

## Physiological Mechanisms Underlying Motion-Induced Blindness

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**Visual disappearance illusions – such as motion-induced blindness (MIB) - are commonly used to study the neural underpinnings of visual perception. In such illusions a salient visual target becomes perceptually invisible. Previous studies are inconsistent regarding the role of primary visual cortex (V1) in these illusions. Here we provide physiological and psychophysical evidence supporting a role for V1 in generating MIB.**

Some of the most striking visual illusions fall into the category of multistable phenomena. These are situations in which an unchanging stimulus generates alternating perceptual states. Some examples are Necker cube reversals, binocular rivalry, ambiguous structure from motion and motion-induced blindness<sup>1</sup>.

Motion-induced blindness (MIB) is a phenomenon of visual disappearance in which a salient target becomes intermittently invisible when surrounded by a field of rotating distractors<sup>1</sup>. Several explanations have been proposed to explain this illusion: slowdown of the attentional switch<sup>1</sup>, interhemispheric competition<sup>2</sup>, depth ordering, surface completion<sup>3</sup> and perceptual filling-in<sup>4</sup> among others. The aim of our first, perceptual, experiment was to test whether having a large surface-inducing mask is necessary for MIB to occur. To do this we compared the effects on the rate of target disappearance of a full mask, a mask that only just surrounded the target and flashing bars around the target<sup>5</sup> (Figure 1A, 1B and 1C). There was no difference between the rates of disappearance or the time the target remained invisible under these conditions

(Figure 1E). To further explore how early in the visual system MIB suppression originates, we asked how MIB is affected by segregating the mask and target across the vertical midline. We arranged target and mask as shown in Figure 1D with the mask only visible at a distance of 1 degree to the left of the target. Then we varied the fixation location so that the mask and target were both on the same side of the midline, or on opposite sides of the midline, and we found that the target disappeared significantly less often when it was on the opposite side of the vertical midline from the mask, compared to the same-side condition (Figure 1F). This result further supports the idea that MIB is generated by suppressive interactions occurring at early visual areas, because only in early visual areas are receptive fields (and their inhibitory surrounds) restricted to one or the other hemisphere<sup>6,7</sup>.

Since the perceptual studies summarized in Figure 1 indicate a role for early visual areas in generating MIB, we looked at the firing patterns of individual V1 neurons in two alert fixating macaques while they viewed the MIB stimulus. One of these monkeys was trained to report the visibility of a peripheral yellow target in the presence of an MIB mask while maintaining fixation on a small spot. Each trial started with the target present in the cell's receptive field, and the monkey was trained to move a lever rightward when he saw the target disappear, and to move it leftward when the target reappeared. In some trials the target actually disappeared and reappeared, and in some trials it remained present throughout the trial. The monkey was rewarded at the end of the trial. Great care was taken to ensure that the lever pulls reflected perceptual reports (see supplementary methods). The pattern of the monkey's reports indicates that macaques,

like humans, perceive disappearances of the salient target in the presence of a moving field of dark blue crosses.

We recorded from single units in V1 while the monkey viewed the MIB stimulus shown in Figure 1A, with the target centered on the receptive field of each cell recorded. A protection zone surrounding the target prevented the mask from entering the activating zone of the V1 cells. We compared V1 neural activity preceding lever presses in trials when the target actually disappeared and re-appeared to the activity in trials when the monkey moved the lever even though the target was continuously present throughout the trial (and we will refer to the lever presses in these latter trials as indicating illusory disappearances). We observed, as expected, an increase in neural activity around 500 ms before lever presses in response to actual target appearances and disappearances, but we also observed a similar, but smaller, average increase in activity before lever presses indicating illusory transitions. However the increases in neural activity preceding illusory transitions were much smaller than the peaks of activity preceding real target transitions and did not reach statistical significance (Fig 2A). We therefore cannot explain the illusory disappearances simply by parallel changes in the activity of V1 cells.

However, we noticed that in the presence of the MIB mask, the responses of the V1 cells to actual appearances and disappearances of the target were often attenuated compared to the mask-absent condition, so we asked whether the mask might weaken or interfere with neural responses to the target in V1. We measured the responses of 25 single cells in V1 to the presentation of the same target with and without the MIB mask in two monkeys during passive fixation. On average, the neurons gave smaller responses to both appearances and disappearances of the target in the presence of a surrounding

mask compared to the no-mask control condition (Fig 2B). On average, there was a significant decrease in the initial peak response to both target ON and target OFF in the presence of the MIB mask (paired t-test,  $p < 0.05$ ), and no significant difference in the sustained responses (300-500ms, paired t-test,  $p > 0.05$ ).

Our physiological recordings from macaque V1 thus showed that although V1 target responses did not parallel target visibility, early signals from V1 in response to target transitions were significantly reduced in the presence of the MIB mask, but the sustained phases of the responses were unaffected. Our failure to observe a reduction in the sustained responses to the target indicates that the perceptual disappearances might not be attributable to the reduction of signals from early visual areas reflecting merely the presence of the target, but rather to changes in signals indicating target transitions. That is, this result raises the question of whether the mask actually does render the target "less visible" or whether it makes the target "more likely to disappear". Therefore we explored this issue perceptually by sinusoidally modulating the luminance of the target in the presence and absence of the MIB mask around two values (a high and a low luminance value). If the MIB mask simply renders the target "less visible" then we expect the target to disappear more frequently during the dimmest periods of the luminance cycle; if the MIB disappearances are caused by changes in the likelihood of "disappearances" then we would expect the target to disappear more frequently during the decreasing brightness phases of the brightness cycle. We found that subjects reported target disappearances much more often right after the target started dimming in the presence of the MIB mask, for both high and low luminance levels (Figure 1G), even though in the absence of the mask the target simply appeared to dim, not disappear. This suggests that

regardless of the absolute value of luminance of the target, under MIB conditions, small transients induce the disappearance of the target, whether this transient originates in the target or within the brain itself.

