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An emergent mechanism of selective visual attention in *Drosophila*

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Abstract. Due to the limited computational capacity of visual systems and the limited capacity to perform several mental operations at once, animals only select a small proportion of the stimuli available at any one time. It remains to be clarified how this process is related to the spatio-temporal dynamics of cell assemblies in the brain. By employing the flight simulator, selective visual attention behavior is studied in *Drosophila*. It has been found that for the visual objects presented, the tethered fruitflies display various attention patterns. Specifically, the learning memory mutants *dunce* and *amnesiac* possess attention patterns totally different from that of the wild-type fly. To explain these results from the viewpoint of dynamic cell assemblies, a neural network has been developed in which a possible link between the activity of cell assemblies, encoding of sensory information, and selective attention in *Drosophila* is proposed.

1 Introduction

Selective visual attention may be particularly appropriate in the case of compound eyes, which unceasingly sample almost all of the visual space (Heisenberg and Wolf 1984). However, in a natural or even experimentally simplified environment, measuring the behavioral input-output relations of a freely flying insect is so difficult that the attention problem of *Drosophila* has seldom been investigated by experimenters and theorists in the past. However, with the introduction of the flight simulator, the visual flight orientation of the fly could be studied under closed-loop conditions. It has been found that if the fly is surrounded by a sufficiently homogeneous distribution of visual landmarks, it may be considerably attracted by a cluster of landmarks (Wehner and Wehner-von Segesser 1973; Horn 1978; Götz 1980). Furthermore, the ability to explore different options, or to focus attention on different segments of the visual field, has been established in closed-loop experiments with two or more targets (Götz 1980; Wolf and Heisenberg 1980; Bülthoff et al. 1982; Heisenberg and Wolf 1984; Götz 1987). To our knowledge, more systematic investigations concerning the attention pattern of *Drosophila* have, to date, not been carried out. In this work, in order to understand the neural mechanism of selective attention in *Drosophila* from the viewpoint of dynamic cell assemblies, behavior experiments were performed; then an attention network was developed to investigate the behavior results.

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2 Selective visual attention of wild-type *Drosophila*

In this section, behavior experiments on wild-type fruit flies are described.

Considering that attention behavior to simple visual stimuli may disclose deeper laws than those under complicate stimuli, we carried out behavior experiments using only two or four visual figure stimuli. Since true attention requires the existence of intentions and of a deep structure of behavior (Heisenberg and Wolf 1984), guessing whether a fruit fly is paying attention and which stimulus becomes the focus of a fruit fly is very complex. Thus, it is supposed in this work that the attention direction is the same as the flight or fixation direction of a fruit fly. This supposition is in accordance with the conclusion that stabilization of a target in the preferred area of the visual field requires continuous visual attention (Götz 1987).

The attention behavior of flies was observed during a long-lasting flight in a flight simulator. Flies were attached to a torque meter with their heads immobilized, and allowed to control with their yaw torque the angular velocity of a vertical drum surrounding them. The fly could control, by its intended turns, the rotation of a surrounding panorama on a cylindrical screen about its vertical body axis. The relation between visual motion, angular velocity of the cylindrical arena, and yaw torque in tethered flight has been extensively investigated in flies (Götz 1975; Buchner 1984; Heisenberg and Wolf 1988;

Wolf and Heisenberg 1990; Wolf and Heisenberg 1991). In this experiment, two dark bars were located on the internal surface of the drum to stimulate the fly visually (Fig. 1a). The two bars were identical except in their position. They were presented in opposite positions on the upper and lower hemispheres, respectively, of the visual field. Each bar was 60° high and 30° wide. Two- to three-day-old female fruit flies of wild-type Berlin, which were reared under standard conditions (Guo and Götz 1997), were used in this experiment. It was found that although the fixation patterns of various fruit flies are very different, they can be roughly divided into three kinds. Three individual flies having typical attention patterns are used here to demonstrate this result. The flight period of each fly is expressed as a sequence of histograms of 0.4-min interval, in temporal sequence from front to back (Fig. 2). Each histogram shows, from left to right, the relative time spent by the visual object at different angular positions between −180° and 180° of the fly's forward direction. The upper bar is located at the middle of the abscissa, and the left (or right) end of the abscissa corresponds to the direction occupied by the lower bar. Figure 1b gives a schematic drawing of such a histogram. As shown in Fig. 2a, the fly attends to one of two bars in turn and seldom fixates other positions, and the probability for attending to each of the two bars is almost equal. Frequent spontaneous attention shifting is involved in this process. The wild-type fly runs between two objects, and may continue to do so for a very long time. This situation is as perplexing to *Drosophila* as it was to Buridan's ass in the early 14th century (Götz 1980; Strauss and Heisenberg 1993). In another pattern (Fig. 2b), besides two bars many angle positions of the panorama attract the fly's interest, even if these positions are not related to bars at all. The last pattern (Fig. 2c,d) describes the situation in which the fly focuses attention on the upper bar after a short period of searching in almost every direction in space. Continuous central peaks in Fig. 2d indicate that attending to the upper bar prevails during the last 48 min. Besides continuous attention, holding the bar in a selected angular position of the visual field requires an effort to overcome fluctuation and drift imparted by the beating wings (Götz 1987). An idea is that the fly counteracts the escape of the visual object from the selected position by intended body saccades (Götz 1987). Based on this explanation, the swaying central peaks in Fig. 2d do not imply unstable attention, but they embody the strategy adopted by a fly to keep its body in the attention direction.

