Lengthy suppression from similar stimuli during rapid serial visual presentation

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The stimulus at any point in the visual field is rarely static during normal viewing: observer and object movement conspire to produce a continually changing series of stimuli. Our aim was to study both the short- and long-term interactions between responses to a series of stimuli presented at a single visual location. We used rapid serial visual presentation (RSVP) in which the stimuli were randomly oriented gratings delivered at the rate of 30 per second. Human subjects pressed a key whenever they saw a target orientation, for example horizontal. The results were analyzed by finding two orientations before each key-press. The first preceded the key-press by the reaction time, and the second preceded the first by an interval of variable duration. There were two main findings. First, the subject was more likely to press the key when the target was immediately preceded by a grating of similar orientation. This facilitation presumably results from the summation of sub-threshold inputs. Second, a key-press was reduced in probability when a target orientation was preceded by a similar orientation with an interstimulus interval of 100–400 ms. The time course of this suppression is similar to that seen in attentional blink experiments.

Keywords: temporal vision, masking, binocular vision, attentional blink, rapid serial visual presentation, reverse correlation


Introduction

We live in a cluttered visual environment. The objects populating this environment are in frequent motion either because we move or the objects themselves move. This means that at any specific location in the visual field, an object frequently replaces its background, the background replaces an object, or one object replaces another. It is therefore of interest to know whether there is an interaction when one visual stimulus takes the place of another: does the visual response to a stimulus interact with the response to another stimulus that obscures the first?

This question has been studied in various ways. One approach is to use a masking stimulus followed by a test stimulus, where the test is designed to measure the interference produced by the mask. A common finding in this type of experiment is that the mask reduces the visibility of the test for interstimulus intervals of several tens of milliseconds (Breitmeyer, 1984). There is increasing evidence, however, that the masking effect may last considerably longer (Breitmeyer et al., 2006; Ogmen, Breitmeyer, & Melvin, 2003). Breitmeyer et al. required their subjects to match test brightness to a reference stimulus and found that test brightness was reduced for several hundred milliseconds after the mask.

Another approach to the issue of mask–test interaction is rapid serial visual presentation (RSVP), in which a series of objects is presented one after the other at the same location. In one variation of this experimental design, the subject was shown a sequence of words and asked to indicate which word was repeated (Kanwisher, 1987). The resulting “repetition blindness” lasted for hundreds of milliseconds. In another variation, the subject is asked to indicate whether an object belonging to a particular class (an alphabetic character, for example) was present in the series. One of the results from this type of experiment is that the identification of a target object reduces the visibility of a second target, an effect known as the attentional blink (Raymond, Shapiro, & Arnell, 1992). The duration of this effect was similar to that for repetition blindness.

These prolonged time courses are suggestive. They are substantially longer than the impulse responses of neurons in primary visual cortex (Ringach, Hawken, & Shapley, 1997) and indicate the involvement of extrastriate mechanisms. The aim of our paper, therefore, is to study the time course of interstimulus interactions in more detail. We used a rapid serial visual presentation technique...
pioneered by Ringach (1998). Our experimental design differs in five ways from that usually employed in repetition blindness (Chun, 1997; Fagot & Pashler, 1995; Kanwisher & Potter, 1990) and attentional blink (Chun & Potter, 1995; Di Lollo, Kawahara, Ghorashi, & Enns, 2005; Raymond et al., 1992) experiments. First, the stimuli were randomly oriented gratings rather than alphanumeric characters. The advantage of gratings is that the difference between one stimulus and another is defined by a single number, the orientation difference.

