the paradox that although dichogamy is traditionally interpreted as an anti-selfing mechanism[2], many dichogamous species also possess physiological self-incompatibility[24]. The apparent redundancy of two mechanisms that prevent selfing[2] is resolved by recognizing inter-floral dichogamy as a mechanism that promotes outcrossed siring success by limiting pollen discounting, a role that self-incompatibility cannot serve. The second example involves heterostyly, a genetic polymorphism in which plants of each morph have anthers and stigmas in dissimilar positions, with the other morph(s) producing the reciprocal arrangement(s). The pronounced separation of sex organs in heterostylous plants reduces pollen transfer within and between plants of the same morph[25] and, consequently, more pollen remains on the pollinator until it visits the alternative morph(s). Like dichogamy, heterostyly may function, in part, to reduce the mating cost of large floral displays. However, whereas dichogamy typically functions within inflorescences, heterostyly limits pollen dispersal between inflorescences of the same morph. These examples imply that the negative relation between selfing and outcrossed siring success demonstrated by our experiment may be an important, though largely unexplored, influence on the evolution of floral design and display. □

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# Dynamics of neuronal interactions in monkey cortex in relation to behavioural events

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**It is possible that brain cortical function is mediated by dynamic modulation of coherent firing in groups of neurons. Indeed, a correlation of firing between cortical neurons, seen following sensory stimuli or during motor behaviour, has been described[1–5]. However, the time course of modifications of correlation in relation to behaviour was not evaluated systematically. Here we show that correlated firing between single neurons, recorded simultaneously in the frontal cortex of monkeys performing a behavioural task, evolves within a fraction of a second, and in systematic relation to behavioural events. Moreover, the dynamic patterns of correlation depend on the distance between neurons, and can emerge even without modulation of the firing rates. These findings support the notion that neurons can associate rapidly into a functional group in order to perform a computational task, at the same time becoming dissociated from concurrently activated competing groups. Thus, they call for a revision of prevailing models of neural coding that rely solely on single neuron firing rates[6–8].**

The neuronal activity of 6–16 neurons in the frontal cortex of a rhesus monkey was recorded simultaneously while the animal performed a spatial delayed response task (Fig. 1). Interactions between pairs of neurons were studied by dynamic cross-correlation (joint peri-stimulus time histogram, JPSTH[9]). This analysis highlights the detailed time structure of the correlation of firing between two neurons and its time-locking to a third event, such as the onset of a stimulus or the initiation of a movement. All JPSTHs were normalized to remove the contributions of stimulus- (or movement-) induced co-variation of single-neuron firing rates. Thus, the normalized JPSTH reflects the net effect of direct and indirect interactions of the two neurons, expressed as correlation coefficients[9]. We also computed the relative deviation of the observed coincidence rate from the expected rate for independently firing neurons. Its maximal absolute value, measured along the coincidence–time histogram (the main diagonal of the JPSTH; Fig. 2) and expressed as a percentage of the expected rate, was denoted as the 'maximal modulation depth'.

Figure 2 shows JPSTHs for two neurons in the premotor cortex for two behavioural paradigms. The peri-stimulus time (PST) histograms for paradigms GO (Fig. 2*a*) and NO-GO (Fig. 2*b*) are very similar, and show very little (*x*-axis) or no (*y*-axis) modulation of the firing rates. Thus, PST analysis indicates that these two neurons, taken individually, neither respond to the ready signal nor contribute to the discrimination between the two behavioural paradigms. Further, the cross-correlograms in Fig. 2*a* and *b*, which both have a wide central peak, are very similar. Thus, firing rates and time-averaged correlation do not discriminate between the two behavioural paradigms.

