

Effects of ISI and flash duration on the identification of briefly flashed stimuli

MICHELE RUCCI* and JACOB BECK

Department of Cognitive and Neural Systems, Boston University, 677 Beacon Street, Boston, MA 02215, USA

Received 20 February 2004; accepted 22 June 2004

Abstract—The identification accuracy of briefly flashed stimuli followed by an interstimulus interval (ISI) of variable length was compared to that obtained with longer flashes that prolonged the exposure of the stimulus throughout the ISI. The interval between the onset of the stimulus and the onset of the mask (stimulus onset asynchrony (SOA)) was the same in the two conditions. Consistent with a dependence of visual identification on SOA, the percentages of correct identification in the two conditions were approximately similar at all SOAs irrespective of the level of noise, stimulus familiarity, and stimulus complexity. However, departures from the onset-onset rule were also present. While the two conditions yielded virtually identical identification accuracy with an SOA of 80 ms, small but significant differences were found for shorter and longer intervals. Possible theoretical explanations of the results are presented.

Keywords: ISI; backward masking; rapid categorization; fixational eye movements; microsaccade; Bloch's law.

INTRODUCTION

The identification of complex stimuli may occur with very brief presentations. For example, a flash of 20 ms duration is sufficient to enable subjects to report whether an unfamiliar natural scene contains an animal (Thorpe *et al.*, 1996), or to categorize an image according to arbitrary predefined categories (Van Rullen and Thorpe, 2001a, b). Similarly, high percentages of recognition can be obtained in experiments involving the rapid sequential visual presentation (RSVP) of images, each displayed for as little as 80 ms, in which subjects are later required to identify the images that were part of the sequence (Rosenblood and Pulton, 1975). In all these experiments, rapid visual processing critically depends on the presence of a blank interval (ISI) following the presentation of the stimuli. In the absence of

*To whom correspondence should be addressed. E-mail: rucci@cns.bu.edu

such an interval, performance drops drastically in both single stimulus presentation (Breitmeyer, 1984; Kahneman, 1968) and RSVP experiments (Potter and Levy, 1969).

It is an interesting question how the presence of an ISI following a brief stimulus exposure compares to a longer presentation of the stimulus. Would a stimulus presented for a very short exposure followed by an ISI give the same identification accuracy as when the stimulus is exposed for an additional interval equal to that of the ISI? A number of observations suggest that a prolonged exposure of the stimulus should facilitate visual identification. For example, small fixational eye movements have been shown to improve the discrimination of stimuli presented for a few hundred milliseconds (Rucci and Desbordes, 2003), a finding that is consistent with the observation that fixational eye movements strongly modulate the responses of neurons in different cortical areas (Gur *et al.*, 1997; Leopold and Logothetis, 1998; Martinez-Conde *et al.*, 2000; Snodderly *et al.*, 2001). Furthermore, with stimulus presentations longer than 100 ms, contextual modulations of neural activity, presumably originating from feedback from higher cortical areas, can be observed in V1 (Lamme *et al.*, 2002). However, studies on backward masking, the perceptual interference on a first stimulus resulting from a following masking stimulus, have reported that in many circumstances performance critically depends on the length of the interval between the onset of the stimulus and the onset of the mask (stimulus onset asynchrony, SOA) (Bridgeman, 1980; Haber and Nathanson, 1969; Kahneman, 1967; Liss, 1968; Liss and Reeves, 1983; Mewhort *et al.*, 1969; Sperling, 1963). According to this onset-onset rule, visual identification is little affected by how the SOA interval is distributed between stimulus duration and ISI. For example, virtually identical accuracies in identifying the position of a 16 ms flash target followed by a 5 ms ISI and that of a 10 ms target followed by a 10 ms ISI were reported by Donchin (1967).

To investigate the coexistence of these two sets of results, we carefully compare identification accuracy with briefly flashed stimuli that were either followed by a variable ISI or exposed through the ISI interval. In the case of metacontrast, departures from the onset-onset rule have already been observed (Eriksen and Eriksen, 1971; Francis *et al.*, 2004; Macknik and Livingstone, 1998; Schiller, 1965). In this paper, we focus on the case of monotonic (Type A) masking functions produced by high energy masks that conformed to Eriksen's (1980) minimal test: when the mask and stimulus were visually superimposed, the stimulus could not be seen at all. These conditions resemble more closely those occurring during natural viewing, when the stimuli produced by successive fixations overlap on the retina and tend to have comparable intensities. Under these conditions, an analysis of identification accuracy with systematically varied values of stimulus duration and ISI was previously performed by Loftus *et al.* (1992). However, few combinations of ISI and stimulus duration had comparable SOA in that study, and the case of very brief stimulus presentations was not considered.

The experiments we report studied the identification of letters of the alphabet and unfamiliar random line patterns presented in the fovea. Their aim was to revisit the onset-onset rule of visual identification and examine the influence of stimulus complexity, degree of familiarity, and level of noise.

METHODS

Stimuli

Stimuli consisted of letters of the alphabet or random line patterns that were flashed for 13 ms (one frame at a refresh rate of 75 Hz) on a Trinitron CRT monitor with P22 phosphors (decay time less than 1 ms). Line patterns were composed of 3 to 5 randomly oriented segments connected at their vertices or midpoints so that the resulting size and number of pixels were approximately equal to that of the letters. Patterns were embedded in a noisy 44 by 44 pixel matrix (the stimulus matrix) that was displayed on a uniform background. The intensity of the pixels composing the letter or the line pattern was set to 255 (100 cd/m^2), while the intensity of the other pixels in the stimulus matrix and in the background was set to zero. Noise of variable density and amplitude was added to increase the difficulty of identification. Each pixel of the stimulus matrix had a fixed probability D (the noise density) of being affected by noise. The intensity values of noisy pixels were replaced with random values selected from a uniform distribution between 0 and 255. Thus, the stimulus display consisted of three regions: (1) a white letter or line pattern that was affected by noise; (2) an immediate local background around the letter that was initially dark, but in which pixels could assume nonzero intensity values because of noise; and (3) a remote black background that was not affected by noise. Adding noise made the letter on average dimmer, and its local background on average brighter, thus reducing letter contrast. A noise density $D = 0.55$ was used in all the experiments, except in one condition where the noise density was increased to 0.66. Figure 1 shows examples of the stimuli. Only the stimulus matrix is represented in the figure (the uniform background is not shown).