In summary, we found both perceptual and physiological evidence that MIB can originate in early visual areas. We established that macaque monkeys, like humans, perceive the MIB illusion, and, even though the activity of V1 cells did not correlate directly with the illusory disappearances of the target, the responses in V1 to the target were diminished by the MIB mask. Furthermore, decreases in target luminosity, regardless of absolute luminosity level, induced perceptual disappearances of the target. Such decreases in target luminosity should cause transient OFF responses in a subpopulation of V1 cells. Since perceptual disappearances tended to occur right after the target decreased in luminance, we deduce that these disappearances were caused by OFF responses. Because we also found that under MIB conditions the initial transient responses of V1 cells were reduced (thus bringing the peak response closer to the noise level), we suggest that spontaneous perceptual transitions during MIB are caused by the 'chance' event that a sufficiently large population of OFF cells in visual cortex happened to fire enough to fool the system into believing that a real transition occurred. This would also explain why we found a weak (but not significant) correlation between V1 activity and perceptual state during MIB.

We found that the responses of V1 cells to target onset or offset were reduced in the presence of an MIB mask. So, even though the mask fell well beyond V1 classical receptive fields due to the protection-zone, it still produced a modulatory influence on V1 responses. Primary visual cortex is likely not the only factor influencing the

disappearances, as contextual surround suppression could arise at any cortical level. But the perceptual and physiological results presented here show that effects of the mask in V1 likely contribute to the phenomenon.

The involvement of early visual areas in MIB has been overlooked because several lines of evidence point away from early topographic visual areas as an important locus for MIB. Aftereffects and adaptations, which are assumed to arise in V1, are not affected by MIB disappearances<sup>8,9,10,11</sup>. Furthermore, factors assumed to be important for MIB, such as attention, object selectivity<sup>1</sup>, surface completion, depth ordering<sup>3</sup> and interhemispheric switch<sup>2</sup> are thought to arise at levels higher than V1. It has also been shown that V1 activity does not correlate with perceptual state for other visual disappearance illusions<sup>12</sup>. On the other hand, Kawabe et al. (2007)<sup>5</sup> and Wilke et al. (2003)<sup>13</sup> provided evidence that low-level signals are involved in visual disappearance phenomena. However, because our results implicate the transient phase of visual responses, we can now argue that adaptations and aftereffects not being affected by MIB is not inconsistent with an effect in early visual areas, since adaptations and aftereffects result from prolonged sensory stimulation and are not dependent on the initial burst response<sup>14</sup>.

Even if high-level effects such as object competition or attentional modulation are the final stages responsible for target visibility, our results suggest that the mask-induced reduction in target responses as early as V1 also play an important role. That is, when the signal from lower levels is noisier, the detection processes in higher-level cells will also be more error prone. In this view, we would expect activity in the whole population of V1 cells that respond to the target to correlate to some degree with the perceptual report,

although this correlation need not be as strong as during real transitions, since errors could be initiated anywhere along the pathway, not just at the first stage. This interpretation fits well with other single-unit studies and studies correlating fMRI signals and local-field potentials in early visual areas to perceptual state<sup>15</sup>.