Such discrimination can be made, however, on examining the dynamics of the correlation. The main diagonal (bottom left to upper right) in each colour-coded matrix, emphasized in the coincidence–time histogram (Fig. 2), reveals strong modulations of co-firing between these two neurons, which are temporally linked to the ready signal. Moreover, the evolution of co-firing is virtually opposite in the two behavioural conditions: during performance of the GO paradigm (Fig. 2*a*) high co-firing occurs only during the first half of the time-window, whereas in NO-GO trials (Fig. 2*b*) it occurs in the second half. Note that in Fig. 2*a* (GO) the co-firing is maximal just after the ready signal, whereas in Fig. 2*b* (NO-GO) the co-firing at that time falls to zero. We stress that this difference in the evolution of co-firing

could not be predicted from the responses of the two neurons alone, nor was it reflected in the time-averaged cross-correlograms. However, the dynamics of the correlation reveal that these two neurons participate in the coding of the sensory event and its behavioural context.

Other examples of correlation dynamics are shown in Fig. 3. Neurons 0 and 1 were recorded by a single microelectrode. We refer to them as neighbouring neurons. The second pair consists of neuron 0 (from the first pair) and neuron 6, recorded by the tip of a different electrode, located 400 μm deeper and 500 μm lateral to the first electrode. Hence, we refer to them as distant neurons.

Figure 3*a*, *b* shows JPSTHs for the two neighbouring neurons (0, 1) during an interval of 3 seconds surrounding the initiation of saccadic eye movements to the right (Fig. 3*a*) and to the left (Fig. 3*b*). The PST histograms show that the firing rates of the neurons were modulated just before and during the saccades. The high peaks in the cross-correlograms indicate that, on average, the amount of correlation between the two neurons is similar and strong in both conditions. The JPSTH analysis, however, clearly reveals that these time-averaged cross-correlations are misleading: whereas the average correlation is indeed similar, dramatic modifications of co-firing occur near the initiation of the saccades. Co-firing increases just as the rightward saccade starts, and reaches its highest level within a few tens of milliseconds. During this brief period (white cluster in matrix *a*) the neurons co-fired on average nine times per saccade, about twice the expected number (maximal modulation depth equals 110%). The opposite change takes place for leftward saccades (Fig. 3*b*), where the correlation decreases to zero (no-correlation) when the saccade starts.

The JPSTHs in Fig. 3*c* and *d* show the same analysis for the distant pair (0, 6). Here, the average correlation is negative. Such correlation can result from reciprocal effects of correlated inputs to the two cells (while these inputs excite one neuron, they inhibit the other). Alternatively, it may reflect mutual inhibition between the two. Again, the JPSTH shows that the average correlation is misleading. In fact, the correlation is only clearly negative just after the initiation of rightward saccades (with a

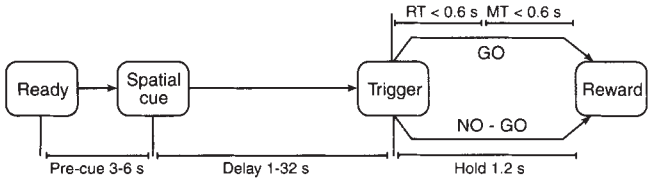


FIG. 1 The spatial delayed-response task. Trials were initiated when the monkey touched a central key and a central red light was turned on ('ready'). After a variable delay (3–6 s), one of two target keys was illuminated for 200 ms ('cue'). Then, after a delay of 1–32 s, the central red light was dimmed ('trigger'), instructing the monkey to exhibit the appropriate behavioural response. In one paradigm ('GO'), the monkey was rewarded for releasing the centre key within 0.6 s (RT, reaction time) after the trigger signal, and touching the correct target key within the next 0.6 s (MT, movement time). In the second paradigm ('NO-GO'), the monkey was rewarded for continuing to touch the centre key for at least 1.2 s after the trigger. Special peripheral lights instructed the monkey to switch paradigms after every fourth correct trial.