Apparatus and procedure

A fixed distance (46 cm) was maintained between the subject and the CRT monitor by means of a head-rest. At this distance, the stimulus matrix subtended 1.25° . As illustrated in Fig. 2, two conditions, ISI and Duration, were compared. In both types of trials, a fixation point was initially presented for 1 second. At the offset of the fixation point, the stimulus was flashed for 13 ms. In an ISI trial, the offset of the stimulus was followed by a blank interval (ISI) of 26, 66 or 227 ms. In a Duration trial, the stimulus remained on the screen for an additional interval equal to the ISI. At the conclusion of both types of trials, a mask (a high-frequency, maximum intensity checkerboard with random phase) was presented for 660 ms,

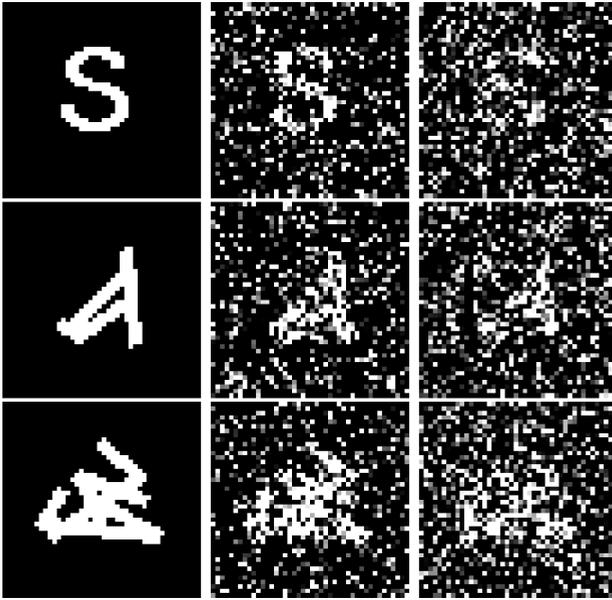


Figure 1. The patterns used in the experiments were letters of the alphabet (top row) and random line patterns with low (middle row) or high number of segments (bottom row). The columns show the effect of varying the level of noise: Left: No noise. Center: Noise density 0.55. Right: Noise density 0.66.

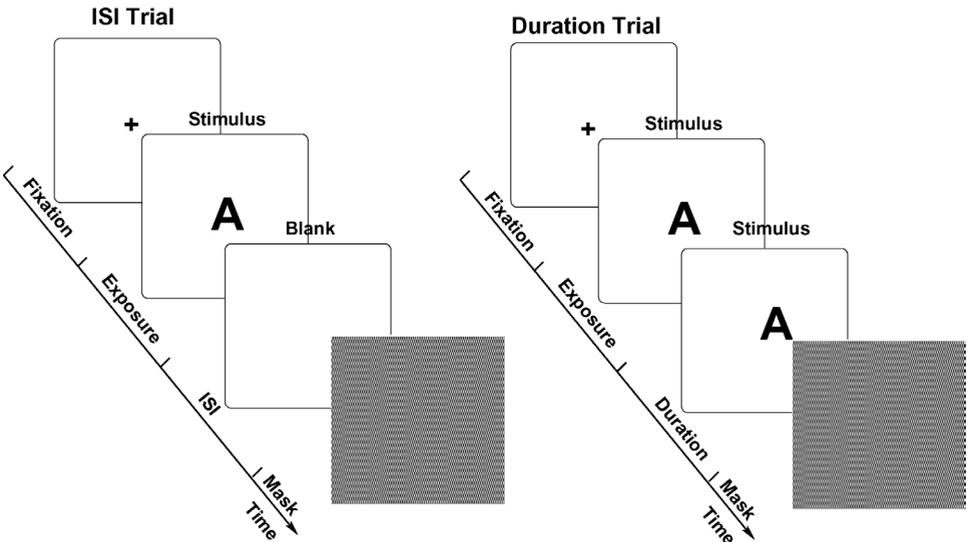


Figure 2. Experimental procedure: Subjects were required to identify a pattern that was flashed on a CRT display. Identification performances in two conditions, ISI and Duration, were compared. Experimental trials for both conditions started with a fixation point and terminated with a mask. In the ISI trials, a blank interstimulus interval followed the presentation of the pattern. In the Duration trials, the stimulus remained visible until the presentation of the mask.

and the subject was required to identify the stimulus by pressing a key on the computer keyboard. In the case of random line patterns, after the presentation of a mask, the stimulus that appeared in the trial was presented together with 9 other line patterns, each matched to a different letter. It should be noted that the probability of correct identification by chance was different in the cases of letters and random line patterns. In one case, stimuli were drawn from 26 possible letters. In the other, the subject identified the correct stimulus among the 10 patterns displayed on the screen.

To evaluate asymptotic performance, each subject received extensive practice involving at least 250 trials prior to the beginning of the experiment. An experimental session was composed of 5 or 6 blocks of 50 trials each. Each block consisted of an equal number of randomly ordered trials for the ISI and Duration conditions. Each subject participated in 2 to 3 experimental sessions of approximately 45 minutes each. Each of the data points was based on 125 (120 with random line patterns) trials for subject MR, 135 (50) for subject GD, and 100 (66) for subject AT.

