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Temporal gating of neural signals during performance of a visual discrimination task

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The flow of neural signals within the cerebral cortex must be subject to multiple controls as behaviour unfolds in time. In a visual discrimination task that includes a delay period, the transmission of sensory signals to circuitry that mediates memory, decision-making and motor-planning must be governed closely by 'filtering' or 'gating' mechanisms so that extraneous events occurring before, during or after presentation of the critical visual stimulus have little or no effect on the subject's behavioural responses. Here we study one such mechanism physiologically by applying electrical microstimulation[1–3] to columns of directionally selective neurons in the middle temporal visual area[4–9] at varying times during single trials of a direction-discrimination task. The behavioural effects of microstimulation varied strikingly according to the timing of delivery within the trial, indicating that signals produced by microstimulation may be subject to active 'gating'. Our results show several important features of this gating process: first, signal flow is modulated upwards on onset of the visual stimulus and downwards, typically with a slower time course, after stimulus offset; second, gating efficacy can be modified by behavioural training; and third, gating is implemented primarily downstream of the middle temporal visual area.

Several lines of evidence indicate a critical role for MT (the middle temporal visual area) in the analysis of visual motion information. Roughly 90% of MT neurons respond selectively to stimulus motion within a restricted range of directions[7]. Furthermore, MT neurons are organized in columns such that neighbouring neurons preferentially respond to similar directions of motion[9]. Electrical microstimulation of these columns can bias a monkey's judgements of motion direction towards the direction encoded by the stimulated neurons, showing that directional signals in MT are important in generating psychophysical performance[1–3]. In earlier microstimulation experiments, trains of stimulating pulses were delivered at the same time as presentation of the motion stimulus to

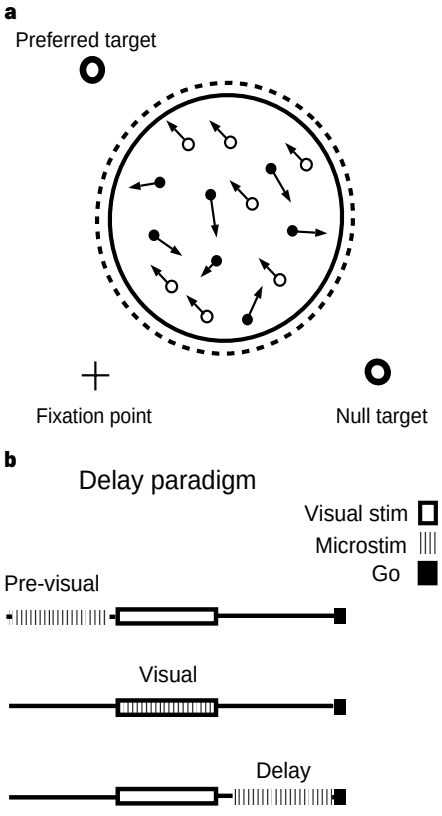

Figure 1 The protocol. **a**, Diagram of the visual display. The visual stimulus aperture (complete circle) was positioned within the multi-unit receptive field (dashed circle) mapped at the microstimulation site. Open dots represent the coherent motion signal (arrows directed upwards and left); solid dots represent the masking motion noise (randomly directed arrows). **b**, The sequence of events. Stimulating pulses were delivered for equal amounts of time in each experimental condition. Control trials with no microstimulation were randomly interleaved among the test trials.

be discriminated by the monkey. We now compare the efficacy of microstimulation delivered before, during and after presentation of the visual stimulus.

We trained four rhesus monkeys to discriminate between opposite directions of motion in a dynamic random dot display (Fig. 1a). In each experiment, a microelectrode was positioned within a column of directionally selective MT neurons. The monkey then performed the discrimination task for a block of several hundred trials in which the direction and the coherence of the motion signal varied randomly from trial to trial. Microstimulation was applied during the stimulus presentation interval or during the delay period for monkey K, and also during a fixation interval before the onset of the visual stimulus for the other three monkeys (Fig. 1b).

