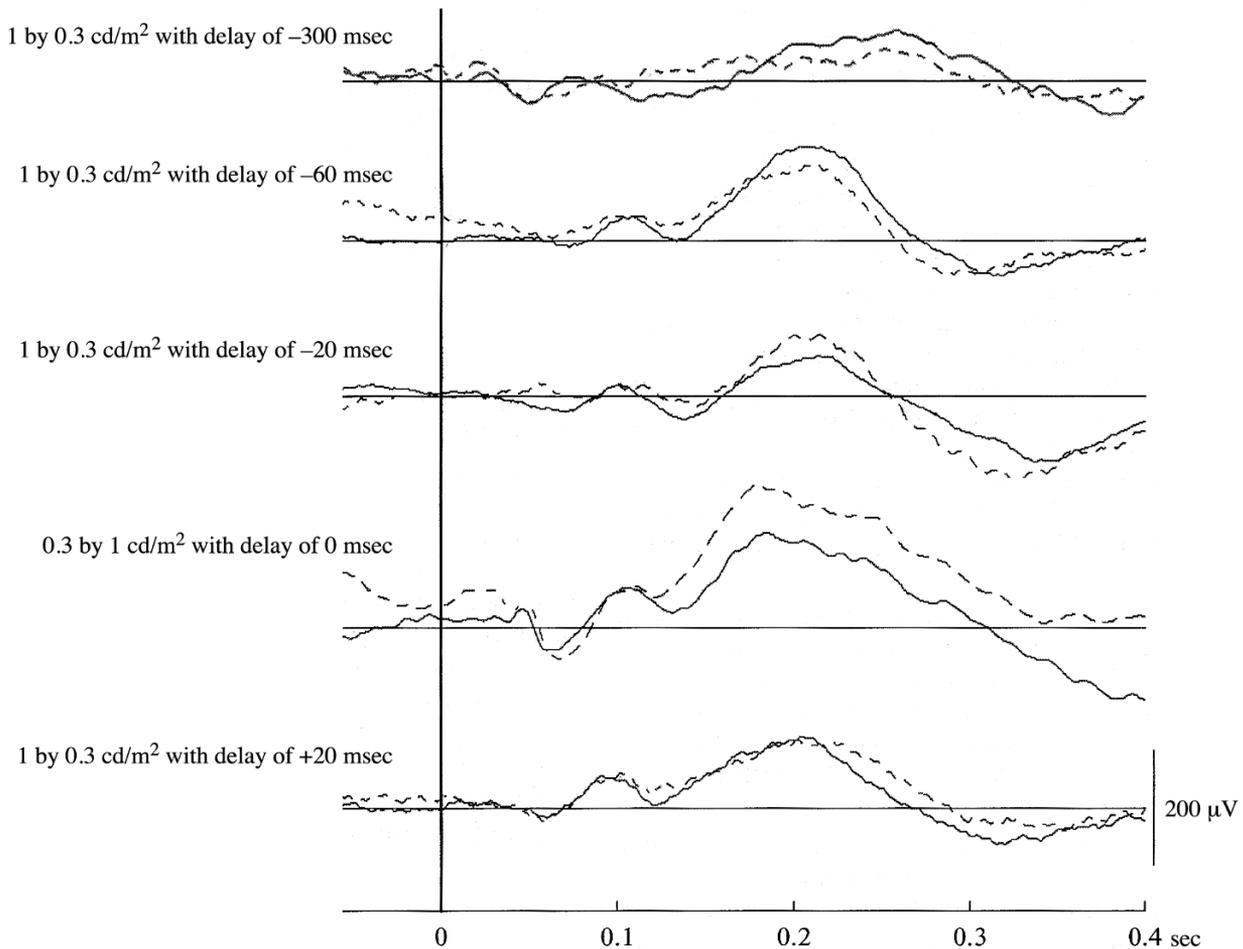
Fig. 3. Examples of original EP traces for sound delay intervals showing significant effects of sound on the amplitude of the P2 phase. Intervals are shown at left. The vertical line shows the moment of light stimulus substitution. The dotted line shows EP to light and the continuous line shows EP to light + sound complexes.

We assessed the sound effect in terms of evoked potentials in the visual cortex. The sound itself, with the parameters used (2000 Hz, 70 dB, 40 msec) produced no response in the visual cortex.