Subjects

Three subjects with normal or corrected to normal vision participated in the experiments. Two were naive about the purposes of the experiments and were paid to participate. A third subject was one of the experimenters (MR).

RESULTS

Figure 3 shows the percentages of correct identification when letters were either flashed for 13 ms and followed by an ISI, or displayed for a longer period with equal SOA. The individual subject data as well as their overall means are shown as a function of SOA. While individual differences were present, all subjects improved significantly in both the ISI and Duration conditions when the SOA was increased from 40 ms to 240 ms. One-tail z -tests of the differences in the percentage of correct identification at 240 and 40 ms were all significant at the 0.05 level. For subject MR, all the improvement occurred from 40 to 80 ms (ISI $z = 4.35$, $p < 0.05$; Duration $z = 2.63$, $p < 0.05$). For subject AT, performances improved both between 40 and 80 ms (ISI $z = 3.07$, $p < 0.05$; Duration $z = 2.87$, $p < 0.05$) and, in the Duration condition, between 80 and 240 ms ($z = 3.83$, $p < 0.05$). For subject GD, the improvement was more gradual in both ISI and Duration conditions, and the changes in performances between 40 and 80 ms and between 80 and 240 ms were not statistically significant.

Results were in first approximation consistent with a dependence on SOA. For all subjects a prolonged exposure of the letter following a presentation of 13 ms did not result in a large improvement in identification percentages over an ISI of the same duration. However, clear departures from the onset-onset rule were also present. After a SOA of 240 ms, all subjects performed better with the prolonged stimulus

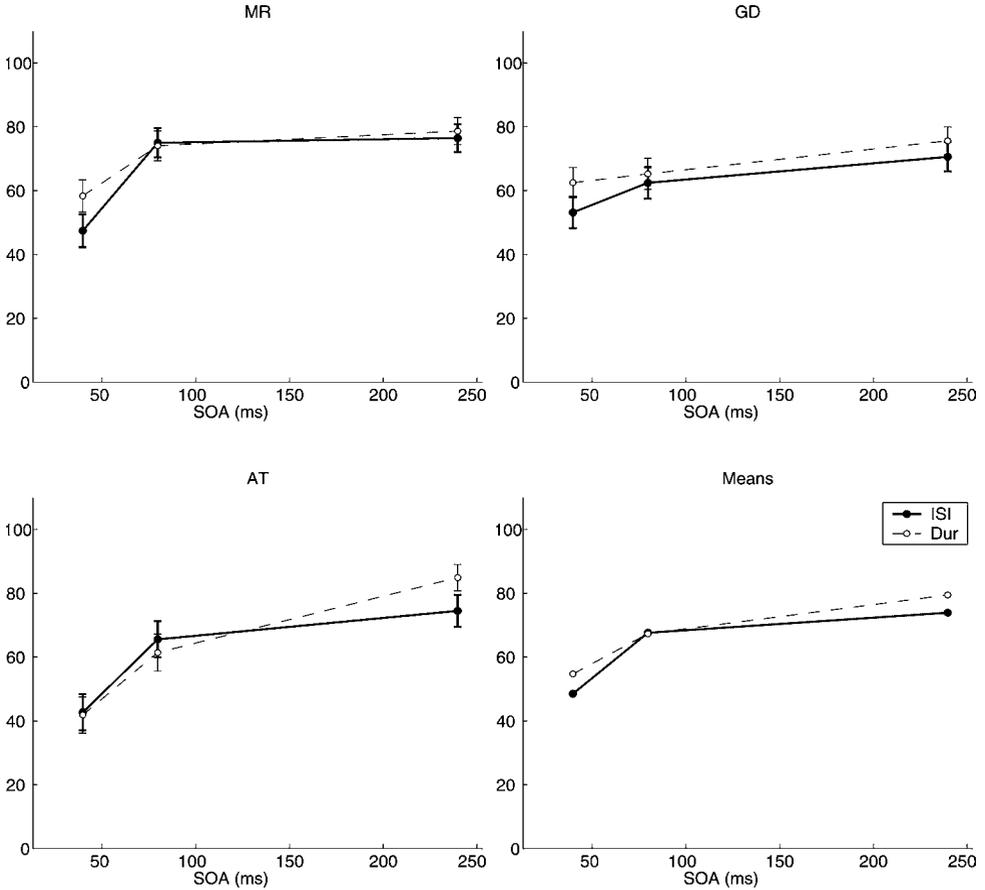


Figure 3. Percentages of correct identification obtained with presentation of briefly flashed letters. The results for each subject as well as the overall means are shown. Filled circles and solid lines show the percentages of correct identification in the ISI condition and open circles and dashed lines in the Duration condition. Error bars at the 0.05 significance level are shown.

presentation. This difference was statistically significant for subject AT ($z = 1.85$, $p < 0.05$; one-tail test) with 85% correct identification in the Duration condition and 74% in the ISI condition. At the 40 ms SOA, a prolonged presentation of the stimulus facilitated identification for subjects GD and MR. Percentages of correct identification in the ISI and Duration conditions differed significantly for subject MR ($z = 1.74$, $p < 0.05$) and fell slightly short of the significance level for subject GD ($z = 1.58$, $p > 0.05$).