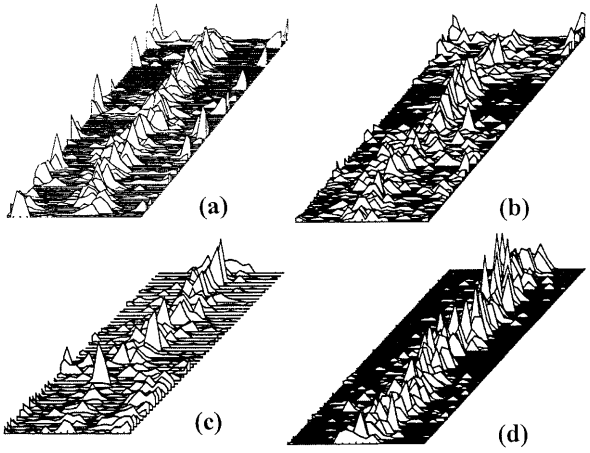

Fig. 2a–d. Object-induced attention of three fruit flies during a successive flight in the closed-loop experiment. Histograms are arranged in the temporal sequence from front to back. **a** A 44-min flight represented by 110 histograms. **b** A 48-min flight represented by 120 histograms. **c, d** The sustained flight consists of two sequences, the first 20 min represented by 50 histograms in **c** and the following 48 min by 120 histograms in **d**. There is no interruption between them

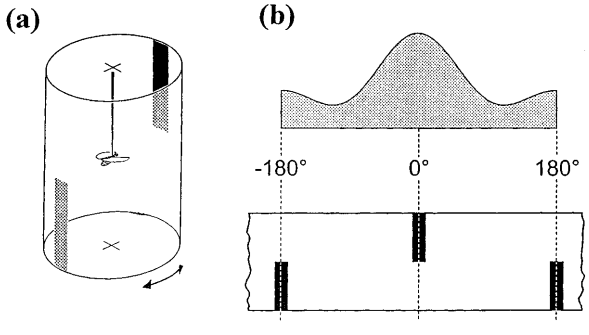

Fig. 1. **a** *Drosophila* during fixed flight in a simulator. A fly is allowed to move a panorama consisting of two dark bars by intended turning. Adapted from Guo and Götz (1997). **b** Schematic drawing of a histogram of the relative time spent on different directions of flight. The projection of the panorama shown below presents these directions in relationship to a spontaneously preferred reference object in the center. From Guo and Götz (1997)

Two identical bars induce rich attention patterns; what is the underlying neural cause for this? The current explanation suggests that guidance towards the object is accomplished by a peculiar asymmetry of the optomotor responses, which favors back-to-front movements of the fluctuating retinal image. This asymmetry thus induces turning of the fly towards the visual object, fixation of the object in the frontal visual field and also tracking of a mobile object (Poggio and Reichardt 1976; Reichardt and Poggio 1976). In contrast to this opinion, we propose that the generation of various attention patterns is the natural result of an emergent property of the dynamical cell assemblies in the *Drosophila* brain. In the following section, an attention network is described to investigate this emergent mechanism.