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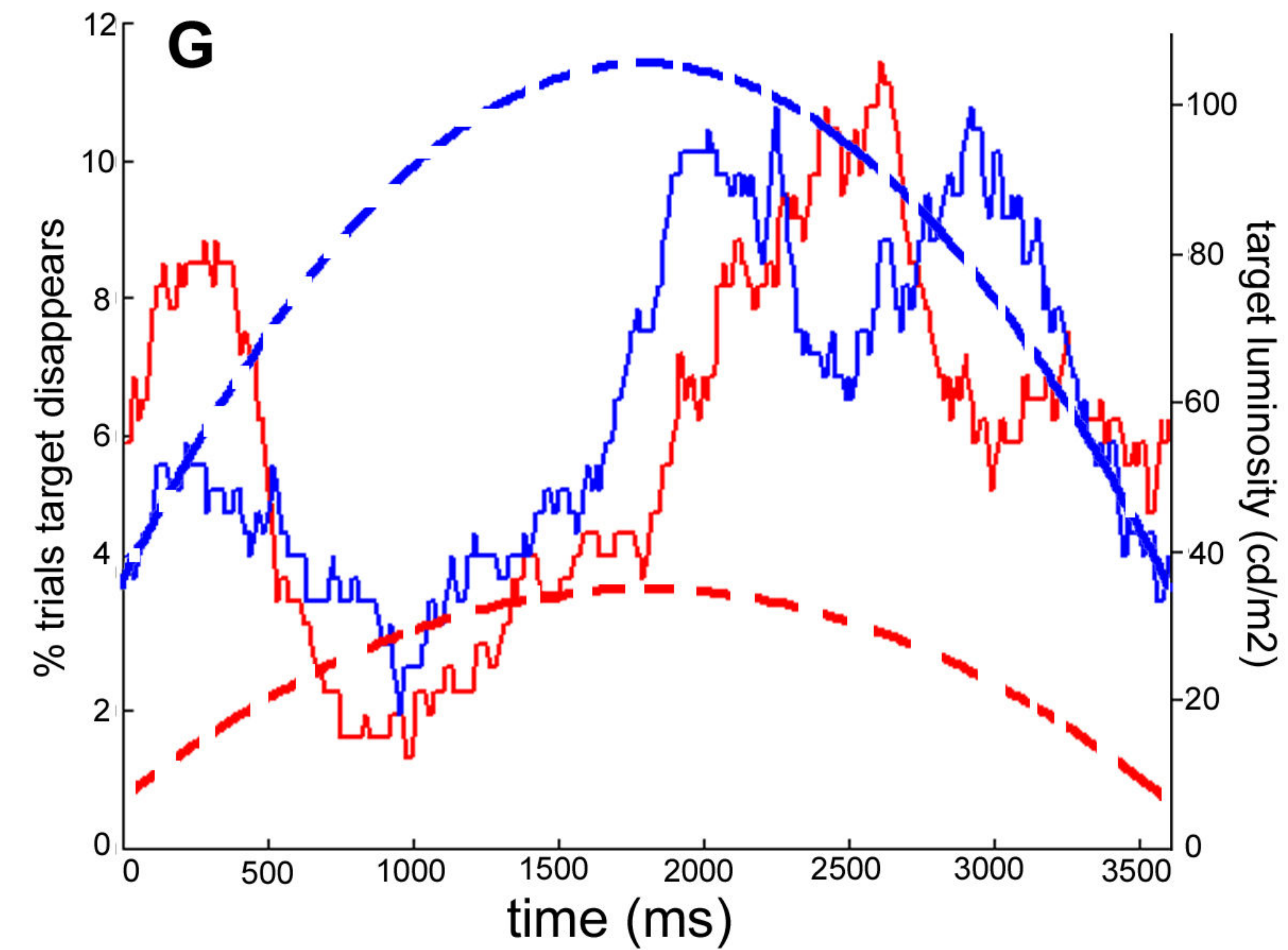
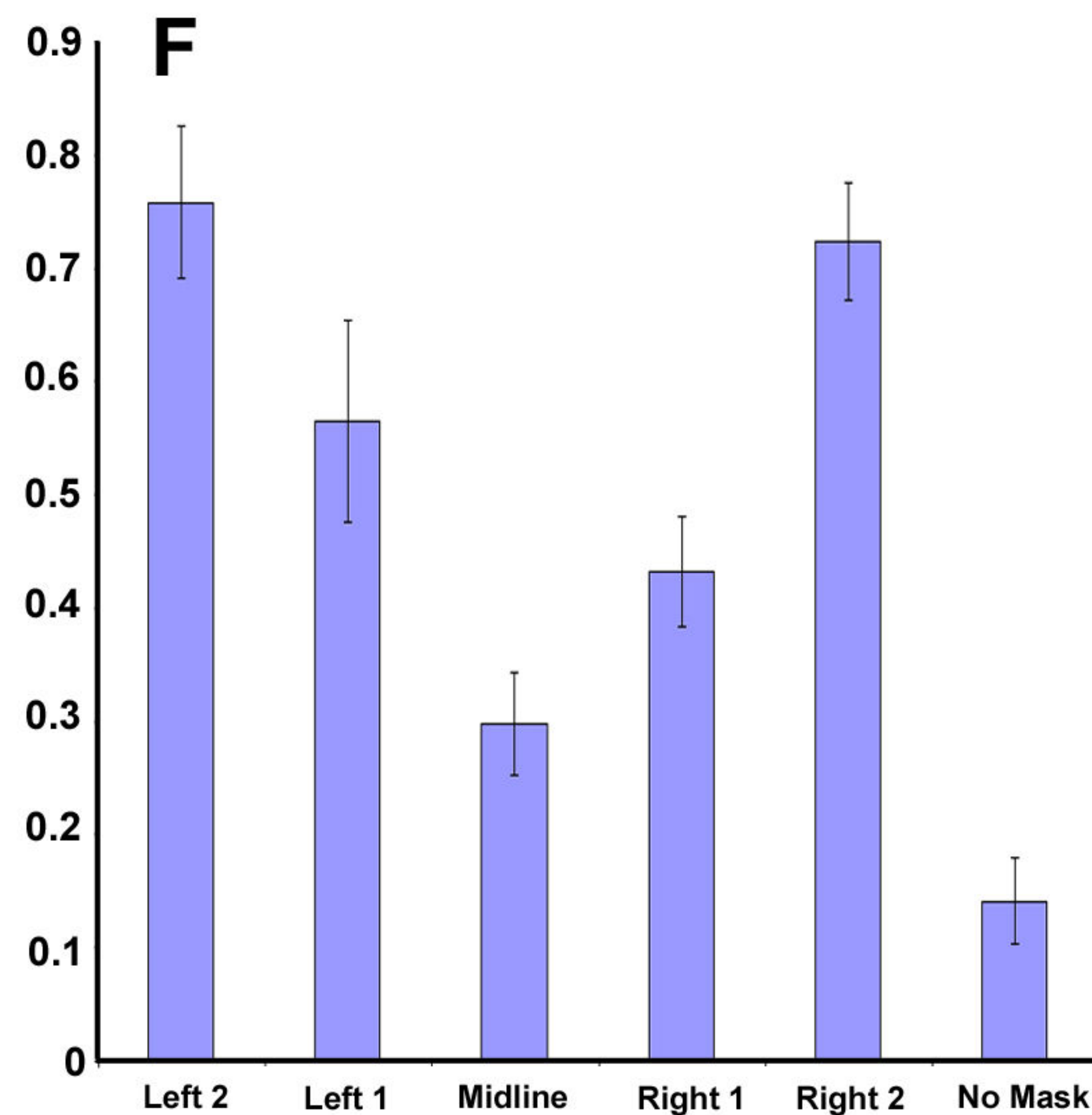
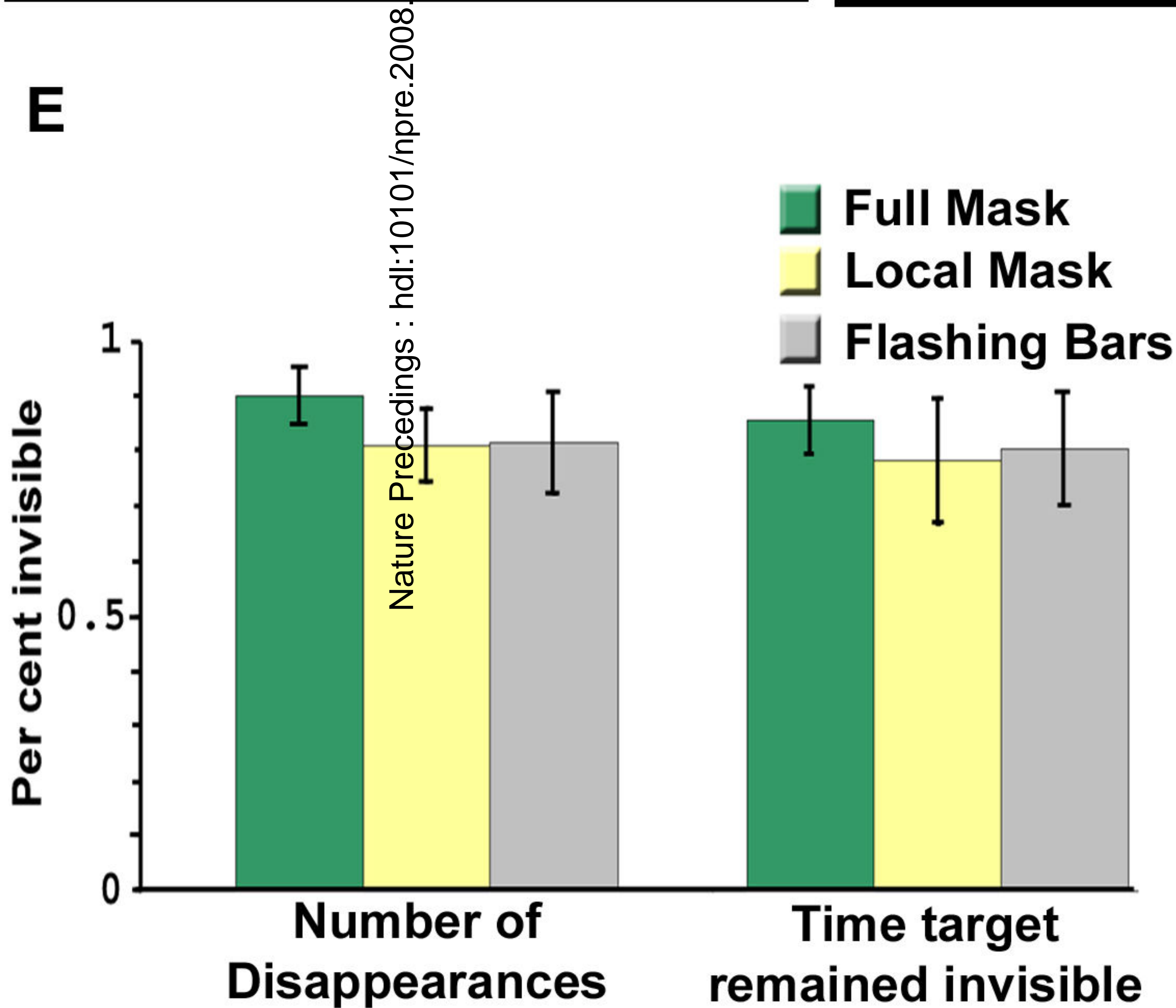
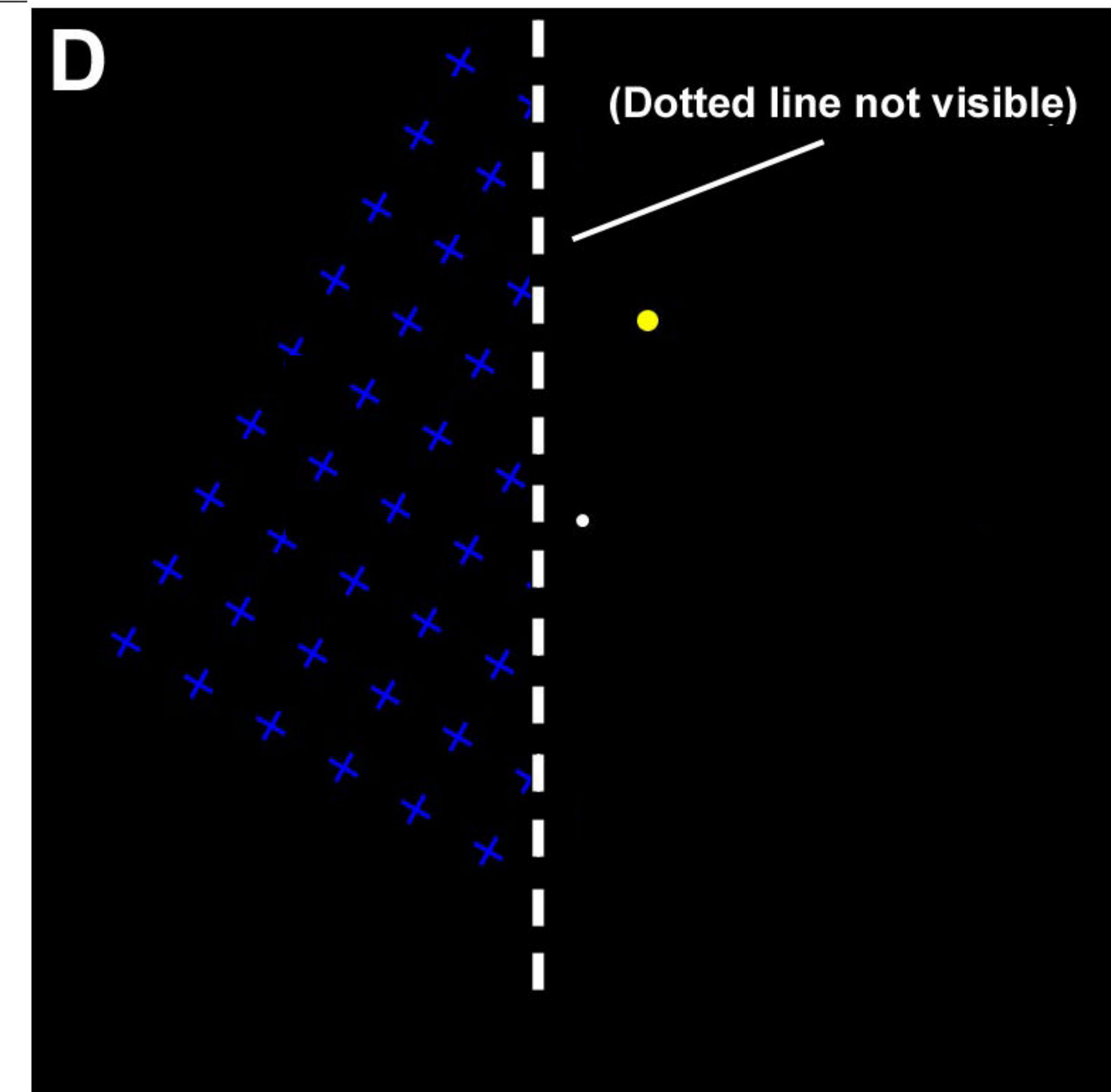
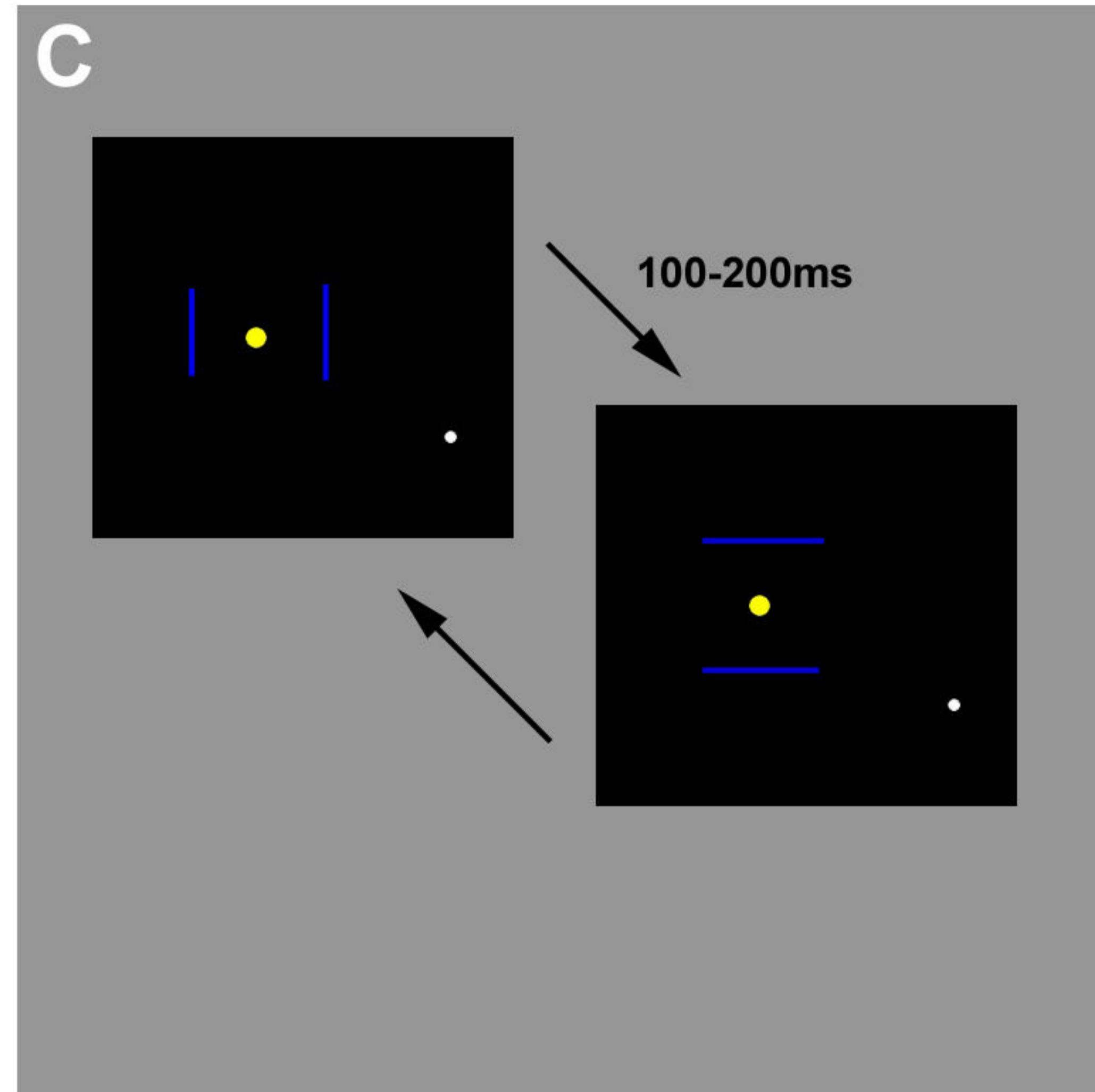
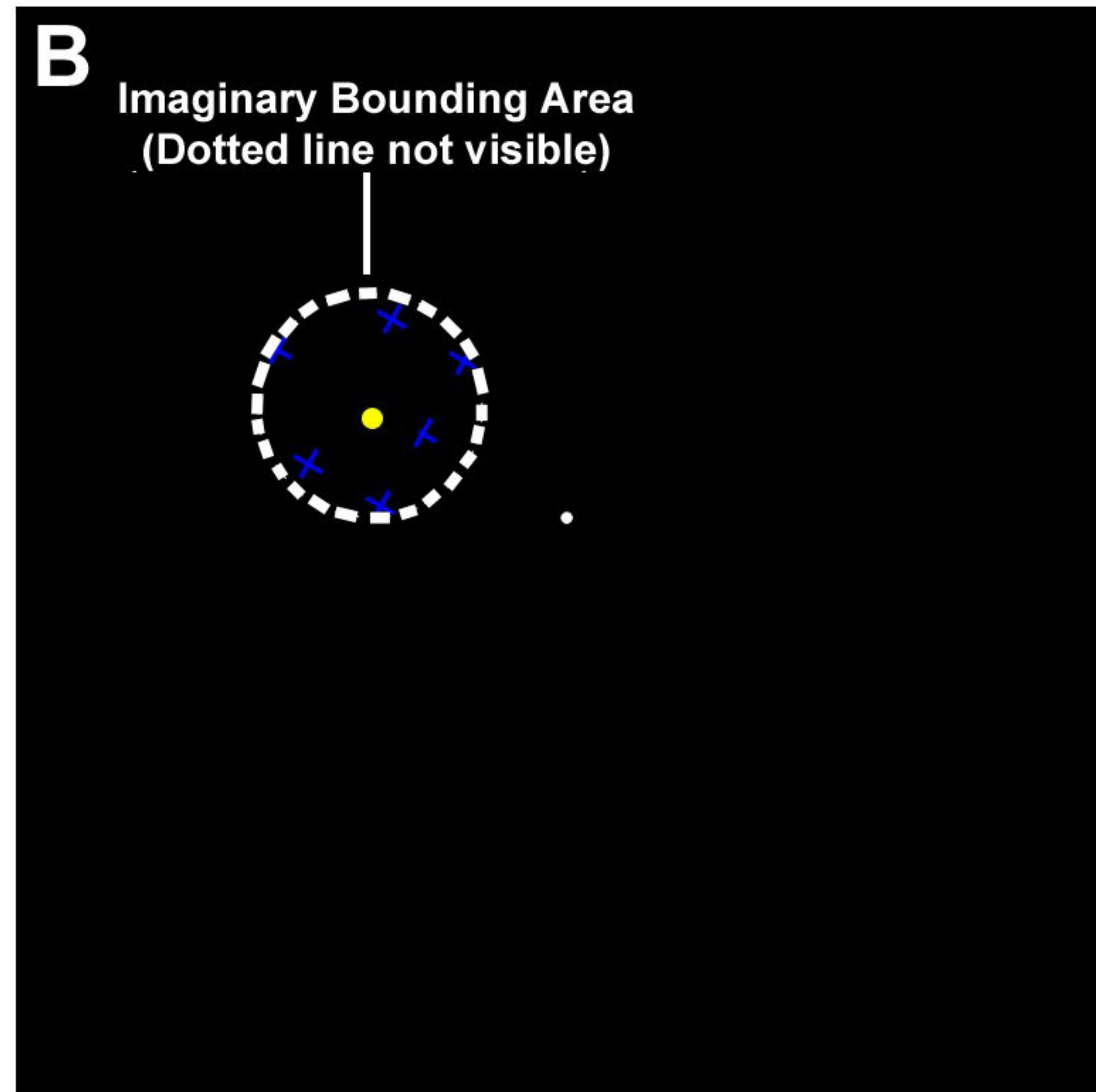
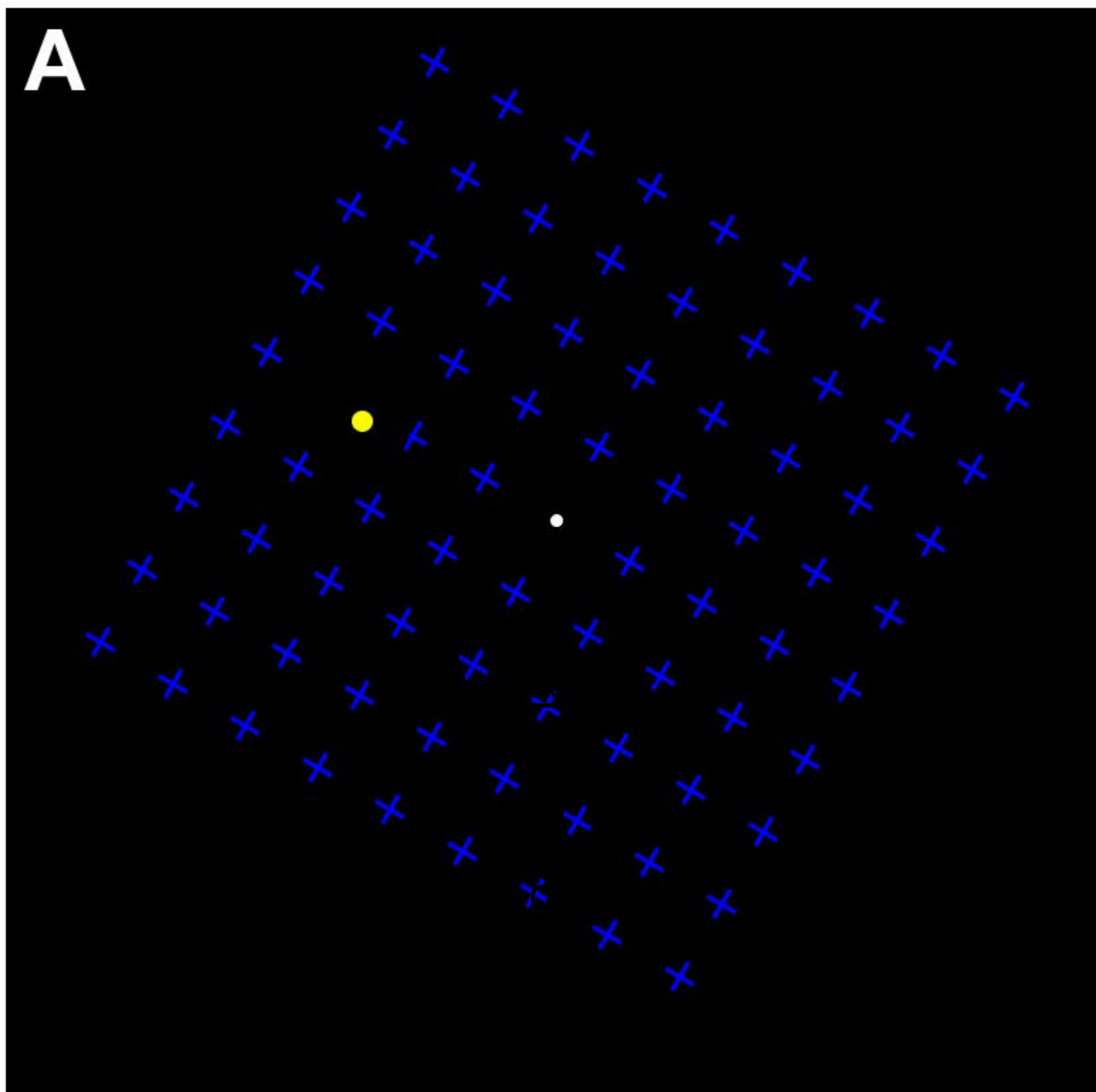