To investigate the possibility that the improvement of identification performances in the ISI condition might reflect some type of saturation effect due to the perceptual simplicity of the patterns, we examined the consequences of increasing the level of noise. Figure 4 compares the performances of subjects MR and GD at 0.65 noise density with their previous results at 0.55. Data points at the higher noise density

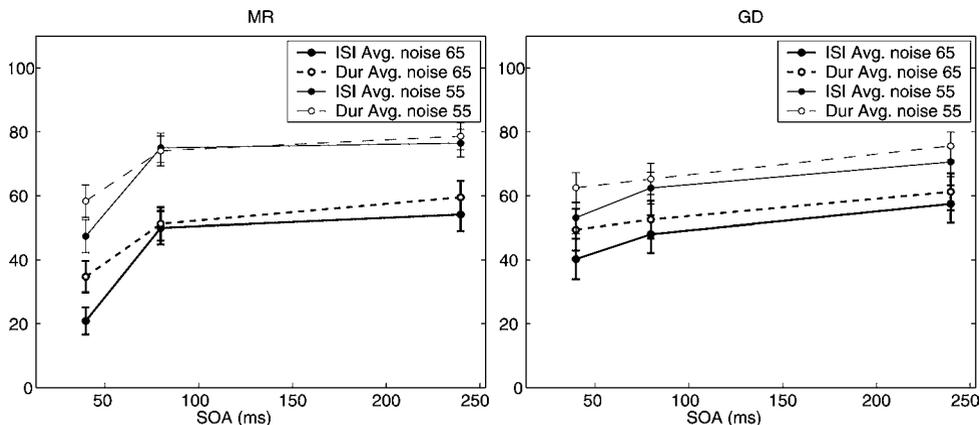


Figure 4. Letter identification with two different levels of noise (noise density 0.55 and 0.65). To allow a direct comparison between performance at different levels of noise, data obtained with noise density 0.55 are plotted again from Fig. 3. Filled circles and solid lines show the percentages of correct identification in the ISI condition and open circles and dashed lines in the Duration condition. Error bars at the 0.05 significance level are shown.

are based on 125 trials for subject MR and on 90 trials for subject GD. As shown in Fig. 4, the ISI and Duration conditions were similarly affected by a higher level of noise. The percentages of correct identification in the two conditions remained close to each other, but a small advantage for a prolonged exposure of the stimulus could still be seen for short and long SOAs. The difference between performances in the ISI and Duration conditions was statistically significant for subject MR at 40 ms ($z = 2.46$, $p < 0.05$).

With an SOA of 240 ms, the small advantage of prolonging the presentation of the stimulus from 13 to 240 ms in the previous experiments should be compared with the case in which, during the presentation, a change in the pattern occurs that reveals additional information on the identity of the stimulus. Figure 5 shows the effect of varying the noise pattern after 120 ms from the onset of the stimulus. The new noise pattern, which was displayed for the remaining 120 ms of the trial, was drawn from the same distribution as the first, but since the pixels affected by the noise were randomly selected, new information on the identity of a letter was effectively displayed in this way. Presentation of the new noise pattern resulted in a substantial improvement in identification performances. After an SOA of 240 ms, percentages of correct identification were now significantly higher in the Duration condition for both MR ($z = 2.64$, $p < 0.05$) and GD ($z = 2.72$, $p < 0.05$), showing that a change in the appearance of the stimulus during the Duration interval is detected and used by the visual system.

It is possible that the high familiarity of subjects with letters contributed to the similarity between the ISI and Duration conditions. For example, cognitive top-down processes may compensate for an incomplete sampling of visual information in the ISI condition, thus raising the percentages of correct identification. To

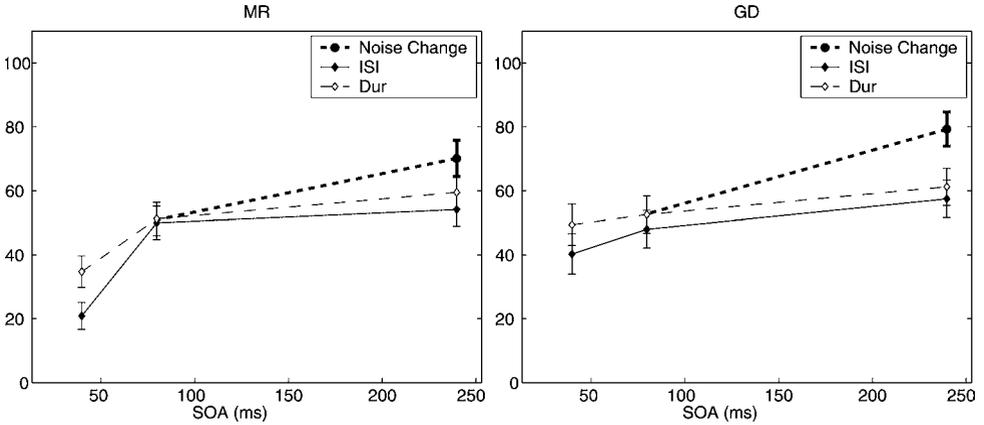


Figure 5. Letter identification with presentation of a new noise pattern after 120 ms. The thick dashed line with filled circles shows percentages of correct identification with the changed noise pattern. The change in the noise configuration occurred only in Duration trials with 240 ms duration interval. Error bars at the 0.05 significance level are shown.

determine the possible role of familiarity, subjects were presented with randomly generated line patterns. The results, shown in Fig. 6, were similar to those obtained with presentation of letters. For subjects MR and GD, improvements in percentages of correct identification occurred mainly from 40 to 80 ms (for subject MR, ISI: $z = 2.25$, $p < 0.05$; Duration: $z = 1.64$, $p < 0.05$; for subject GD–ISI: $z = 2.04$, $p < 0.05$; Duration: $z = 0.81$, $p > 0.05$). For subject AT, improvements were more uniform (ISI 40–80 ms: $z = 1.82$, $p < 0.05$; Duration 40–80 ms: $z = 2.2$, $p < 0.05$. ISI 80–240 ms: $z = 1.99$, $p < 0.05$; Duration 80–240 ms: $z = 2.32$, $p < 0.05$). Similar to the previous case, performances in the ISI and Duration conditions were similar in magnitude, but statistically significant differences between the two conditions were present at the long and short SOAs. For a 240 ms SOA, the difference between 75% correct identification in the Duration condition and 65% in the ISI condition for subject MR was statistically significant ($z = 1.67$, $p < 0.05$). At 40 ms, the difference between 62% in the Duration condition and 44% in the ISI condition was statistically significant for subject GD ($z = 1.70$, $p < 0.05$). The similarity of these data with the results obtained in the case of letters indicates that the degree of familiarity with the stimuli had little influence on how identification accuracy improved with longer intervals in the ISI and Duration conditions.