3 Attention model

Previous studies (Heisenberg and Wolf 1984) have verified that olfactory or wind signals can guide the attention of *Drosophila*; this seems to indicate that the control of attention might occur outside of the visual system. In *Drosophila* brain, is there a system whose function is analogous to that in the mammalian cortex to control selective attention? It has been shown that mushroom bodies (MBs) function as a multimodal integration center (Ferrús and Canal 1994; Heisenberg 1998; Strausfeld et al. 1998). Even the absence of direct

inputs to the MB calyx from the optic lobes in certain species does not preclude their MBs from integrating visual information (Strausfeld et al. 1998). Other evidence supports the central complex being involved in visual flight control too (Bausenwein et al. 1994; Ferrús and Canal 1994; Ilius et al. 1994). More important, MBs receive multimodal sensory information from protocerebral regions and send output back to the same neuropil regions, and the central complex is connected to many protocerebral regions but has no direct connection with MBs (Strausfeld et al. 1998). According to the above experiment results, there exists the possibility that both MBs and the central complex have a specific influence on the visual selective attention, although it may still be a long time until the function of these brain regions is understood at the circuit level. Since the question "What is the specific neuroanatomical constraint for visual selective attention in the insect brain?" largely remains to be answered, our attention network is generally assumed to simulate the brain region responsible for visual selective attention in the *Drosophila* brain.

This network is developed on the inspiration of the model suggested by Lisman and Idiart (1995) and it consists of identical integrate-and-fire neurons. To simplify analysis, it is assumed that all the neurons are arranged in a line. The visual stimuli constitute the information inputs for this network. A hypothesis is that sensory stimuli can be represented by a dynamical cell assembly which is spontaneously organized and shows correlated firing (Fujii et al. 1996). Experimental results also support spatio-temporal coding; it is suggested that olfactory inputs to the MB, are structured spatially and temporally in a stimulus-specific manner (Laurent et al. 1998). A simple way to imagine these spatio-temporal activity patterns is to consider the representation as a dynamic assembly that is updated gradually and rhythmically during odor presentation (Laurent et al. 1998). These studies encourage us to assume that from retina to the central brain, a visual stimulus is mapped to a set of spike trains possessing a stimulus-specific spatio-temporal structure. To account for the ability of the brain to perform selective attention between two bars in Fig. 2, we elaborate such a spatio-temporal structure. Each bar is assumed to enable an assembly of six adjacent neurons to receive a brief suprathreshold informational input at an interval of 5 ms; then these six adjacent neurons will fire successively at an interval of 5 ms. Due to different heights and different angular positions of two bars in the panorama (Fig. 1a), two sets of spike trains encoding two bars are supposed to have different spatio-temporal structures. Such a difference is described by two parameters, δt and δn. When two spike trains are incident on this network, the times of their arrivals are different (the difference is denoted by δt) and the two assemblies of the neurons receiving them are nonoverlapping. The space distance between the two assemblies is measured by the number of neurons between them, and is denoted by δn.

The membrane potential for each spiking neuron in this network is modeled by:

$$V_i(t) = V^{\text{rest}} + V^{\text{osc}}(t) + V_i^{\text{ADP}}(t) + V^{\text{inh}}(t) + V_i^{\text{exc}}(t) \ , \tag{1}$$

and it is reset to $V^{\text{rest}} = -60$ mV when it exceeds $V^{\text{thresh}} = -50$ mV, the threshold for spike generation. $V^{\text{osc}}(t)$ describes subthreshold oscillation of the membrane potential which has been shown to be an intrinsic property of various neurons in the central and peripheral nervous system of many animals (Llinas et al. 1991; Braun et al. 1994; Gutfreund et al. 1995; Longtin and Hinzer 1996), including insects (Laurent and Naraghi 1994; Laurent et al. 1998). During periods of brain oscillation, the induced afterdepolarization effect (Lisman and Idiart 1995) is given by V_i^{ADP}. The specific function V_i^{ADP} is assumed to be the same as described in Lisman and Idiart (1995), i.e. $V_i^{\text{ADP}}(t) = \alpha(t - t_i)$, where t_i is the time of action potential in cell i and α is the alpha function $\alpha(t) = A^*(t/\tau^*)\exp(1 - t/\tau^*)$ with an amplitude A^{ADP} and a time constant of $\tau^{\text{ADP}} = 200$ ms. To simplify analysis, a sine function is usually employed to simulate subthreshold oscillation (Hopfield 1995; Lisman and Idiart 1995). In (1), the oscillatory input is supposed to be $V^{\text{osc}}(t) = B\sin(2\pi ft)$, with $f = 6$ Hz and $B = 5$ mV. The sine function is used for illustration; in general, the periodic subthreshold oscillation will have a more complex form.