Second, the stimuli were presented at a higher rate (30 per second) than in previous experiments in order to improve the temporal resolution of the measured time courses. Third, the stimulus series was continuous rather than being broken into short trials, and the subject signaled each time a target was seen. This approach is designed to improve the efficiency of data collection. Fourth, we did not attempt to estimate the correctness of a subject’s response. Instead, we asked subjects to signal a target and used a reverse correlation procedure to find what types of stimulus preceded a response. This approach avoids having to adjust the stimulus so that it produces sufficient incorrect responses. Finally, we wished to know about the neural location of any long-term suppression effects revealed by our experiments. We therefore presented a series of gratings to the left eye that was independent of the series presented to the right eye, allowing interocular interactions to be examined along with intraocular ones. Interocular interactions that mimic intraocular ones provide strong evidence for a cortical locus.

Our results include the finding that a subject is less likely to detect a target when a grating of similar orientation precedes it by at least 100–400 ms, and that the time course of this suppression is similar to that of the attentional blink. We wished to see whether this result could be reproduced with a more conventional experimental design. Experiment 2, which employed forward masking, provided extra evidence for a long-lasting suppression. Some of this work has been previously presented in abstract form (Freeman, Wong, & Roeber, 2008).

### Experiment 1: Rapid serial visual presentation

#### Methods

**Stimulus**

The stimulus and data collection methods have been previously described in Roeber, Wong, and Freeman (2008). In brief, stimuli were presented on a computer monitor with a video frame rate of 60 Hz, and a gray background (58 cd/m²). Left and right eye stimuli were presented on the left and right sides, respectively, of the monitor screen and viewed through a mirror stereoscope. Each half of the screen showed a black fusion circle with an inner diameter of 3° and a width of 0.25°, and subjects adjusted the stereoscope to fuse the two circles. Each fusion circle contained a sinusoidal grating with a spatial frequency of 2 cycles/deg and a contrast of 1. Contrast was calculated by subtracting background luminance from peak luminance and dividing the difference by background luminance. Each grating had one of 10 orientations spaced 18° apart and one of four spatial phases spaced a quarter of a cycle apart. There were therefore 40 possible gratings. Each monocular stimulus consisted of a series of gratings, as shown in Figure 1, with a new grating chosen every 33.3 ms (2 video frames). The choice was made from the 40 available gratings with equal probability. Each experimental run lasted 60 s. On any run the series for one eye was independent of that chosen for the other eye, and both series were independent of those presented in other runs.

#### Procedure

One orientation was nominated as the target and the subject’s task was to press a key whenever the target was seen. There were three targets—horizontal, vertical, and 45° to the vertical—and four and a half hours of data collection for each target.

#### Analysis

The first step of the analysis was to find the orientations present at a specific time before each key-press. The example shown in Figure 2A comes from one subject. For any given time prior to a key-press (shown on the oblique axis) it shows the probability density of the orientations presented at that time. The density was compiled across all four grating phases. Given that responses were similar for left-eye gratings, right-eye gratings, and all three targets, densities were averaged across eyes and targets. The density peaks at the target orientation for times close to 400 ms before the key-press and is flatter at other times. This means that the subject was pressing the key after a target presentation, as required, and that the reaction time was about 400 ms.

A more precise description for reaction time is shown in Figure 2B. It was obtained from probability densities such as those in Figure 2A by computing how much each density differed from a flat line. The measure used was chi-square computed by comparing the frequency histogram of key-presses with the mean number of key-presses:

\[
X^2 = \sum_{i=1}^{10} \frac{(\text{count}_i - \text{mean count})^2}{\text{mean count}},
\]

(1)
where count, is the number of key-presses preceded by orientation \(i\). Chi-square is shown on the vertical axis versus time prior to a key-press on the horizontal axis, for the five subjects in this experiment. The resulting curves peak at differing times across subjects, but the peaks are clustered around 400 ms. Figure 2C shows the same data as in Figure 2B but at an expanded vertical scale in order to show the significance level for chi-square (9 degrees of freedom, \(\alpha = 0.05\)) obtained with a goodness-of-fit test. This graph therefore shows the range of times prior to a key-press at which the probability densities differed significantly from flatness.