We also investigated how identification in the Duration and ISI conditions is affected by the complexity of the stimuli. In a further experimental session, subjects MR and GD were presented with random line patterns composed of a larger number of segments, which varied randomly between 7 and 9. Increasing the number of segments made the identification task more difficult as the patterns looked more alike and a finer discrimination was required for correct identification (see Fig. 2).

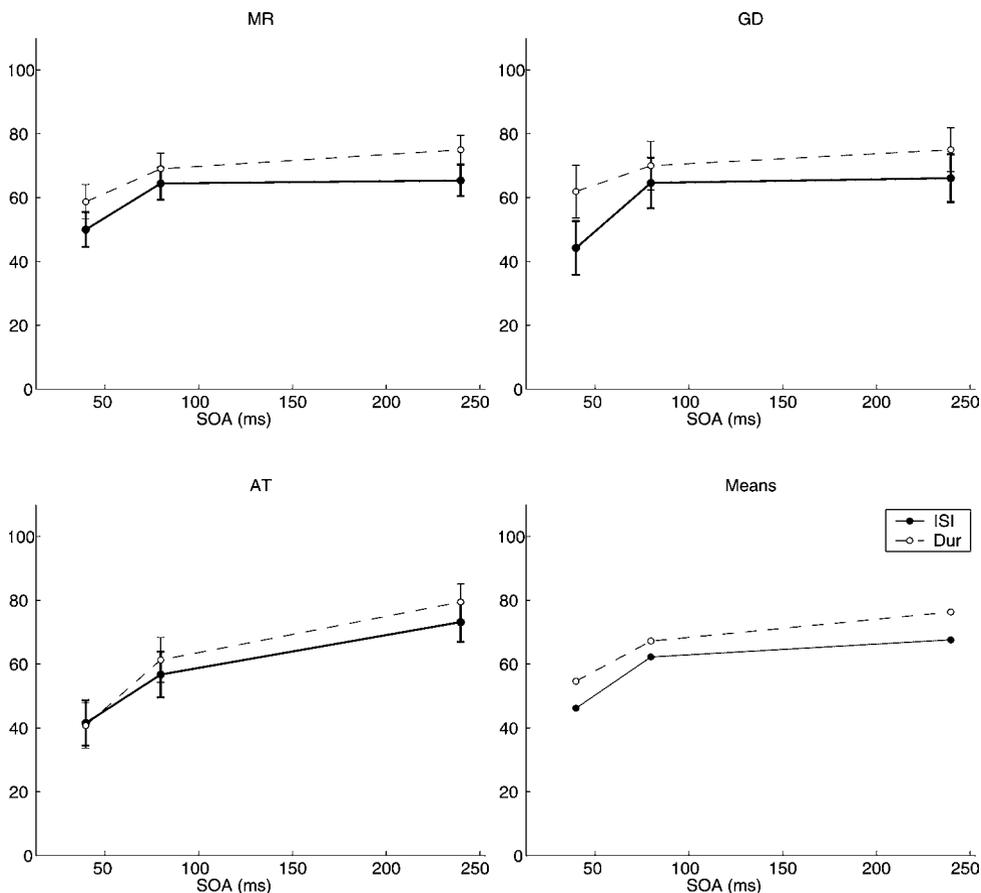


Figure 6. Percentages of correct identification with presentation of randomly generated line patterns. The results for each subject as well as the overall means are shown. Filled circles and solid lines show the percentages of correct identification in the ISI condition and open circles and dashed lines in the Duration condition. Error bars at the 0.05 significance level are shown.

The data shown in Fig. 7 are based on 66 trials for subject MR and 125 for subject GD. In this case, the ISI and Duration curves were more similar and no statistically significant differences between the two conditions were found.

To summarize, although the differences between ISI and Duration conditions were always small, systematic advantages for the duration condition were visible at SOAs of 40 and 240 ms. More specifically, in all experiments and for all subjects, the percentages of correct identification after a 40 ms SOA were greater for the Duration condition in 7 of 10 cases. In 3 cases the differences between ISI and Duration conditions were statistically significant at the 0.05 level: twice for subject MR (11% and 14%) and once for subject GD (18%). At the intermediate interval of 80 ms, the percentages of correct identification in the Duration condition were also higher in 7 of 10 cases, but these differences were never statistically significant. At 240 ms,

