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Neuroscience Letters 344 (2003) 75–78

Neuroscience Letters

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Figure–ground activity in primary visual cortex (V1) of the monkey matches the speed of behavioral response

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Received 28 January 2003; received in revised form 17 March 2003; accepted 18 March 2003

Abstract

To look at an object its position in the visual scene has to be localized and subsequently appropriate oculo-motor behavior needs to be initiated. This kind of behavior is largely controlled by the cortical executive system, such as the frontal eye field. In this report, we analyzed neural activity in the visual cortex in relation to oculo-motor behavior. We show that in a figure–ground detection task, the strength of late modulated activity in the primary visual cortex correlates with the saccade latency. We propose that this may indicate that the variability of reaction times in the detection of a visual stimulus is reflected in low-level visual areas as well as in high-level areas.

Keywords: Neurophysiology; Figure–ground; Contextual modulation; Reaction time; Primary visual cortex; Saccade; Eye movement; Monkey

The time it takes to react to a stimulus is related to the transformation of the sensory signal into a motor command. In the visual system, neural correlates of visuo-motor processes have been observed in the parietal and frontal cortex [2,3,7,11,12,17–19]. In these areas, the late component of neuronal activity (after ~130 ms) evoked by a visual stimulus is transformed into motor-related activity that correlates with the speed of the behavioral response, i.e. a voluntary eye movement, where stronger responses lead to faster reaction times [5,7,14,18,19]. However, prior to this movement-related activity, discrimination of the visual target has to occur.

Neuronal correlates of target discrimination or stimulus segregation have been found in the primary visual cortex (V1) [20]. In a figure–ground discrimination task, the late activity (after ~100 ms) of V1 neurons is larger when their receptive field is on the figure than when it is on the background. This enhanced neuronal activity depends on the global context of the stimulus in the visual scene, and is referred to as contextual modulation. It can be elicited by several cues that segregate figure from ground, such as orientation, motion, disparity or color differences [8]. In this study, we examined to what extent this late visual processing relates to the speed of the behavioral response to a stimulus. Therefore, we analyzed the properties of contextual modulation as a function of the reaction time.

For this study we tested two monkeys (*Macaca mulatta*) in a figure–ground detection task. Stimuli were presented on a 21-inch monitor (28° × 21° of visual angle, resolution 1024 × 768 pixels, refresh rate 72.34 Hz). In each trial, a square of 3° was randomly presented at one out of three possible locations at an eccentricity of 2.74–4.4° from the fixation point (a central red spot of 0.2°). Trial onset consisted of the abrupt transition from a texture of randomly oriented line segments into a texture of oriented line segments with a 90° orientation difference between figure and ground (Fig. 1A). Line segments (0.44° × 0.027°) could have 135° or 45° orientation. Both orientations were used for both figure and background. Animals were trained to fixate at the fixation point on the monitor and to make a saccade towards the figure, as soon it appeared (300 ms after onset fixation). The maximum time allowed for responding to the figure was 500 ms. Reaction time was measured by calculating the time at which the saccade towards the position of the 'figure' was initiated. Trials where the

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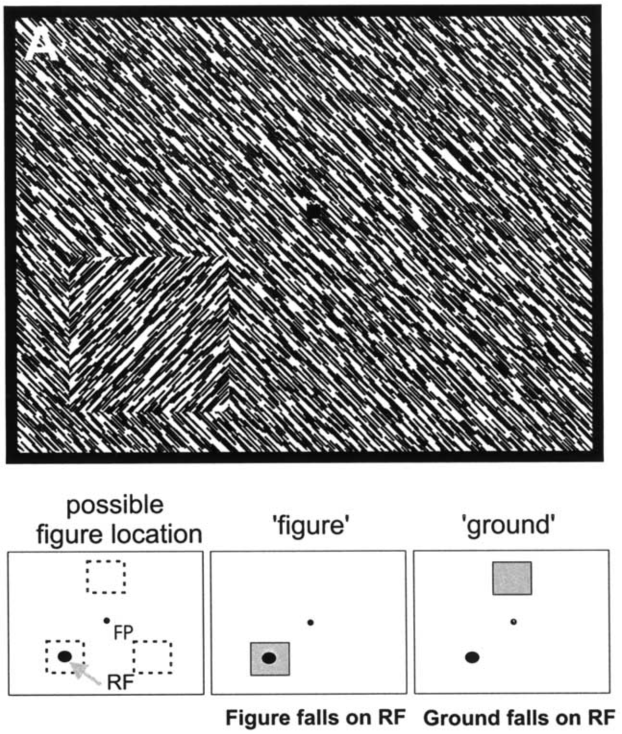
doi:10.1016/S0304-3940(03)00360-4