METHODS. Two monkeys (*Macaca mulatta*, female, 3–4 kg) were trained to perform the task. Recording sessions began after the monkey was well trained. In each session we simultaneously recorded the activity of 6–16 neurons during the performance of 400–800 correct trials, with 100–200 alternations between the two behavioural paradigms. Six microelectrodes (glass-coated tungsten, 0.2–1.5 MΩ impedance) were inserted into the frontal cortex in a circular array, with 500–1,000 μm inter-electrode distance. Spike-sorters were used to isolate the activity of 1–3 single units from each electrode. Typically, in each session we recorded 6–10 well-isolated units and 6–10 clusters with a mixture of 2–3 spike-shapes in each cluster. Eye movements were monitored by Ag–AgCl′ cup-electrodes. The locations of the electrodes' tracks in the cortex were reconstructed by standard histological techniques. Statistical significance of JPSTH correlation coefficients was evaluated using the 'surprise'-measure[23]. Statistical tests for the time-averaged cross-correlograms were described by Abeles[24]. All procedures were carried out in accordance with the NIH and Hebrew University regulations for animal care.

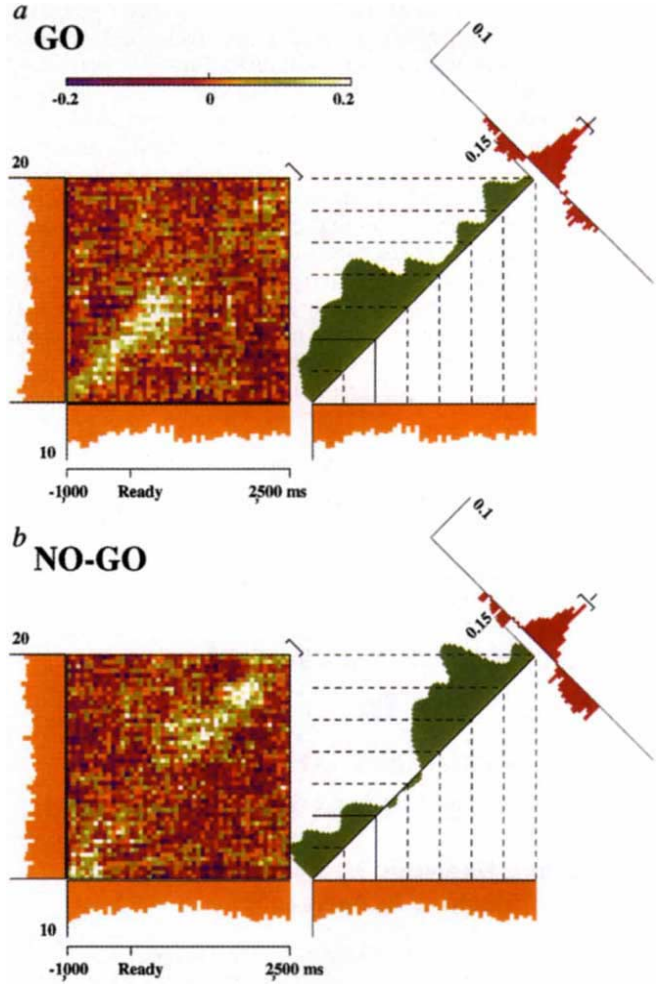


FIG. 2 Dynamic modification of correlated firing of two frontal cortex neurons in relation to the 'ready' signal. *a*, JPSTH constructed from 221 GO trials, with 4,414 spikes of neuron 1 and 10,121 spikes of neuron 2. Observe the gradual build-up of excess correlation, which starts before the ready signal, reaches a peak 400 ms after the signal (at that point the maximal modulation depth is 50%) and then decays. *b*, JPSTH constructed from 194 NO-GO trials for the same neurons (neuron 1: 3,764 spikes; neuron 2: 8,715 spikes). Note the different temporal evolution of the correlation compared with *a*. Each JPSTH is composed of four displays. (1) A colour-coded matrix of correlation coefficients (left half of plots *a* and *b*), with each bin depicting the amount of correlation of the two neurons at the corresponding pair of time delays, relative to the ready signal; colour scale (shown in *a*) from blue (minimum) to white (maximum). (2) Peri-stimulus time histograms (PSTHs; in orange), along the *x*–*y* axes of the matrix, depicting the firing rates of the two neurons relative to the time of the ready signal; *x*-axis: neuron 1, full scale, 10 spikes per s, *y*-axis: neuron 2, full scale: 20 spikes per s (the PSTH of neuron 1 is duplicated along the *x*-axis in the right-hand plot). (3) Coincidence–time histogram (in green; full scale, 0.15) showing the temporal evolution of the correlation coefficient relative to the ready signal. This histogram measures excess correlation within the time-window marked by the ] sign at the upper-right corner of the matrix. (4) The conventional, time-averaged cross-correlogram (in red; full scale, 0.1). Grid line intervals, 500 ms. The timing of the ready signal is marked by solid grid lines. Bin width, 70 ms (PSTHs) and 70 ms × 70 ms (matrix).

