Late responses and perceptual awareness

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An electrophysiological study in monkey primary visual cortex reveals that a late component of neural activity is correlated with perceptual awareness of an object.

The activity of neurons in the brain does not necessarily affect the mind. Most notably, several lines of evidence indicate that certain types of visual stimuli evoke clear responses in neurons in the primary visual cortex (V1) without entering into the awareness of the person (or monkey)[1–3]. What features of responses determine whether they are correlated with perceptual awareness? A study in this issue by Supèr and colleagues addresses this question directly[4].

The authors trained monkeys in a detection task. While the monkey looked at a fixation point in a random texture field composed of line segments of multiple and random orientations, the random texture field was replaced with another texture field containing a square-shaped figure region (Fig. 1), defined by a discontinuity in the orientation of line segments: the line segments within the figure were parallel to each other; those in the outside were also parallel to each other, but they were orthogonal to those within the figure. The position of the figure was randomly selected from three positions. The monkey's task was to detect the figure and make a saccade to it within 500 ms after the stimulus onset. In some 'catch' trials, there was no figure: the whole stimulus field was composed of line segments of a single orientation, and the monkey had to continue fixating for 500 ms to get a reward. Such a figure defined by texture discontinuity is less salient than figures defined by clear luminosity contrast, especially when it is presented peripherally. Indeed, the monkey occasionally continued to fixate even in the trials in which a figure appeared, as if it had failed to detect the figure.

Spike activity of V1 neurons was recorded extracellularly with chronically implanted electrodes while the monkey was performing the task, and the authors examined neural responses to the switch from the random texture to the texture with a figure. Because the monkey reported whether or not it was aware of the figure (by making a saccade versus continuing fixation), the responses of the neurons could be examined in reference to the monkey's perceptual awareness. There were four types of trials, according to whether the figure covered the receptive fields of the recorded cells (figure trials) or the figure was presented at a far distant location (background trials), and whether the monkey detected the figure and made a correct saccade (seen trials) or the monkey continued the fixation neglecting the actually present figure (not seen trials). The orientation of line segments at the receptive fields was identical in all four cases.

In the trials in which the monkey correctly responded with a saccade to the inside of the figure (seen trials), the response was larger in the figure trials than the background trials (Fig. 1). However, only the late component of the response differed (after about 100 ms from the stimulus onset); the initial 60 ms of the responses (following a 40 ms delay) were similar. Because the shortest latency of saccades was about 250 ms in this experiment, the difference was not due to the presence or absence of saccades. Interestingly, there was no such difference in trials in which the

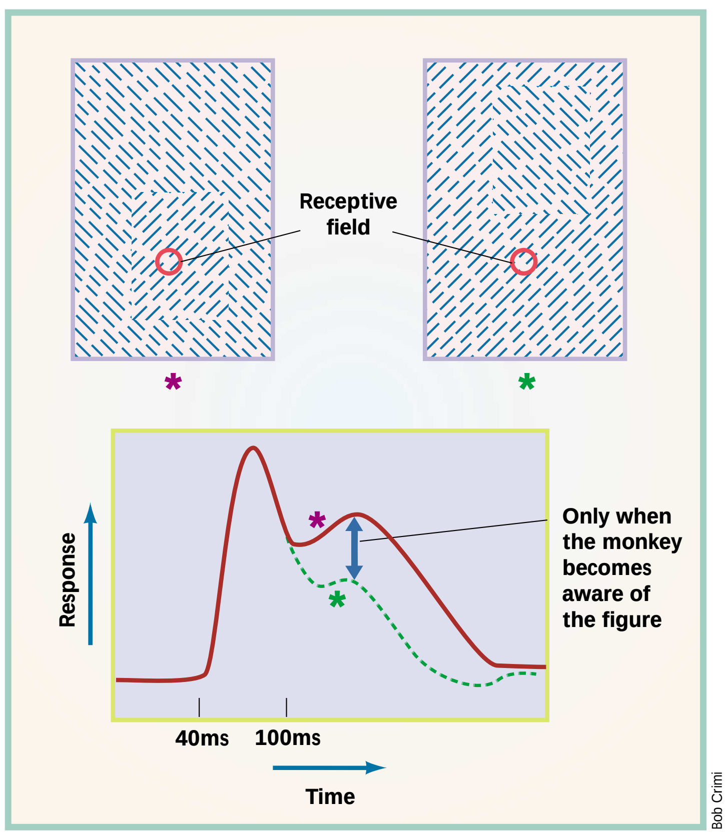

Fig. 1. Context-dependent modulation of late responses in monkey V1 neurons occurs only when the monkey becomes aware of the figure. While the monkey is fixating a point, a texture field (figure) appears, which is defined by a discontinuity in the orientation of line segments. The late response is larger when the receptive field of the recorded V1 cell is located at the inside of the figure than when the figure is distant from the receptive field, even though the stimuli at the receptive fields are identical in the two conditions. The novel finding of this study is that this modulation occurs only when the monkey becomes aware of the figure. The onset of the differential response occurs at about 100 ms—about 60 ms later than the onset of the non-differential initial responses.