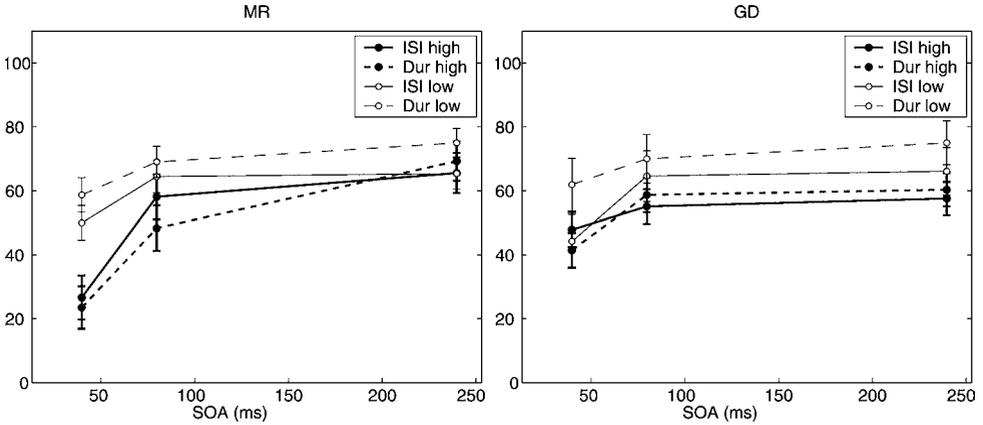


Figure 7. Identification of randomly generated line patterns with two different levels of complexity. Curves with open circles show performances in the ISI and Duration conditions with patterns composed of 3–5 segments. Curves with filled circles show performances in the ISI and Duration conditions with patterns composed of 7–9 segments. Error bars at the 0.05 significance level are shown.

the percentages of correct identification in the Duration condition were greater in all 10 cases. In 2 cases these differences reached the level of statistical significance and corresponded to a 10% improvement of identification in the Duration condition for subject AT and subject MR. We examined these differences over all subjects and experimental conditions in a second level t -test. The mean difference in percentages of correct identification in the ISI and Duration conditions was 5.8% for a 40 ms SOA ($t(9) = 2.28, p < 0.05$), 1.0% at 80 ms ($t(9) = 0.65, p > 0.05$), and 5.6% at 240 ms ($t(9) = 6.02, p < 0.05$). Thus, although the advantage was small, a longer exposure of the stimulus was beneficial for SOAs of 40 and 240 ms.

DISCUSSION

The results of this paper show that while the accuracy of identification of briefly flashed stimuli can be described in a first approximation by a dependence on the interval between the onset of the stimulus and the onset of the mask, small but statistically significant deviations from the onset-onset rule occur as the SOA is varied.

It may appear surprising that, independent of the level of noise and specific familiarity of the stimulus, percentages of correct identification with a presentation of 240 ms, a time comparable to the average duration of visual fixation, did not differ more substantially from those obtained with a stimulus flash of only 13 ms followed by a blank interval of 227 ms. Since the stimulus intensity was the same in the two conditions, one may imagine that the higher level of energy in the Duration condition should lead to a significantly higher level of performance. However, it is

known that time-intensity reciprocity does not hold for the perception of form under conditions of backward masking (Kahneman, 1966). As shown by Donchin (1967), the SOA law applies for stimuli with durations as brief as 10 ms when the stimulus is followed by a mask with comparable or higher intensity.

While in our experiments the departures from the onset-onset rule were relatively small, more substantial deviations have been observed in the case of metacontrast (Eriksen and Eriksen, 1971; Francis *et al.*, 2004; Macknik and Livingstone, 1998; Schiller, 1965). In particular, by using an approach similar to the one of our experiments, Eriksen and Eriksen (1971) reported a significant advantage for the Duration condition in the case of sequential presentation of three stimuli (a number, an arrow, and a letter). Thus, the type of mask appears to play a role in the validity of the onset-onset rule. It should also be noted that some of the conditions of our experiments might have enhanced the similarity between performances in the ISI and Duration conditions. For example, stimuli were always presented at a nominal contrast of 100% (in the absence of noise) and performance was evaluated after the occurrence of substantial training. Training may have a significant impact in these experiments, as subjects may learn to pick up information with very brief exposure duration.

The departure from the onset-onset rule at 40 ms is not surprising. A similar deviation has been previously reported for briefly flashed stimuli with pattern and light masks (Kahneman, 1966; Kaswan and Young, 1963; Turvey, 1973), and it appears to be consistent with a transition from additive to multiplicative interaction between stimulus duration and ISI (Monahan and Steronko, 1977; Turvey, 1973). Whereas SOA has been reported to be the critical parameter in a number of backward masking conditions, including metacontrast (Kahneman, 1967, 1968), pattern masking by a spatially uniform field (Donchin, 1967) and masking by structure (Spencer and Shuntich, 1970; Turvey, 1973), experiments using sparse noise masks have shown a multiplicative interaction between ISI and stimulus duration (Kinsbourne and Warrington, 1962a, b; Turvey, 1973). Since additive and multiplicative mechanisms tend to occur in different visual conditions (dichoptic *versus* monoptic) and with different types of masks, they have been proposed to originate from neural processes at different levels, either in the periphery of the visual system or at a more centrally located processing stage (Turvey, 1973). A multiplicative mechanism requires the critical ISI (the ISI that allows evasion of masking) to be inversely proportional to the duration of the stimulus. Thus, the critical ISI for a flash of 13 ms should be approximately three times the critical ISI required after a stimulus presentation of 40 ms. A simple calculation reveals that a multiplicative mechanism is consistent with an advantage for the Duration condition if the critical ISI for a 13 ms flash is longer than 39 ms.