maximal modulation depth of 70%), whereas it is even slightly positive near leftward saccades (Fig. 3*d*). Similar dynamics of negative correlation were found between neurons 1 and 6 (not shown).

Again, these changes of correlation could not be predicted from the neurons' firing rates. The correlation either increased (Fig. 3*a*) or decreased (Fig. 3*c*) near the saccade, whereas the firing rates of the neurons increased, regardless of saccade direction.

Analysis of 947 neuronal pairs revealed correlated activity in 499 pairs. Analysis of all 499 pairs in detail using the JPSTH method revealed that modulation of correlation between neurons is quite frequent; rapid changes of the rate of co-firing in relation to behaviour were observed in 308/499 cases (61%), with time constants of modulation down to a few tens of milliseconds.

The time-averaged cross-correlograms of these pairs had a peak centred around time delay 0 ('positive' correlation), a trough centred around 0 ('negative' correlation), or an asymmetrical pattern around 0, which included both a peak and a trough ('compound' correlation). The peaks and troughs decayed within tens to a few hundred milliseconds (Figs 2 and 3). To test whether the pattern of correlation depends on the distance between neurons, as shown in Fig. 3, we compared the distribution of correlation patterns for neuronal pairs recorded by the same electrode and the correlations of pairs recorded by different electrodes (Fig. 4). A positive time-averaged correlation was observed between neighbouring neurons as well as between distant neurons, but more frequently between neighbouring ones. By contrast, a negative correlation was found only between distant neurons, and never between neighbouring ones.

Our results show that many cortical neurons exhibit rapid modulations of discharge correlation in relation to behavioural events. Epochs with a particular correlation may last from few tens of milliseconds to several seconds. The observed modulations of correlation may be, but do not have to be, associated with changes in the individual neurons firing rates. These findings support the notion that a single neuron can intermittently participate in different computations by rapidly changing its coupling to other neurons, without associated changes in firing rate.

Previous correlation studies concentrated mainly on relatively precise coincidences, with a resolution of only few milliseconds[10–12], the assumed time jitters of direct synaptic interactions. Here we chose to describe the phenomenon of loose synchrony, also measured in the visual cortex[13]. As we described elsewhere[14], however, precise coincidences do occur in these data. For example, JPST analysis of the recordings in Fig. 2*a*, using a narrower bin of 5 ms, revealed that the modulation depth