B	Figure	Ground
Early 135	260±15	256±18
Late 135	321±33	332±43
Early 45	257±17	260±16
Late 45	318±35	325±39

Fig. 1. Illustration of a figure–ground display and reaction times. (A) A texture of random line segments with a difference of 90° in line orientation results in a figure–ground percept (not drawn to scale). Animals had to fixate at a central point (FP) for 300 ms before the appearance of the stimulus. At stimulus onset, a texture appeared with a figure in one of three possible locations (indicated by dotted squares) and the animals had to make a saccade towards the figure (indicated by the rectangle). The circle indicates the location of the receptive fields (RF). When the figure was overlying the receptive fields responses to 'figure' were recorded. In the two other figure locations, 'ground' responses were obtained. (B) The table shows mean reaction times in ms and standard deviation for early and late saccades for figure and ground. The numbers 135 and 45 indicate the degree of line orientation of the figure and ground textures.

animals made incorrect eye movements were discarded. Eye movements were monitored using scleral search coils and digitized at 400 Hz.

While the animals were performing the figure–ground task, multi-unit activity of V1 neurons was recorded through chronically implanted micro-wire electrodes (16 out of ~40 electrodes per animal). Prior to the experiments, aggregate receptive field size and positions at each recording site were determined. Receptive field size ranged from 0.7° to 1.4°, and eccentricity from 1.3° to 5.2°. For each monkey, figure positions and electrodes were chosen such that the figure covered the receptive fields of the recording sites simultaneously. When the figures were on the other two locations, the receptive fields were covered with background. These two locations were used for the 'ground' response. For each recording site the responses were divided by the maximum peak response, so that the relative differences between conditions (figure, ground, early, late) were maintained in spite of this normalization. The strength of contextual modulation was calculated by subtracting the ground activity from the figure activity. In this way we obtained the neural responses related to the perception of the figure [8] although other responses, e.g. saccade-related activity, may be included.

The performance of detection of the figure was 95.8% for monkey 'U' and 92.4% for monkey 'T'. To analyze the neuronal responses as a function of the reaction time we divided the neurophysiological data according to the saccade latencies. For each trial, the saccade latency was calculated and the neuronal data were accordingly placed into the early or late saccade latency group. This was done in such a way that the distributions of early saccades for the figure trials did not overlap with the late saccades for the ground trials and that for both conditions an approximately equal amount of trials for fast and short saccade latencies were obtained (Fig. 1B). In addition, the responses were separated according to the orientation of the line segments (indicated by 135° and 45°) of the figure–ground textures. To calculate contextual modulation, we compared figure responses from a particular orientation with ground responses from the same orientation. A difference in response to figure compared to ground would thus have to come from a mechanism that is sensitive to the global context (figure or background) of the line segments that are on the receptive fields and not from a difference in, for example, orientation tuning [8,20].

The neurophysiological data from the figure–ground display show that the initial neuronal response is similar for figure and ground (Fig. 2). The late (>100 ms) activity,

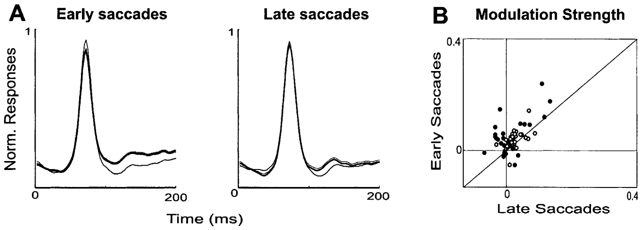


Fig. 2. Average neurophysiological figure–ground responses for fast and slow reaction times. (A,B) An example of the averaged neuronal activity for figure and ground. After ~100 ms, the figure response (thick line) is stronger than the ground response (thin line). This differential response is called contextual modulation (shaded areas). SEM is plotted as dots above the figure responses. (B) Average modulation strength (figure–ground response) for each recording unit for late vs. early saccades. Filled circles indicate the 135° line orientation and open circles the 45° line orientation of the stimulus.