It is interesting that after the initial advantage for the Duration condition with a 40 ms SOA, performances in the ISI and Duration conditions were virtually identical at 80 ms and then differed again with a 240 ms SOA. While several explanations could account for this pattern of results, in Fig. 8 we propose one

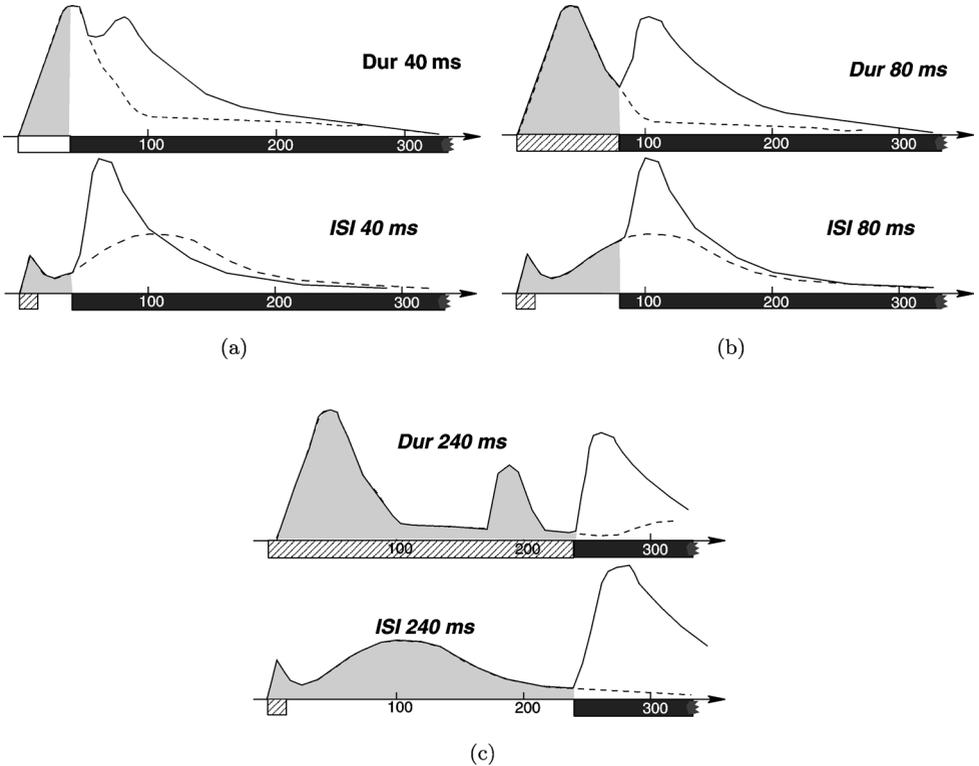


Figure 8. Hypothetical responses of neurons in the primary visual cortex in the Duration and ISI conditions. Each panel illustrates the situation for a specific SOA. The horizontal bars under the time axis represent the experimental sequence of events. The striped light bar represents the exposure of the stimulus. The dark bar indicates the presence of the mask. Solid lines indicate putative neuronal responses due to both the stimulus and the mask. The dashed lines represent the response to the stimulus that would have occurred without presentation of the mask. The shaded area under the trace of neural activity represents the amount of stimulus information transmitted by neuronal firing.

that is consistent with the firing of neurons in the primary visual cortex of the macaque, as measured by recent neurophysiological recordings. Neurons in different visual areas including the retina, the lateral geniculate nucleus, and the primary visual cortex respond strongly both at stimulus onset and at the disappearance of the stimulus (Gawne and Martin, 2002; Humphrey and Weller, 1988; Macknik and Livingstone, 1998; Mastrorarde, 1987). In the macaque, a species with psychophysics of visual masking very similar to that of humans, long transient off-responses in V1 cortical neurons have been correlated with backward masking. That is, a post-stimulus mask that produces visual masking in humans has been found to selectively inhibit neuronal after-discharges in the primary visual cortex (Macknik and Livingstone, 1998). Figure 8 illustrates the putative responses of a V1 neuron for ISI and Duration intervals of different lengths. The curves are based on traces of neural activity recorded in alert monkeys (Macknik and

Livingstone, 1998). In the Duration condition, the onset of the stimulus elicits a strong excitatory response (on-response) that, if undisturbed, decays quickly. In the ISI condition, due to the brief duration of the flash, the onset of the stimulus produces only an incomplete on-response. This initial response is then followed, for long ISI intervals, by a strong discharge generated by the offset of the stimulus (off-response). In both the Duration and ISI conditions, the appearance of a mask gives rise to a new on-response, which interferes with the activity evoked by the stimulus. For an SOA of 40 ms (see Fig. 8a), it is possible that the amount of information about the stimulus conveyed by neural responses (represented in the figure as a shaded area under the firing rates) is greater in the Duration condition than in the ISI condition, thus accounting for the superior performance we found in this condition. At 80 ms (see Fig. 8b), the appearance of the mask may disrupt responses in both conditions in a way that gives rise to a similar amount of transmitted information, thus yielding identical percentages of correct identification in the two conditions. Figure 8c depicts the situation at 240 ms, when transient neuronal discharges in both conditions were presumably little affected by masking, as the stimulus-evoked responses have already decayed at the time of appearance of the mask. In this case, the superiority of performance in the Duration condition may be due to a larger amount of net information conveyed by the on-responses, or to an increased level of neuronal activity with a longer stimulus presentation due to either recurrent excitation from higher cortical areas (Lamme *et al.*, 2002) or additional on- and off-discharges originating from small fixational eye movements (Gur *et al.*, 1997; Leopold and Logothetis, 1998; Martinez-Conde *et al.*, 2000; Snodderly *et al.*, 2001). The burst of activity around 200 ms depicted in Fig. 8c represents the neuronal discharge occurring after a fixational saccade.

The results of this paper illustrate how recent neurophysiological and psychophysical observations supporting an improvement of performance with a prolonged exposure of the stimulus can coexist with well-established results of backward masking. While the onset-onset rule does provide a good first-order approximation of identification accuracy, small but significant improvements are present with a stimulus exposure comparable to the average duration of visual fixation. This advantage can become important in normal viewing conditions when stimuli do not suddenly disappear and when longer fixation periods may allow better discrimination. Further studies are needed to revisit the onset-onset rule of visual identification in the presence of different stimuli and conditions, and determine the implications of an advantage for longer stimulus exposures during natural viewing.