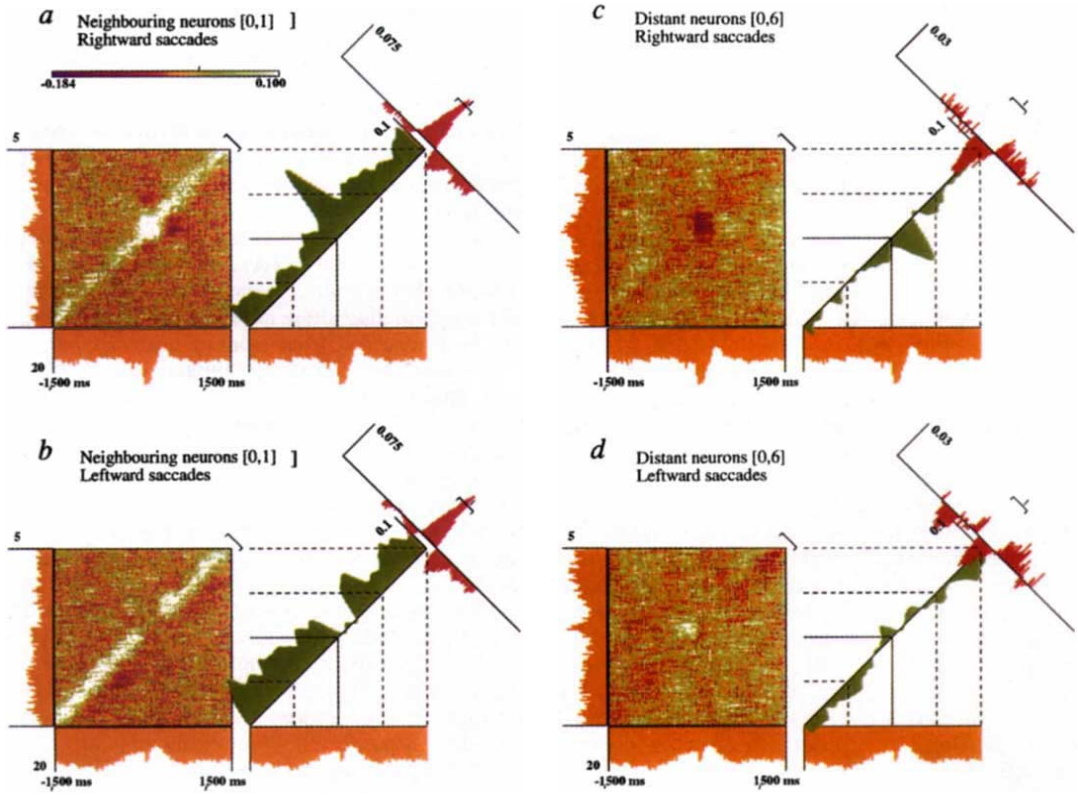


FIG. 3 Dynamic modification of correlated firing between neurons in the frontal eye field in relation to the onset of saccadic eye movements. *a*, *b*, JPSTHs for neurons (0, 1), recorded by one microelectrode ('neighbouring' neurons). *c*, *d*, JPSTHs for neurons (0, 6). Neuron 0 is from the first pair, neuron 6 was recorded by another electrode ('distant' neurons). The following features are apparent. First, the averaged cross-correlograms (in red) for each pair are very similar. However, the correlation dynamics are temporally linked to the saccades and depend strongly on their direction, as shown by the matrix and the (green) coincidence–time histograms (*a* compared with *b* and *c* compared with *d*). Second, the time-averaged correlation between neighbouring neurons (*a*, *b*) is positive (that is, the probability that either of the neurons will fire a spike is higher around the times the other neuron fires), whereas the correlation between distant neurons (*c*, *d*) is negative. Third, the temporal changes of correlation could not be predicted from the firing rates of the two neurons. The correlation either increased (*a*) or decreased (*c*) near the time of saccade initiation, whereas the firing rates of both neurons increased around the onset of saccades, regardless of its direction. The normalization and format of the JPSTHs are the same as in Fig. 2. Bin size, 30 ms. The JPSTHs around onsets of rightward saccades (*a*, *c*) were constructed from 776 saccade, 33,882 spikes of neuron 0 (*a*, *c*), 4,299 spikes of neuron 1 (*a*) and 6,927 spikes of neuron 6 (*c*). The JPSTHs in *b* and *d* were constructed from 734 saccades, 32,621 spikes of neuron 0 (*b*, *d*), 4,167 spikes of neuron 1 (*b*) and 5,992 spike of neuron 6 (*d*).