Figure 2 shows the results of a representative experiment from each of two of the monkeys. The psychometric functions show, for each motion condition tested, the proportion of trials in which the monkey chose the direction preferred by neurons at the stimulation site. Microstimulation during the visual stimulus interval caused both monkeys to make substantially more decisions favouring the preferred direction, resulting in a large leftward shift of the psychometric function relative to the control function (22.6% and 19.5% coherence in Fig. 2a, b, respectively; see Methods). Microstimulation during the delay period influenced both monkeys, but to different degrees: the delay-period effect was substantially smaller than the visual-period effect in monkey K (8.4% coherence), but the effects were equivalent in monkey R (26.4% coherence). In contrast to the large effects in the delay period, monkey R's choices were completely unaffected by microstimulation delivered before the onset of the visual stimulus (Fig. 2b), consistent with our previous results[1].

Figure 3 shows average results from each of the four monkeys. In monkeys K and T, delay-period effects were much smaller than visual-stimulus-period effects (Fig. 3a, b; paired t-test, $P < 0.005$ for both monkeys). In monkeys R and S, on the other hand, delay-period effects were roughly equal to visual-period effects (Fig. 3c, d; paired t-test, $P > 0.5$ for both monkeys). Stimulation before the visual-stimulus interval was ineffective in monkey R, and only weakly effective in monkeys T and S.

The data indicate that the behavioural efficacy of microstimulation is modulated upwards at the time of stimulus onset, and, in monkeys K and T, is modulated downwards again at stimulus offset. The large delay-period effect in monkeys R and S was quite surprising as no visual stimulus was present during this interval. One could explain this result if some MT neurons are active during the delay period, signalling the remembered direction of motion. In this case, microstimulation during the delay period could influence behaviour by modifying the ongoing representation of past stimuli. We did not, however, observe such delay-period activity in single-unit recordings from MT neurons in either monkey R ($n = 21$ cells) or monkey K ($n = 16$ cells; E.S. and W.T.N., unpublished observations). We therefore wondered whether the efficacy of the pathway linking MT and premotor circuitry might also be modulated downwards during the delay period in monkeys R and S, but over a longer time course than in monkeys K and T.

To test this possibility, we carried out additional experiments in monkey R, applying microstimulation after increasingly longer delays following the offset of the visual stimulus. Figure 4 shows that the effect of microstimulation indeed waned substantially as the stimulating pulses were progressively delayed relative to the offset of the visual stimulus. Averaged across ten experiments, microstimulation applied after the longest delay was only 32% as effective as

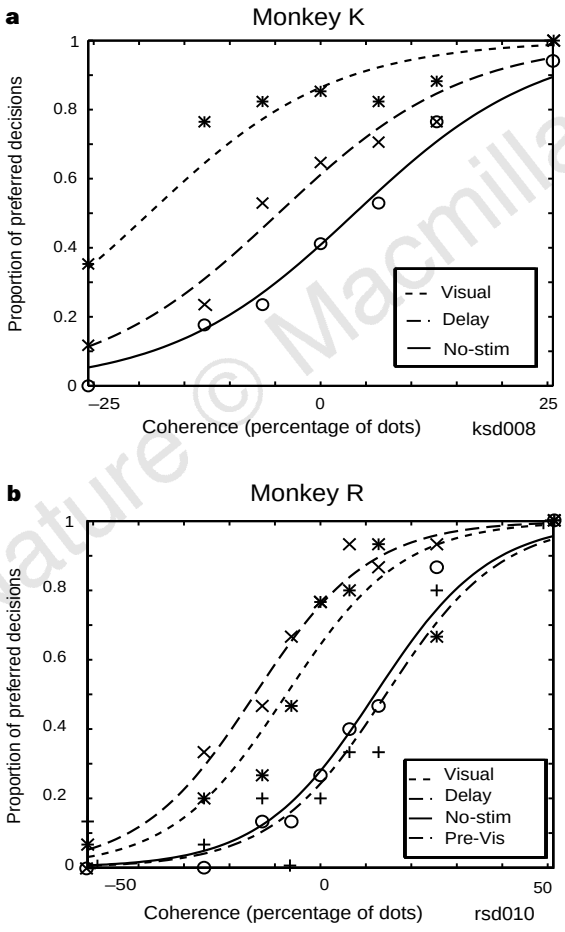

Figure 2 Data from representative experiments in monkeys K and R. **a**, Results from monkey K; and **b**, from monkey R. Each data point indicates the proportion of the monkey's decisions that favoured the preferred direction of the stimulated neurons (ordinate) as a function of stimulus coherence and direction (abscissa). Stimulus motion in the preferred direction is indicated by positive coherence values; motion in the null direction is indicated by negative values. The symbol for each data point indicates the control or test condition: no stimulation (open circles); microstimulation before (plus symbols), during (asterisks) and after (crosses) presentation of the visual stimulus. Sigmoids illustrate the fitted curve for each condition.