Acknowledgements

This material is based upon work supported by the National Science Foundation under Grant No. 0130851. We thank Dr. Adam Reeves for his useful comments and suggestions.

REFERENCES

- Breitmeyer, B. G. (1984). *Visual Masking: An Integrative Approach*. Clarendon Press, Oxford, UK.
- Bridgeman, B. (1980). Temporal response characteristics of cells in monkey striate cortex measured with metacontrast masking and brightness discrimination, *Brain Res.* **196**, 347–364.
- Donchin, E. (1967). Retroactive visual masking: Effects of test flash duration on the masking interval, *Vision Res.* **7**, 79–87.
- Eriksen, C. W. (1980). The use of a visual mask may seriously confound your experiment, *Perception and Psychophysics* **28**, 89–92.
- Eriksen, C. W. and Eriksen, B. A. (1971). Visual perceptual processing rates and backward and forward masking, *J. Exp. Psychol.* **89**, 306–313.
- Francis, G., Rothmayer, M. and Hermens, F. (2004). Analysis and test of laws for backward (metacontrast) masking, *Spatial Vision* (in press).
- Gawne, T. J. and Martin, J. M. (2002). Responses of primate visual cortical neurons to stimuli presented by flash, saccade, blink, and external darkening, *J. Neurophysiol.* **88**, 2178–2186.
- Gur, M., Beylin, A. and Snodderly, D. M. (1997). Response variability of neurons in primary visual cortex (V1) of alert monkeys, *J. Neurosci.* **17**, 2914–2920.
- Haber, R. N. and Nathanson, L. S. (1969). Processing of sequentially presented letters, *Perception and Psychophysics* **5**, 359–361.
- Humphrey, A. L. and Weller, R. E. (1988). Functionally distinct groups of X-cells in the lateral geniculate nucleus of the cat, *J. Comp. Neurol.* **268**, 429–447.
- Kahneman, D. (1966). Time-intensity reciprocity under various conditions of adaptation and backward masking, *J. Exp. Psychol.* **71**, 543–549.
- Kahneman, D. (1967). An onset-onset law for one case of apparent motion and metacontrast, *Perception and Psychophysics* **2**, 577–584.
- Kaswan, J. and Young, S. (1963). Stimulus exposure time, brightness and spatial factors as determinants of visual perception, *J. Exp. Psychol.* **65**, 113–123.
- Kinsbourne, M. and Warrington, E. K. (1962a). The effect of an aftercoming random pattern on the perception of brief visual stimuli, *Quart. J. Exp. Psychol.* **14**, 223–224.
- Kinsbourne, M. and Warrington, E. K. (1962b). Further studies on the masking of brief visual stimuli by a random pattern, *Quart. J. Exp. Psychol.* **14**, 235–245.
- Lamme, V. A., Zipser, K. and Spekreijse, H. (2002). Masking interrupts figure-ground signals in V1, *J. Cognitive Neurosci.* **14**, 1044–1053.
- Leopold, D. A. and Logothetis, N. K. (1998). Microsaccades differentially modulate neural activity in the striate and extrastriate visual cortex, *Exp. Brain Res.* **123**, 341–345.
- Liss, P. (1968). Does backward masking by visual noise stop stimulus processing? *Perception and Psychophysics* **4**, 328–330.
- Liss, P. and Reeves, A. (1983). Interruption of dot processing by backward mask, *Perception* **12**, 513–529.
- Loftus, G. R., Duncan, J. and Gehrig, P. (1992). On the time course of perceptual information that results from a brief visual presentation, *J. Exp. Psychol., Human Perception and Performance* **18**, 530–549; discussion 550–561.
- Macknik, S. L. and Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system, *Nature Neuroscience* **1**, 144–149.
- Martinez-Conde, S., Macknik, S. and Hubel, D. H. (2000). Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys, *Nature Neuroscience* **3**, 251–258.
- Mewhort, D. J. K., Merikle, P. M. and Bryden, M. P. (1969). On the transfer from iconic to short-term memory, *J. Exp. Psychol.* **5**, 359–361.
- Monahan, J. S. and Steronko, R. J. (1977). Stimulus luminance and dichoptic pattern masking, *Vision Research* **17**, 385–390.

- Potter, M. C. and Levy, E. I. (1969). Recognition memory for a rapid sequence of pictures, *J. Exp. Psychol.* **81**, 10–15.
- Rosenblood, L. K. and Pulton, T. W. (1975). Recognition after tachistoscopic presentations of complex pictorial stimuli, *Canad. J. Psychol.* **29**, 195–200.
- Rucci, M. and Desbordes, G. (2003). Contributions of fixational eye movements to the discrimination of briefly presented stimuli, *J. Vision* **3**, 852–864.
- Schiller, P. (1965). Metacontrast interference as determined by a method of comparisons, *Perceptual and Motor Skills* **20**, 279–285.
- Snodderly, D. M., Kagan, I. and Gur, M. (2001). Selective activation of visual cortex neurons by fixational eye movements: Implications for neural coding, *Vision Neuroscience* **18**, 259–277.
- Spencer, T. J. and Shuntich, R. (1970). Evidence for an interruption theory of backward masking, *J. Exp. Psychol.* **85**, 198–203.
- Sperling, G. (1963). A model for visual memory tasks, *Human Factors* **5**, 19–31.
- Thorpe, S. J., Fize, D. and Marlot, C. (1996). Speed of processing in the human visual system, *Nature* **381**, 520–522.
- Turvey, M. T. (1973). On peripheral and central processes in vision: Inferences from an information processing analysis of masking with patterned stimuli, *Psychol. Rev.* **80**, 1–52.
- Van Rullen, R. and Thorpe, S. J. (2001b). The time course of visual processing: from early perception to decision-making, *J. Cognitive Neurosci.* **13**, 454–461.