It proved very useful to collapse the probability densities such as those in Figure 2A into a single density. This was done by weighting each individual density by its chi-square (with the significance level subtracted) and summing across weighted densities. All probability densities shown in the Results section were calculated in this way. Given the low variability in the time interval between a key-press and the target orientation that precedes it, we assume a causal relationship between the two and will refer in what follows to the target stimulus producing a key-press.

**Results**

Our aim in this paper was to measure the time course of interactions between masking and test stimuli. We start by describing a procedure for measuring mask–test interactions using rapid serial visual presentation. We then plot the time course for these interactions. Figure 1 illustrates a stimulus sequence in which one orientation, \(\theta_1\), is preceded by another, \(\theta_2\). To demonstrate the effect of \(\theta_2\) on the response to \(\theta_1\) we plot in Figure 3A the probability that a key-press is preceded by \(\theta_1\) and, immediately before that, \(\theta_2\). The interstimulus interval here is 33 ms, orientation \(\theta_1\) is given on the horizontal axis and \(\theta_2\) on the vertical axis. The gray level at each point codes the probability, \(p_{\text{obs}}(\theta_1, \theta_2)\), that a key-press is preceded by the combination \((\theta_1, \theta_2)\), and the scale at the right of the plot shows the relationship between probability and gray level.

There is a bright area in the middle of the plot, indicating that a key-press is likely to be preceded by two target orientations, one immediately following the other. This is not surprising as each target orientation could contribute to a key-press independently of the other target. What is more interesting is whether there is any interaction between the two stimuli in producing a response. To examine this possibility we first calculated the probability density expected if orientations \(\theta_1\) and \(\theta_2\) contribute to a key-press independently of each other. This density was calculated from the observed probabilities in three steps. First, probabilities were summed across \(\theta_2\) to find the marginal density for \(\theta_1\), \(p(\theta_1)\). Second, probabilities were summed across \(\theta_1\) to give the
other marginal density, \( p_2(\theta_2) \). Third, the two marginal densities were multiplied to find the independence model:

\[
p_{\text{ind}}(\theta_1, \theta_2) = p_1(\theta_1)p_2(\theta_2). \tag{2}
\]

The results are shown in Figure 3B. The final step in the analysis was performed by subtracting the independence model from the observations, to find the interaction between \( \theta_1 \) and \( \theta_2 \) in producing a key-press:

\[
p_{\text{interaction}} = p_{\text{obs}} - p_{\text{ind}}. \tag{3}
\]
The interaction plot is shown in Figure 3C. It is not uniformly gray, indicating that there are interactions. There is a bright area in the middle indicating that the combination of two targets is more likely than expected if the two stimuli acted independently. In other words, $\theta_2$ facilitates $\theta_1$ in producing a key-press. Elsewhere in the plot the probability differences are negative, producing dark areas. This means that $\theta_2$ has a suppressive effect, making it less likely that $\theta_1$ will evoke a key-press.

We have previously described the facilitatory influence of consecutive orientations (Roeb et al., 2008) and will not dwell on that theme here. Instead, the focus of this paper is on suppression and its time course. We therefore calculated the interaction plot for several interstimulus intervals, as shown in Figure 4. Intraocular and interocular interactions are shown on the left and right columns of the figure, respectively. The left column of the figure shows densities for which the two orientations were delivered to the same eye; data from the left eye and right eye are averaged. The right column shows densities for which $\theta_1$ was presented to one eye and $\theta_2$ to the other eye. Again there are two cases ($\theta_1$ to the left or right eye), and the mean is shown. The interstimulus interval, the time by which $\theta_2$ preceded $\theta_1$, is shown to the right of each row. There is no intraocular plot for an interstimulus interval of 0 because only one orientation was presented to each eye at any given time.