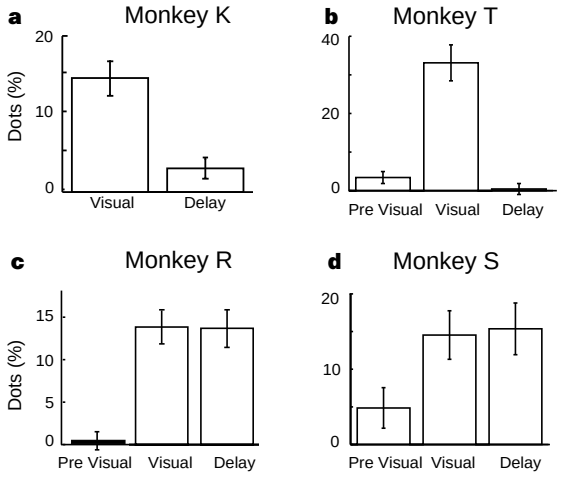

Figure 3 Average microstimulation effects in the four monkeys. Microstimulation effects (ordinate) are given as the leftward shift of the psychometric function in per cent coherent dots. For an experiment to be included in this analysis, microstimulation had to generate a significant positive shift of the psychometric function in at least one test condition (logistic regression analysis, $P < 0.05$). Negative microstimulation effects were observed in only four experiments and were excluded from this analysis. Error bars indicate the standard error of the mean. **a**, Monkey K ($n = 12$). **b**, Monkey T ($n = 13$). **c**, Monkey R ($n = 13$). **d**, Monkey S ($n = 9$).

microstimulation delivered after a short delay. This decrease in microstimulation efficacy is not simply due to the lengthening of the delay. Microstimulation effects remained high in other test conditions, randomly interleaved among those in Fig. 4, in which microstimulation was applied only during the first 900-ms interval after offset of the visual stimulus (mean shift is 15.5, 11.8 and 14.3% coherence for short, medium and long delays, respectively). Thus the behavioural efficacy of microstimulation is indeed modulated downwards in monkey R after offset of the visual stimulus, the time course of modulation being longer than in monkeys K and T.

Interanimal differences in the time course of the downward modulation were unexpectedly large, and we wondered whether the differences might be reduced if monkeys R and S were trained explicitly to ignore irrelevant information arriving during the delay period. To test this, we constructed a new behavioural task in which an irrelevant visual stimulus appeared during the delay in place of the microstimulation pulses. The first time period contained a red random dot stimulus that carried the signal for the direction discrimination; the second period contained a green random dot stimulus that was irrelevant to the discrimination. After the animals learned to ignore the green dots effectively, we repeated the standard microstimulation experiment outlined in Fig. 1, which contained a single visual stimulus period. In both monkeys, after being trained with the red–green paradigm, microstimulation during the delay period exerted a substantially weaker effect relative to stimulation during the visual stimulus period (compare Figs 3c, d and 5a, b). Before training on the red–green task, the efficacy of microstimulation in the delay period had remained roughly constant over the course of several months. Thus the change in efficacy shown in Fig. 5a, b can be attributed unambiguously to training with the red–green task. The reduced efficacy of delay-period microstimulation shows that past experience can strongly affect the gating process that prevents irrelevant neural signals from influencing premotor circuitry. These results also indicate that the neuronal signals that are produced in MT by visual stimuli and by electrical microstimulation are subject to the same gating mechanism.

Finally, we recorded single-unit activity in MT while monkeys R and T performed the red–green task in order to determine whether the gating effect occurs at the level of MT. Weaker responses to the green (ignored) dots than to the red (attended) dots would indicate that the gating mechanism is probably expressed in MT, whereas equivalent responses to the red and the green dots would indicate that the gating operation is implemented downstream of MT. Across 42 MT cells from monkeys R and T, responses were only slightly stronger to the red dots than to the green dots (8% difference). These effects are an order of magnitude smaller than attentional effects recently observed in the MT[10]. In our task, therefore, the gating mechanism that prevents irrelevant stimuli from affecting psychophysical decisions seems to reside primarily downstream from MT.