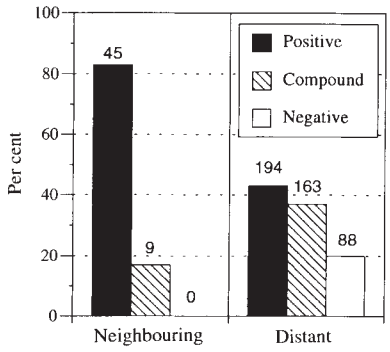


FIG. 4 Distribution of cross-correlogram patterns in neighbouring and distant neurons. Time-averaged cross-correlograms between pairs of neighbouring neurons are, in most cases, characterized by positive peaks. Note that negative cross-correlograms are completely missing in the population of neighbouring neurons. The number of neuronal pairs in each class is given above the bars. The difference between the two populations is statistically significant at a level of 0.001 ($\chi^2 = 318.77$).

of precise coincidences (with jitters of only ±2.5 ms) reached values up to 620%.

The wide peaks and troughs (tens to hundreds of milliseconds wide) indicate that the time-constraints of the underlying processes are loose. The mechanisms of such dynamic correlation (including precise coincidences) are unknown. The correlation could emerge from repeated volleys of direct synaptic interactions between the neurons; or, more probably, it could arise from changes in the pattern of activity of a large number of neurons, interacting with the sampled neurons in a correlated manner. Regardless of the mechanism, however, the modifications of correlation between two neurons in relation to stimulation and behaviour most probably reflect changes in the organization of spike activity in larger groups of neurons. Indeed, recent model studies have shown that similar dynamic organization can be accomplished in large networks, even without associated modifications of the synaptic weights[15–17].

Our results also support and extend anatomical and physiological findings indicating that functional groups are organized in spatial clusters[3,11,18–22]. Our findings suggest that neighbouring neurons tend to share common inputs of the same sign (either inhibitory or excitatory), whereas the effects on more distant neurons (in our study 500–1,000 μm apart) are mixed. Therefore, when the common drive is increased, neighbouring neurons tend to be activated in unison, enabling them to operate as a coherent functional group for a short while. Concurrently, the negative correlation between neurons in one group and those in another, more distant group can accentuate the demarcation among groups. Thus, the spatio-temporal organization of activity in the network allows for the rapid association of neurons into a functional group, at the same time dissociating such a group from concurrently activated, competing groups. □

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# Neuronal correlates of inferred motion in primate posterior parietal cortex

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**For many types of behaviours, it is necessary to monitor the position or movement of objects that are temporarily occluded. The primate posterior parietal cortex contains neurons that are active during visual guidance tasks: in some cases, even if the visual target disappears transiently[1,2]. It has been proposed that activity of this sort could be related to current or planned eye movements[1,2], but it might also provide a more generalized abstract representation of the spatial disposition of targets, even when they are not visible. We have recorded from monkey posterior parietal cortex while the animal viewed a visual stimulus that disappeared, and then, depending on experimental context, could be inferred to be either moving or stationary. During this temporary absence of the stimulus, about half of the neurons were found to be significantly more active on those trials in which the stimulus could be presumed to be moving rather than stationary. The activity was thus present in the absence of either sensory input or motor output, suggesting that it may indeed constitute a generalized representation of target motion.**

Two rhesus monkeys were trained to maintain fixation within a 1° window while they viewed the trial types shown in Fig. 1*a*. On full vision trials, a stimulus 0.25° across appeared 12° from the fovea, and then, after a brief delay, moved towards the fixation spot. On occlusion trials the stimulus appeared as above, but then disappeared without moving and reappeared at 2° eccentricity moving towards the fixation spot, with the reappearance timed to be consistent with the stimulus moving continuously during the time that it was not visible. Full vision and occlusion trials were randomly interleaved during a block of trial presentations. Blocks of full vision and occlusion trials were interleaved with blocks of a third trial type, blink trials. On these trials, the stimulus appeared and disappeared exactly as in the occlusion trials, but then it reappeared in the same location, as if it had been stationary during the time it was not visible. Until the reappearance of the stimulus, the visual stimulation was identical on the occlusion and blink trials, the only difference being that the animal presumably inferred that the stimulus was moving during the time it was invisible on occlusion trials and inferred that the stimulus was stationary during the same period on blink trials.