There is a progressive change in the interaction plot as the interstimulus interval increases: an area of suppression develops at the center of the plot. Whereas the central suppression is evident in all the interocular plots, it is not well established in the intraocular plot until the interval between the stimuli reaches 133 ms. To quantify this time course we summed values within the central area of the plot. In order to find the best summation area the interaction plot was averaged over interstimulus intervals, as shown at the bottom of Figure 4. This mean shows a circular suppression region surrounded by facilitation. A circular summing area was therefore used, and its radius was set so that the sum of values within the contour was minimized: a smaller radius would not include all the negative values representing suppression and a larger radius would encroach on the positive values indicating facilitation. The dashed circle shows the optimal contour, which had a radius of 35°.

Summation of interaction values within this optimal contour results in the time course shown in Figure 5A. Intraocular data are shown on the left and interocular on the right, with one line for each subject. All data in this figure have been smoothed using a moving average over five consecutive values. Interactions in the intraocular case are strongly facilitatory at short interstimulus intervals and the interaction only becomes suppressive at longer intervals. The suppression is shown more clearly in Figure 5B by using an expanded vertical scale. The
intraocular and interocular plots are similar: suppression is strongest at an interstimulus interval of 100–300 ms and continues up to about 400 ms.

Whereas the suppression phase of the intraocular and interocular time courses are similar, the facilitatory phases differ markedly. This suggests that the time courses have two components—facilitatory and suppressive. Indeed, Figure 4 shows that the pattern of interactions at short interstimulus intervals differs substantially from that at long interstimulus intervals. To test this idea we broke the

Figure 4. Interstimulus interactions. Interaction plots are shown for the interstimulus intervals shown at right. The left column is for interactions when the two orientations are presented to the same eye, and the right column for presentation to differing eyes. All plots in this figure have been smoothed using a Gaussian convolution with a standard deviation of 18°. A central dark area develops with time, indicating a long-lasting suppression of one stimulus by another of similar orientation. The mean over a range of interstimulus intervals is shown at the bottom.

Figure 5. Suppression time course. (A) The time course of the interactions shown in the previous figure was quantified by summing interactions in the dashed circle shown at the bottom of that figure. The sum is shown on the vertical axis versus interstimulus interval on the horizontal axis, with one line for each subject. Intraocular interactions are shown in the column at left and interocular interactions on the right. There is a strong facilitatory interaction between two stimuli when both are presented to the same eye with only a small intervening interval. This facilitation is small or absent for the interocular case. (B) The data in (A) are shown on an expanded vertical scale to more clearly depict the time course of suppression. The interaction between two stimuli is most suppressive when they are separated by 100–300 ms. (C) The time courses in (A) were decomposed into facilitatory and suppressive components by using the pattern of interactions seen in Figure 4. Representative error bars are shown: they provide 95% confidence intervals.
time courses into two additive components with the following model:

\[
\text{Interaction}(t, \theta_1, \theta_2) = f(t)b(\theta_1, \theta_2) + s(t)l(\theta_1, \theta_2), \tag{4}
\]

where \( t \) is time, \( b \) is the pattern of interactions at the briefest interstimulus interval (33 ms for the intraocular case and 0 ms for the interocular case), and \( l \) is the pattern of interactions averaged over the longer interstimulus intervals (the bottom pattern in Figure 4). This analysis has an advantage over that in parts A and B of the figure: it uses all the data in the interaction plots, not just those data within a contour. The model in Equation 4 was fitted to the observations using least-squares regression, and the resulting time courses, \( f(t) \) and \( s(t) \), are shown in Figure 5C labeled Facilitation and Suppression, respectively. For both the intraocular and interocular cases, model-fitting reveals a rapid decline in the facilitatory component and a suppressive component that takes 100–200 ms to reach its trough, followed by a long decay period. A one-tailed \( t \)-test on the unsmoothed data showed that the suppression differed significantly from zero at the 5\% level for interstimulus intervals of 100–400 ms for the intraocular case, and 67–400 ms for the interocular. The General discussion section takes up the mechanisms that may underlie these time courses.