The behavioural efficacy of microstimulation in MT is temporally modulated during single trials, indicating that an active gating mechanism controls information flow from MT to premotor circuitry. Microstimulation allowed us to study the time course of the gating process; signal flow was modulated upwards rapidly at stimulus onset and downwards, with a variable time course, at stimulus offset. Using microstimulation as a probe, we found that the time course of downward modulation can be affected strongly by the monkey's past experience. The gating mechanism operates primarily downstream of MT. Our data place no constraints on the length of the pathways that link MT to preoculomotor circuitry; we can only say that the gating mechanism acts at some point on these pathways, whatever their length. Similarly, our experiments place no constraint on the cellular mechanisms underlying the gating process: facilitation of relevant signals and inhibition of irrelevant signals (or both) are equally plausible.

Gating of information flow according to its behavioural significance must be ubiquitous within the central nervous system; its existence can be inferred from numerous psychophysical and physiological studies, including those on the effects of visual attention (reviewed in refs 11, 12). Thus our observations concerning temporal gating are related to earlier studies that show modulation of neural signals by spatial- or feature-based attentional mechanisms[13–17]. An important outcome of our study is the establishment of a physiological paradigm by which a neuronal signal that is subject to gating can be delivered at will by experimenters to a precise location in the central nervous system. An important goal for the future will be to follow this signal from MT to premotor circuitry in order to localize the site at which irrelevant signals are filtered out. Identification of such a site may allow cellular analysis of the gating mechanism and circuit-level analysis of the higher-level signals that control the operation of the gate. □

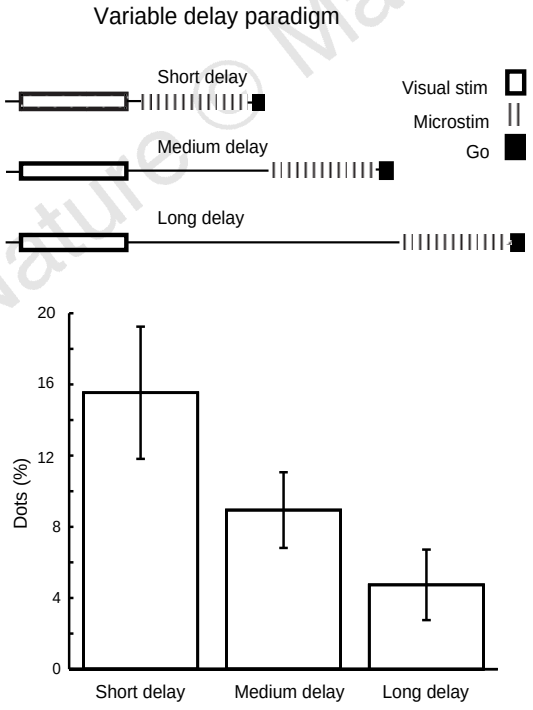

Figure 4 Sequence of events and average microstimulation effects in the variable delay paradigm. For each test condition, the amplitude of the microstimulation effect was considered to be the shift of the test psychometric function relative to a control function (no microstimulation) obtained using a matched delay period. The microstimulation effect decreased significantly as the delay period lengthened (one-way analysis of variance, $P < 0.05$). Error bars denote the standard error of the mean.

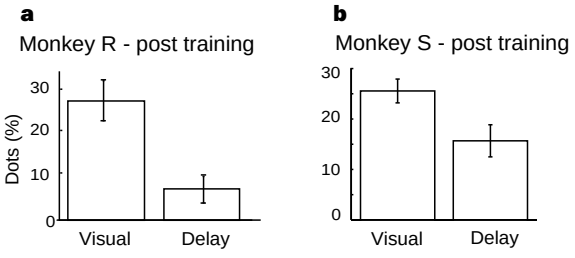

Figure 5 Average microstimulation effect in monkeys R and S following training on the red–green task. In contrast to the results shown in Fig. 3c and d, delay-period stimulation caused significantly weaker effects than microstimulation during the visual stimulus (paired *t*-test, $P < 0.005$ for both monkeys). **a**, Monkey R ($n = 14$). **b**, Monkey S ($n = 12$).

Methods

The treatment of the monkeys was in accordance with the guidelines set by the US Department of Health and Human Services (NIH) for the care and use of laboratory animals.