Figure 1. (A) Full mask, a 9 x 9 field composed of 81 equally spaced blue crosses rotated about its center-point (fixation spot) at 45°/s. A yellow target was located 2° from the fixation spot. (B) Local mask. This was the same stimulus as the full mask (A) except that the only part of the mask still present was a 0.5° annulus around the yellow target. (C) Flashing bars. This was the same stimulus as the full mask (A) except that the mask was replaced by two sets of sequentially flashing bars. The frequency of the flashes was 5 – 10 Hz. (D) Stimulus used in experiment 2. Here the mask was only present beyond an imaginary line 1 degree from the target. There are 6 conditions, in all of which the target is 2 degrees from the fixation spot. In Midline, the target is located ½ a degree to the right of the fixation spot. In the Left 1 and Left 2 conditions the target is moved to the left by ½ and 1 degree respectively. And the opposite is true for the Right 1 and Right 2. In the No Mask condition, no mask is present. (E) Average of normalized (to full-mask value) number of disappearances (left) and time of invisibility (right) under Full Mask (green), Local Mask (yellow) and Flashing Bars (grey). Error bars represent 1 standard error. (F) Effect of having mask and target in different hemifields. Stimuli as in Figure 1D. (G) Disappearance rate (percent of times target disappeared each cycle) of the target (continuous lines) and luminosity of target (dotted lines) over time. Red and blue lines represent low and high luminance respectively.