Discussion

We have shown here that a grating stimulus increases the visibility of an aligned grating that follows soon after it. Breitmeyer et al. (2006) and Ogmen et al. (2003) found that a mask can improve the visibility of a test stimulus presented shortly after the mask. They suggested that this facilitation derives from non-specific activating systems in the brainstem. Is there a simpler explanation? Probability summation can be ruled out because we have subtracted out the effects of the two stimuli when acting independently. Rather, the facilitation is most likely to be due to sub-threshold summation. To see this it must first be appreciated that the individual stimuli used in our stream of gratings are weak: subjects detect, on average, only one in 30 targets, and when they do signal a detection the probability of a hit is only slightly higher than the probability of a false positive (Figure 2A). We suggest, therefore, that the brief facilitation we have measured is due to neural summation within orientation detectors.

Legge (1979) carried out a series of masking experiments in which a test grating was presented simultaneously with a masking grating of the same orientation. When the mask’s contrast was low, the threshold for test detection was lower than when the mask was absent. This is the “dipper effect” and our facilitation is probably another demonstration of this effect. Legge used both intraocular presentation, where the mask and test were shown to the same eye, and interocular presentation, where the mask was shown to one eye and the test to the other. The dipper effect was less marked for interocular presentation. Baker and Meese (2007) extended this result by showing that varying the relative phase of mask and test further weakened the interocular dipper effect. We agree with previous results, therefore, in that the facilitation we measured was smaller for the interocular case than for the intraocular.

We have also shown that a grating stimulus reduces the probability that an aligned grating will be detected when the interval between the two is between 100 and 400 ms. The time course of this long-lasting suppression when the two stimuli are presented to differing eyes is similar to the intraocular time course. This finding, which is consistent with previous work (Breitmeyer, Ziegler, & Hauske, 2007), provides clear evidence that the suppression has a cortical origin. The biphasic nature of the time course in Figure 5B suggests that orientation detectors have a biphasic response. Indeed, a significant population of orientation-selective cells in primary visual cortex does display biphasic responses to a brief stimulus (Ringach et al., 1997). The timing, however, does not support this explanation because the negative part of the cellular response is complete within 100–150 ms.

Instead, it is likely that the source of the long-lasting suppression lies beyond the initial stages of processing in primary visual cortex. Consider, for example, the links between the results found here and those of previous experiments using rapid serial visual presentation. A target stimulus loses visibility when the subject is required to make a judgment about a preceding target, a phenomenon known as the attentional blink (Raymond et al., 1992). The loss of visibility starts about 100 ms after the first stimulus, peaks at 200–300 ms, and has disappeared by 500 ms. This is a time course very similar to the one we have measured. Attention also plays a vital role in our experiment because the subject is monitoring the stimulus stream closely in order to signal a target. We therefore believe that we have demonstrated the attentional blink using a technique distinct from those used previously.

Experiment 2: Forward masking

We showed in Experiment 1 that a briefly presented stimulus reduced the visibility of a following stimulus for up to half a second. The experimental design, which used a rapid stream of randomly oriented gratings, was unconventional. A more conventional approach to measuring the time course is to present a single masking stimulus followed, at a variable time interval, by a single test stimulus. In this approach, it is typically found that the
masking stimulus elevates the threshold for detecting or discriminating some aspect of the test stimulus, and that the threshold elevation dies away as the interstimulus interval is lengthened to several tens of milliseconds (Breitmeyer, 1984). We therefore performed a forward masking experiment with the aim of exposing a long-lasting suppression like that found in Experiment 1. As the results will show, we were only partially successful in this aim.