Behavioural tasks. The behavioural task and physiological techniques used here have been described[1]. Briefly, in each trial, a fraction of the dots moved coherently in one direction while the remaining dots appeared at random locations within the stimulus aperture, creating a masking motion noise. The strength of the coherent motion (per cent coherence) ranged from 0% (fully random noise) to 51.2%. Each trial began when the monkey fixated a small point of light on a video display (Fig. 1a). The monkey then viewed the random dot display for a brief interval while gazing steadily at the fixation point. Following a brief delay period, the monkey indicated the perceived direction of motion by making a saccadic eye movement to one of two visual targets corresponding to the two possible directions of motion. Extinction of the fixation point and appearance of the two visual targets signalled the end of the delay period. Eye movements were measured throughout all experiments by the scleral search coil technique[18]. The monkey received fluid rewards for correct choices.

Microstimulation techniques. For each microstimulation experiment, the multi-unit receptive field was mapped and the preferred direction identified using a bar of light or a patch of moving dots. To maximize the likelihood that the monkey would use directional information supplied by neurons at the stimulation site, the dot patterns were presented within the receptive field, and the axis of the directional discrimination was aligned with the preferred-null axis of the receptive field. Microstimulation (200 Hz, 10 μA, biphasic pulses) was applied during the stimulus presentation interval or during the delay interval for monkey K, and also during a fixation interval before the onset of the visual stimulus ('previsual') for the other three monkeys (Fig. 1b). For monkeys R, S and T, each microstimulation interval lasted 800 ms; 200 ms separated stimulation intervals. For monkey K, microstimulation duration was 1 s with 500 ms separation between the two microstimulation intervals. In an extra ten experiments, monkey R was tested with same time course as monkey K; the results remained essentially the same as in Fig. 3c. The latter time course was also used in the red–green experiment. In the variable delay experiment (Fig. 4), microstimulation was applied in the last 800 ms of the delay period; the duration of the delay period was varied randomly among three values—900 ms (short), 1,800 ms (medium) and 2,700 ms (long).

Data analysis. Data were analysed using a standard logistic regression model[19]. Microstimulation effects were measured as the horizontal shift of the psychometric function in stimulated trials relative to control trials. The amplitude of this shift was measured in units of the abscissa (coherence, in percentage of dots), where leftward shifts were considered to be positive. Throughout this study, microstimulation did not significantly affect the slopes of the psychometric functions.

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Seeing only the right half of the forest but cutting down all the trees?

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Unilateral neglect following damage to the right hemisphere of the brain can be characterized by failure of the global attentional mechanisms of the right hemisphere to direct the local detail processors of the left hemisphere towards the contralesional left hemispace. This is suggested by patients who recognize the global form of the left side of shapes (the forest) but fail to cancel out its local details (the trees)[1]. Here we report the opposite behavioural dissociation in a patient (Q.M.) with damage to the right hemisphere of the brain. Q.M. detected local details (such as the tail of a dog) on the left or right side of visual shapes, regardless of whether these details belonged to predefined target shapes (a dog in this case) or to distractor shapes differing on the opposite side (a dog with a swan's neck and head, for example). Psychological testing showed an abnormal tendency of this patient to respond to local features, but perfect accuracy in interpreting global features when the local features could not interfere in global processing. The results indicate that the left hemisphere can integrate multiple local features simultaneously but loses global awareness as soon as local features individually compete for response selection. However, awareness of the whole is not necessary for the sequential processing of the parts.

Q.M. is a 57-year-old right-handed woman who suffered right-hemisphere ischaemia (Fig. 1). Two months after the stroke, the patient had severe contralesional neglect and hemianopia. We examined this patient extensively in light of the following observations. When presented with an array of 3s and Bs (Fig. 2a, test a1) and required to cancel out the 3s, Q.M. cancelled out both 3s and Bs on the right side of the array, disregarding the presence of the vertical bar on the left side of the Bs. Tilting the items and varying the thickness of the vertical bar (Fig. 2a, tests a2, a3) did not modify the patient's performance. Unexpectedly, the same behaviour was observed when the items were mirror-reversed about the vertical axis so that the difference between the two stimuli was on the right, not left, side. These findings were replicated using 6s and Ss (Fig. 2a, test b). When asked about her strategy, the patient answered that she looked for items with 'two little humps' when cancelling out Bs, and for items with an upper 'hook' when cancelling out 6s.