however, is stronger when the receptive field is covered by a figure than when it is covered by background. This part of the response thus segregates figure from ground (= contextual modulation). Analyzing the averaged responses separately for early and late saccade trials shows that contextual modulation is stronger for trials in which the animals responded faster than for the late saccade latency trials (Fig. 2A; both animals $P < 10^{-4}$, *t*-test). In addition, we calculated the strength of modulation between 100 and 200 ms after stimulus onset for each recording site and for each orientation separately (Fig. 2B). The findings revealed that contextual modulation is stronger for fast than for slow saccades (differences between early and late saccades: 'T' 135°: $P < 0.0001$; 'T' 45°: NS; 'U' 135°: $P < 0.005$; 'U' 45°: $P < 0.001$, paired *t*-test).

By comparing the figure responses with the ground responses, it is assumed that they are elicited by an identical receptive field stimulus. However, the receptive fields of some of the recorded neurons lie partly on the border of the figure (Fig. 3). Therefore, we analyzed the averaged responses from recorded units with receptive fields partly lying on the border of the figure and the ones with the receptive fields in the center of the figure separately. These results show that in both conditions (center, border) modulation is stronger for the early saccades than for the late saccades (both animals: border $P < 0.007$; center $P < 0.005$, *t*-test).

It is conceivable that the saccade latencies found are correlated with the onset of the neuronal correlate of figure–ground segregation. Hence, we looked at the time at which contextual modulation started. The onset of modulation was calculated as the first sample of the first epoch of eight samples (~20 ms) of the figure response that significantly ($P < 0.01$) differed from the ground response. These results show that the onset latencies of modulation for early saccades are not different from the onset latencies of modulation for late saccade latencies (mean latency ± SEM: early 135°: 'T' 107 ± 13 ms, 'U' 97 ± 10 ms; late 135°: 'T' 106 ± 17 ms, 'U' 106 ± 11 ms; early 45°: 'T' 110 ± 10 ms, 'U' 142 ± 10 ms; late 45°: 'T' 124 ± 4 ms, 'U' 103 ± 14 ms; differences between all conditions: $P > 0.2$, except 'U' early 45° vs. 'U' late 45°, $P < 0.05$). Thus, no systematic correlations are observed between onset latencies of contextual modulation on the one hand and saccade latency on the other hand.

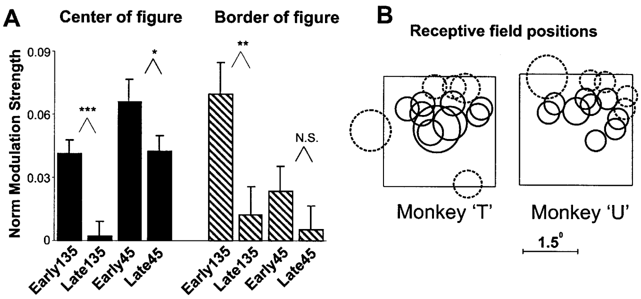


Fig. 3. Strength of contextual modulation for the center and border of the figure. (A) Average modulation strength for receptive fields that are fully within the margins of the figure (center, black bars), and for those that touch the figure–ground contour (border, striped bars). $^{***}P < 0.0005$, $^{**}P < 0.005$, $^{*}P < 0.01$. (B) Receptive field locations relative to the position of the figure (square). Dashed circles indicate receptive fields that touch the border.

In conclusion, the strength (and not the latency) of the figure–ground signal shows a relationship with the moment of the generation of an eye movement, i.e. stronger modulation leads to shorter reaction times, whereas no difference in the onset of modulation between early and late saccades is found.