Methods

Stimulus

As in Experiment 1, the two eyes were independently stimulated. There were therefore two stimulus conditions: the masking and test stimuli were delivered either to the same eye or to different eyes. The intraocular masking condition is illustrated on the left of Figure 6. Both mask and test were Gabor patches constructed by multiplying a sinusoidal grating by a two-dimensional Gaussian envelope. The grating had a spatial frequency of 3 cycles/deg, the standard deviation of the Gaussian envelope was 0.3 deg in both dimensions, and peaks of both grating and envelope were centered within the fusion box. Grating orientation was vertical for the mask and 30 deg clockwise or anticlockwise of vertical for the test—the subject’s task was to signal test orientation. The mask had a duration of 100 ms and a contrast of 1. The test’s duration was 14 ms and its contrast was adjusted, as described below, to find threshold. Intraocular masking was achieved by delivering both stimuli to the right eye and interocular masking, illustrated on the right of Figure 6, by switching the mask to the left eye.

Procedure

Each trial consisted of a masking stimulus, an interstimulus interval of variable duration, a test stimulus, and an interval leading to the subject’s response. Luminance within the fusion box was set at the background level during the intervals between the stimuli and following the test. The subject responded by pressing one of two keys to indicate the apparent tilt direction of the test. Auditory feedback was given for incorrect choices. Test contrast was constant throughout a run, there were 25 trials per run, and at least six runs for each test contrast. There were therefore at least 150 trials from which to calculate a probability of correct choice for each test contrast. Sufficient test contrasts were used to construct a psychometric function. Threshold was measured by fitting a cumulative Gaussian profile to the psychometric function and finding the test contrast at which the probability of correct choice was 75%.

Subjects

There were four subjects, all of whom were females aged between 24 and 33 years of age. Their visual acuities, corrected to normal if necessary, were 6/6 or better in each eye. Stereo-resolution was 60 s or better. Apart from the author (EW), subjects were unaware of the aims or results of the research, gave written consent before participating in the experiments, and were paid for their time.

Results

Figure 7 shows the results. The horizontal axes give the interval between the end of the masking stimulus and the
start of the test stimulus. Subjects discriminated between left- and right-tilted test gratings, and the contrast required to perform this task is shown on the vertical axis versus, on the horizontal axis, the interval between mask and test. There is one line for each subject. (B) The thresholds in (A) have been divided by the value at the longest interstimulus interval in order to show the time course more clearly. Intraocular thresholds drop smoothly for interstimulus interval of 10 ms or more, but for interocular thresholds there is a plateau in the time course at around 50 ms. Representative error bars are shown: they provide 95% confidence intervals.

Discussion

We have shown that when a mask and test are presented to the same eye, the suppressive effect of the mask declines rapidly after the mask and has largely disappeared by 100 ms. This finding is consistent with previous work (Foley & Boynton, 1993; Macknik & Livingstone, 1998). In contrast, the interocular masking time course in Figure 7 does not fall smoothly, but plateaus at an interstimulus interval of about 50 ms. Fitting an exponential decay to these time courses accounted well for the intraocular data but produced poor fits in the interocular case. A model using two functions, one with a slower decay than the other, produced a much better fit to the interocular data; the models are described in the General discussion section. This suggests, therefore, that two processes contribute to restoring full sensitivity in the case of interocular masking. If there are two processes at work, the long-term one presumably peaks at or beyond the plateau, giving it a time course like the long-term suppression found in Experiment 1. To this extent, the long-term process in the masking experiment matches that found with rapid serial visual presentation.

Why, then, is the same plateau not seen in the time course for intraocular masking? There are at least two possible answers to this question. The first depends on the subject’s task. Raymond et al. (1992) found that the interference between two stimuli largely disappeared when the subject had to report the characteristics of only one of them. Similarly, our masking design requires the subject to report the orientation of the test but to make no judgment about the mask’s characteristics. This may explain why there is no long-lasting suppression for our intraocular results, but it cannot explain the difference between the intraocular and interocular results. A more likely answer lies in masking magnitude. Intraocular masking at short interstimulus intervals is about twice the magnitude of interocular masking; the shorter term process may well hide a second recovery process at long interstimulus intervals.
General discussion