The results from these experiments showed that sound had a mainly facilitatory action on the discrimination of low intensities in the range from –300 to +20 msec (Tables 1–3, Figs. 2 and 3). This is generally consistent with studies using psychophysiological methods in humans [Kauser and Logothetis, 2007; Liu et al., 2007; Shams and Kim, 2010] and experimental animals [Polyanskii et al., 2011]. In human studies, subjects had to identify whether different modalities presented with different time intervals relative to each other were discriminable or whether they fused into a single percept, or image. This is clearly a different aim from that of the present study. Our interest was in identifying the time intervals between a sound and a light at which the sound would have significant influence on the light response (the response to substitution of low light intensities, 0.3 and 1 cd/m²). These psychophysiological methods cannot be used in rab-

bits. Objectively, we can only establish the time intervals at which the sound has significant effects on the light response. However, many of the basic mechanisms of activity of the sensory systems (for example, vision) are clearly reflected in both neurophysiological and psychophysiological studies, with results which correlate positively with each other. We can therefore note that the time window established in psychophysiological studies for the interaction between light and sound, of the order of –200 to +200 msec, will also be seen on analysis of objective measures of activity in the visual cortex, particularly as VEP [Lewald et al., 2001; Lewald and Guski, 2004; Molholm et al., 2002; van Wassenhove, 2007].

In our experiments, sound started to have significant effects on the light response with an interval of –300 msec (Tables 1–3, Figs. 2 and 3), after which significant influences were apparent from –100 msec (the N1 phase in this case is slightly inhibited by sound, while the N2 phase is amplified on addition of sound).

At intervals of –60, –40, –20, 0, and +20 msec, sound significantly increased the response to substitution of weak

intensities (Tables 1–3, Figs. 2 and 3). As regards intervals of –200, –150, and –80 msec, our view is that the lack of effect may be due to instability in the functional state of the rabbits. If the rabbit were in its natural environment and its mobility unrestricted, sound would have clear effects at these and other delay intervals. In the experimental conditions, only those intervals at which the effects of sound were stable and sufficiently large were statistically significant.

It can be suggested that the presence of the additional sound with an interval of –300 msec serves as an early signal for danger or a significant event. At intervals close to 0 (–60, –40, –20, +20 msec), sound in complex with light enhances the action of the visual stimuli, helping the rabbit to obtain better orientation in conditions of low illumination.

As regards intervals with sound delays of +50, +100, and +150 msec, the effects of the pause on the response to substitution of light intensities were inhibitory. It is possible that if we were to study the subsequent intervals (+200, +250 msec), we would find an additional influence of sound on the light response.

A further aspect of analysis of the sound modulation of the response to light is that the main effect of sound is reflected in the P2 phase of the evoked potential (120–150 msec) – with a total of seven significant differences in the response to the complex compared with the response to light at different sound-to-light delay intervals, in contrast to the N1 phase (80–110 msec) and the N2 phase (180–250 msec), where there were only three significant differences in each case (Tables 1–3, Figs. 2 and 3). The extent of the effect of sound on the light response was also significantly greater for the P2 phase (1.19–1.35) than the N1 and N2 phases (1.09–1.12) (Tables 1–3, Fig. 2).

These data provide evidence that the early phases P1 and N1 were less susceptible to the effects of sound than the P2 phase. It is possible that the sound signal arrives in the visual cortex with a delay, passing via the auditory cortex, the parietal cortex, the superior colliculi, and other parts of the brain [Jaeckl and Harris, 2009; Molholm et al., 2002].

We plan further analysis of the mechanisms of the effect of sound on the light response over time, with analysis of the responses of visual cortex neurons in rabbits.

Conclusions

1. A sound tone at a frequency of 2000 Hz, loudness 70 dB, and duration 40 msec, which alone did not induce any response in the primary visual cortex, was found to produce significant increases in the response to substitution of low light intensities when presented with delays of –300 to +50 msec relative to the light.

2. The effect of the sound on the light response was most completely apparent in the increase in the amplitude of the P2 phase of visual evoked potentials (120–150 msec from the moment of substitution of light stimuli). While seven sound delay periods were shown to have significant effects on the P2 phase of the response to the change in the light stimulus, the N1 phase (80–110 msec) and N2 phase (180–250 msec) showed significant changes with only three intervals each.

3. The results reported here show that the amplitude of the P2 phase not only underwent the most significant changes in responses to light with different delay intervals for the sound, but also demonstrated the largest increases in the effect of sound on discrimination of low light intensities. While the increase in the response to light as indicated by the P2 phase was by 19–35%, the increases for the N1 and N2 phases were by 11% and 8–12%, respectively.

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