Figure 2. **(A)** Average response of V1 cells when the monkey report target ON (left) and target OFF (right) under illusory (red) or real (blue) transitions. Dotted lines indicate time of lever press. Shaded area denotes the standard error. **(B)** Population average of V1 cells during passive fixation (mean  $\pm$  standard error) to target ON (left) and target OFF (right) of cells with larger response to no-mask condition. Blue line represents the average firing rate when no mask was present and red the average firing rate when the MIB mask was present. Responses were aligned by time to peak and normalized by the maximum firing rate for each cell.



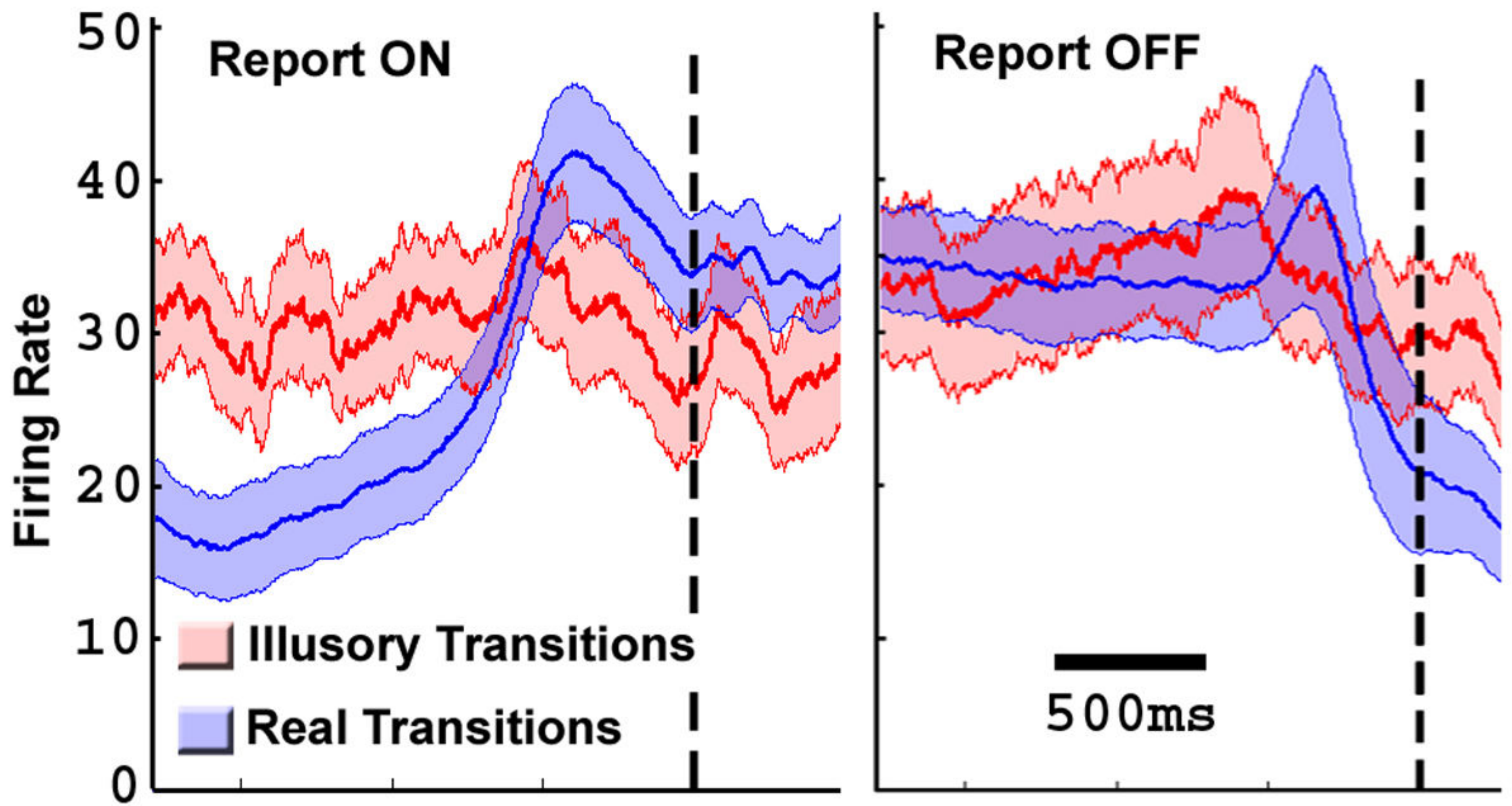
Figure\_1\_Libedinsky





Figure\_2\_Libedinsky

**A**



**B**