In two experiments we have found evidence for both short- and long-term influences of one stimulus on the response to a similar stimulus presented at a later time. Can these results be tied together? One difficulty in doing so lies in the similarity of the two stimuli. The deepest long-term suppression in Experiment 1 was found at the center of the interaction plot, that is, where the two stimuli had the same orientation (Figure 4). Threshold elevations in Experiment 2, on the other hand, were measured using stimuli whose orientations differed by 30°. There are two reasons, however, for believing that long-term suppression in the two experiments can still be usefully compared. First, the contour within which interactions were summed in Experiment 1 had a radius of 35°, which encompasses the 30° orientation difference used in Experiment 2. Second, and more importantly, the time courses in Figure 5C were calculated using the complete interaction maps, not just interactions in the region where orientation differences were small. This means that the time courses of Figure 5C take account of all interstimulus orientation differences and can therefore be fruitfully compared with the results of Experiment 2.

The following discussion attempts to find the links between the two experiments. We start with Experiment 1, which provided separate time courses for the brief facilitation and long-term suppression found between two stimuli in a series of stimuli (Figure 5C). Figure 8A shows the average of those data across subjects (but without smoothing) along with a fitted time course. The model for the facilitation was an exponential function of time:

\[
b(t) = k_1 e^{-t/\tau_b},
\]

where \(b\) stands for brief, and for the suppression it was a gamma density

\[
l(t) = k_2 t e^{-t/\tau_l},
\]

where \(l\) stands for long-term, \(t\) is the interstimulus interval, \(\tau_b\) and \(\tau_l\) are time constants, and \(k_1\) and \(k_2\) are constants.

The major hurdle to overcome in applying these models to Experiment 2 is that the brief process in Experiment 1 is facilitatory whereas it is a threshold elevation, and therefore suppressive, in Experiment 2. This difference does not, however, rule out the possibility that the two processes derive from a single mechanism. As we have already noted, the individual gratings in Experiment 1 are weak stimuli and the facilitation has all the characteristics of sub-threshold summation. Compare that with Experiment 2 where the mask is plainly visible and therefore relatively strong. We suggest that in this case the response to the mask overactivates the detector for the test stimulus, forcing it into a less sensitive region of its intensity–response relationship. We therefore assume that, as in single cortical cells (Albrecht & Hamilton, 1982), a brief, intense, stimulus produces threshold elevation through response saturation.

In fitting the results of Experiment 2 we make the simplest possible assumption, namely, that the measured time course is the sum of the previously identified brief and long-term time courses, along with an additive constant:

\[
\text{Threshold elevation} = k_1 e^{-t/\tau_b} + k_2 t e^{-t/\tau_l} + k_3,
\]

where the time constants and the \(k\)s may differ from those used in Equations 5 and 6. The result of fitting this model to the mean over subjects in Experiment 2 is shown in Figure 8B. The goodness of fit, while not perfect, suggests that the model is a useful characterization of the measured time courses. Time constants are provided in Table 1. As expected from electrophysiological experiments (Shapley & Enroth-Cugell, 1984), the time con-
constants obtained with the strong stimuli used in Experiment 2 tend to be lower than those obtained with the weak stimuli of Experiment 1.

What does this model-fitting exercise tell us about underlying mechanisms? One clue comes from the analysis of linear signal-processing systems. When the input signal is a brief and intense pulse (an impulse), the output, or impulse response, of a first-order low-pass filter is an exponential function of time (Aseltine, 1958), such as that in Equation 5. The impulse response of two first-order low-pass filters in series is the gamma density shown in Equation 6 (Aseltine, 1958). Clearly, the results of Experiment 2 include nonlinear signal processing because visual sensitivity is altered by the presentation of the mask. Nevertheless, the humped form of the long-lasting suppression suggests that at least two processing stages are involved in its production.

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References