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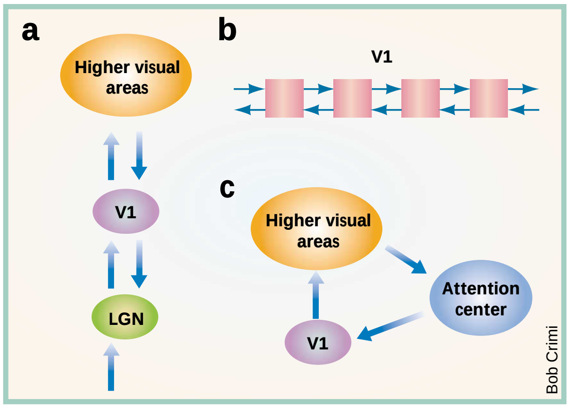

Fig. 2. Three possible mechanisms for the delay of context-dependent modulation. (**a**) The figure is detected in a higher visual area, and the signal is passed back to V1 along the serial pathway. (**b**) The texture borders are detected by V1 cells distant from the recorded V1 cells, and the signals are propagated to the recorded cells along the intrinsic horizontal connections within V1. (**c**) The detection of the figure triggers spatially specific attention, which in turn facilitates V1 neurons with receptive fields around the figure, and suppresses V1 neurons with receptive fields at the background. Feedback, lateral propagation or attention, rather than perception of the figure itself, may fail when the monkey does not become aware of the figure.

monkey continued fixation, neglecting the actually present figure: responses in the not-seen background condition were as strong as those in the not-seen figure condition. Thus, the modulation of late responses appeared when the monkey detected the figure, but not when the monkey failed to detect it. Only the late responses of V1 neurons were correlated with the monkey's perceptual decision. The initial responses were always the same, regardless of the figure position or monkey's decision.

However, when the proportion of the catch trials was increased, the monkey more often continued to fixate in trials in which the figure was actually presented, and the difference in V1 neuron responses between the figure and background trials appeared even in these not-seen trials. Unlike the results in the first experiment, therefore, the modulation of late responses in V1 neurons in this second experiment was no longer correlated with the decision of the monkey. To explain both results consistently, we have to introduce an intermediate stage between a more mechanistic part of perception and the decision making. The modulation of late responses in V1 neurons reflects the activity of the intermediate stage, whereas the unmodulated parts of responses, including the initial responses, represent the mechanistic perception. An increase in the proportion of the catch trials raised the threshold of the decision making, and therefore resulted in a partial dissociation between the intermediate and decision-making stages. In the second experiment, the signal of the figure entered into the second stage, but did not cause a saccade in many trials because of the high threshold. Thus, the authors suggest that the late responses of V1 cells do not reflect the perceptual decision itself, but rather some process at an intermediate stage between mechanistic sensation and decision making.

Why does the context dependence of V1 cell responses (the difference between figure and background trials) appear late? There are at least three possibilities (Fig. 2). One possible explanation of the delay is that the modulation is caused by feedback from higher visual areas. The texture borders are detected as early as in V1 (refs. 5, 6), and neurons in the inferotemporal cortex respond to shapes defined by texture borders as well as those defined by luminosity contrast[7,8]. Therefore, the signal could travel along the serial connections from V1 to a higher visual area and then return to V1 in the opposite direction along the same pathway, which takes time. Another possibility is that the texture borders are detected by V1 neurons with receptive fields located at the borders, and the signals propagate along the intrinsic horizontal connections within V1 to the recorded cells. There is evidence that subthreshold excitation linearly propagates in V1 with constant speed[9]. A third possibility is that the detection of the figure, probably in a higher visual area, is conveyed to an attention center, in prefrontal or parietal cortex, or somewhere else, to evoke spatially selective attention, which enhances responses in the part of V1 corresponding to the figure.

The same group of authors previously found that this context-dependent modulation of V1 cells disappears when the monkey is anesthetized[10]. However, even when monkeys are anesthetized, detection of texture borders by V1 neurons is preserved[6], and inferotemporal neurons still strongly respond to various shapes[11,12], although the influence of anesthesia on their responses to shapes defined by texture discontinuity has not been examined. Therefore, the failure to evoke modulation, and the monkeys' detection of the figure, is likely to be caused by the failure of backward signal propagation, horizontal propagation within V1, or an attentional mechanism—but not by failure of the detection of the figure itself.

Supèr and colleagues also found that late responses in V1 cells were suppressed when the figure at a distance from their receptive fields was detected compared when it was not detected; the late response was larger in the seen figure trials than in the not-seen figure trials, whereas it was smaller in the seen background trials than the not-seen background trials[4]. This can be easily explained by the spatial attention hypothesis. Spatial attention facilitates responses to stimuli in the attended visual field, whereas it may suppress stimuli in the unattended field. It is more difficult to explain this suppression in the framework of the feedback or horizontal propagation hypotheses. In any case, the findings by Supèr and colleagues open a new window toward the neural basis of consciousness[13].

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