The execution of a saccade is controlled by neurons in the frontal eye field (FEF) in the prefrontal cortex [5, 14–16]. By the time that movement-related activity in the FEF is initiated (>130 ms) [1,14,15,18,19] contextual modulation in V1, which starts around ~100 ms after stimulus onset (present results and Refs. [8,20]), is however already present. This means that during a period of approximately 100–300 ms both V1 and FEF have enhanced activity carrying information about the subsequent saccade latency. V1 is reciprocally connected with numerous extra-striate cortical areas [4], whose late activity also conveys information about saccade latencies [2,3,11,12,17], and contextual modulation in V1 partly depends on feedback from these higher visual areas [6,9,10, 13]. The feedback projections may have an attentional influence on V1 or may send a corollary discharge to inform V1 about the saccade processing. Alternatively, the present results may also indicate that the generation of a saccade occurs by distributed activity. We propose that saccade processing occurs through recurrent interactions between sensory and motor areas and that the variability of the reaction times is a reflection of the variability of the cooperation between these areas.

Acknowledgements

We thank Kor Brandsma and Jacques de Feiter for biotechnical support, and Peter Brassinga and Hans Meester for technical assistance. Hans Supèr is supported by a grant from Medical Sciences (MW), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

References

[1] J. Assad, Now you see it: frontal eye field responses to invisible targets, Nat. Neurosci. 2 (1999) 205–206.

[2] C.L. Colby, J.-R. Duhamel, M.E. Goldberg, Visual, presaccadic and cognitive activation of single neurons in monkey lateral intraparietal area, J. Neurophysiol. 76 (1996) 2841–2851.

[3] C.L. Colby, M.E. Goldberg, Space and attention in parietal cortex, Annu. Rev. Neurosci. 22 (1999) 319–349.

[4] D.J. Felleman, D.C. Van Essen, Distributed hierarchical processing in the primate cerebral cortex, Cereb. Cortex 1 (1991) 1–47.

[5] D.P. Hanes, J.D. Schall, Neural control of voluntary movement initiation, Science 274 (1996) 427–430.

[6] J.M. Hupé, A.C. James, B.R. Payne, S.G. Lomber, P. Girard, J. Bullier, Cortical feedback improves discrimination between figure and background by V1, V2, and V3 neurons, Nature 394 (1998) 784–787.

[7] J.-N. Kim, M.N. Shadlen, Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque, Nat. Neurosci. 2 (1999) 176–185.

[8] V.A.F. Lamme, The neurophysiology of figure–ground segregation in primary visual cortex, J. Neurosci. 15 (1995) 1605–1615.

[9] V.A.F. Lamme, H. Supèr, H. Spekreijse, Feedforward, horizontal, and feedback processing in the visual cortex, Curr. Opin. Neurobiol. 8 (1998) 529–535.

[10] B.R. Payne, S.G. Lomber, A.E. Villa, J. Bullier, Reversible deactivation of cerebral network components, Trends Neurosci. 19 (1996) 535–542.

[11] M.L. Platt, P.W. Glimcher, Neural correlates of decision variables in parietal cortex, Nature 400 (1999) 233–238.

[12] J. Quintana, J.M. Fuster, From perception to action: temporal integrative functions of perceptual and parietal neurons, Cereb. Cortex 9 (1999) 213–221.

[13] P.-A. Salin, J. Bullier, Corticocortical connections in the visual system: structure and function, Physiol. Rev. 75 (1995) 107–154.

[14] J.D. Schall, N.P. Bichot, Neural correlates of visual and motor decision processes, Curr. Opin. Neurobiol. 8 (1998) 211–217.

[15] J.D. Schall, K.G. Thompson, Neural selection and control of visually guided eye movements, Annu. Rev. Neurosci. 22 (1999) 241–259.

[16] P.H. Schiller, I.-H. Chou, The effects of frontal eye field and dorsomedial frontal cortex lesions on visually guided eye movements, Nat. Neurosci. 3 (1998) 248–253.

[17] M.N. Shadlen, W.T. Newsome, Motion perception: seeing and deciding, Proc. Natl. Acad. Sci. USA 93 (1996) 628–633.

[18] K.G. Thompson, N.P. Bichot, J.D. Schall, Dissociation of visual discrimination from saccade programming in macaque frontal eye field, J. Neurophysiol. 77 (1997) 1046–1050.

[19] K.G. Thompson, D.P. Hanes, N.P. Bichot, J.D. Schall, Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search, J. Neurophysiol. 76 (1996) 4040–4055.

[20] K. Zipser, V.A.F. Lamme, P.H. Schiller, Contextual modulation in primary visual cortex, J. Neurosci. 16 (1996) 7376–7389.