The inhibitory feedback signal $V^{\text{inh}}(t)$ comes from the inhibitory interneuron which is not explicitly modeled (Lisman and Idiart 1995). This inhibitory interneuron is activated by each spike in a pyramidal cell and it inhibits all pyramidal cells. This inhibition input is assumed to be a linear superposition of inhibitory postsynaptic potentials, so that $V^{\text{inh}}(t) = \sum \alpha(t - t_n)$, where t_n is the time of the nth spike in the network and α is the alpha function (Lisman and Idiart 1995). In detail, the inhibition has the form $V^{\text{inh}}(t) = \sum A^{\text{inh}}\left[(t - t_n)/\tau^{\text{inh}}\right] \exp\left[1 - (t - t_n)/\tau^{\text{inh}}\right]$ with $A^{\text{inh}} = -4.5$ mV and $\tau^{\text{inh}} = 5$ ms. It can be seen that the inhibition includes both self-inhibition and lateral inhibition, as shown in Fig. 3 (Lisman and Idiart 1995).

The essential difference of this network from the model proposed by Lisman and Idiart (1995) is the consideration of excitatory postsynaptic potential $V_i^{\text{exc}}(t)$. From well-known neurophysiological facts, the excitatory input from other neurons to neuron i plays a crucial role in its firing, thus $V_i^{\text{exc}}(t)$ is viewed as a principal term in our model. To simply simulation, it is assumed that each neuron receives excitatory inputs from the nearest six neurons in its neighborhood. In

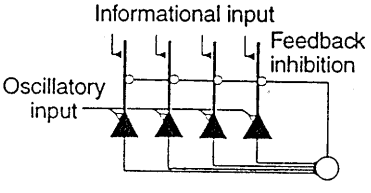

Fig. 3. Network in which pyramidal cells make converging excitatory synapses onto an inhibitory interneuron that produces feedback inhibition of pyramidal cells. From Lisman and Idiart (1995)

detail, it is supposed that the excitatory input has the form $V_i^{\text{exc}} = \sum_{j=i-3}^{i+3} \alpha(t - t_j)$, where $A^{\text{exc}} = 2.1$ mV, $\tau^{\text{exc}} = 15$ ms, $j \neq i$, and t_j is the time of the spike fired by the nearest six neurons. Note that excitatory connections in the network are not illustrated in Fig. 3.

In our simulation, $\delta t = 50$ ms and $\delta n = 8$. The spatio-temporal structure of the visual stimuli is reflected in the network's activity pattern in the first cycle of intrinsic oscillation, as shown in Fig. 4. Most of the parameters in this network, such as $A^{\text{exc}}, A^{\text{inh}}, \tau^{\text{exc}}, \tau^{\text{inh}}$, and τ^{ADP}, etc. have influences on the dynamical behavior of this network. Note that the network receives informational input only once, then evolves according to (1). Here, we select A^{ADP} as the adjustable parameter. The biological meaning of A^{ADP} is the extent of a transient increase in excitability which is resulted in by the after-depolarization effect (Lisman and Idiart 1995). A larger value of A^{ADP} represents a greater increase in excitability of a neuron. When $A^{\text{ADP}} = 10.0$ mV, two assemblies fire in turn and the dynamics of the neural pool behave like period-2 (Fig. 4a). Along the information flow, it is easy to judge that the upper active assembly encodes the upper bar and the lower assembly encodes the lower bar. Since at each cycle of intrinsic oscillation only one cell assembly is active, it naturally determines the attention target in the brain. This means that at any given time, the visual stimulus encoded by the only active cell assembly becomes the attention focus. In Fig. 4a, both bars have an equal probability of being the attention target. From a neurocomputational point of view, this result provides a possible neural mechanism underlying the selective attention patterns in Fig. 2a. It is worth noting that there is a difference between results of simulation and behavior experiments. As shown in Fig. 4a, the neural network produces periodic attentional switches. However, the behavioural changes of attention between the two stimuli (upper bar and lower bar) are random (Fig. 2a), rather than periodic. One possible reason for such a difference may be the employment of periodic intrinsic oscillation $V^{\text{osc}}(t)$ in (1). Experimental recordings (Llinas et al. 1991; Silva et al. 1991) show that subthreshold oscillations are not simply sinusoidal, but have complex forms. Usually they are similar to periodic waves superimposed by noise. If a more realistic intrinsic oscillation is used for simulation, we suggest that the above difference will be substantially reduced. Further

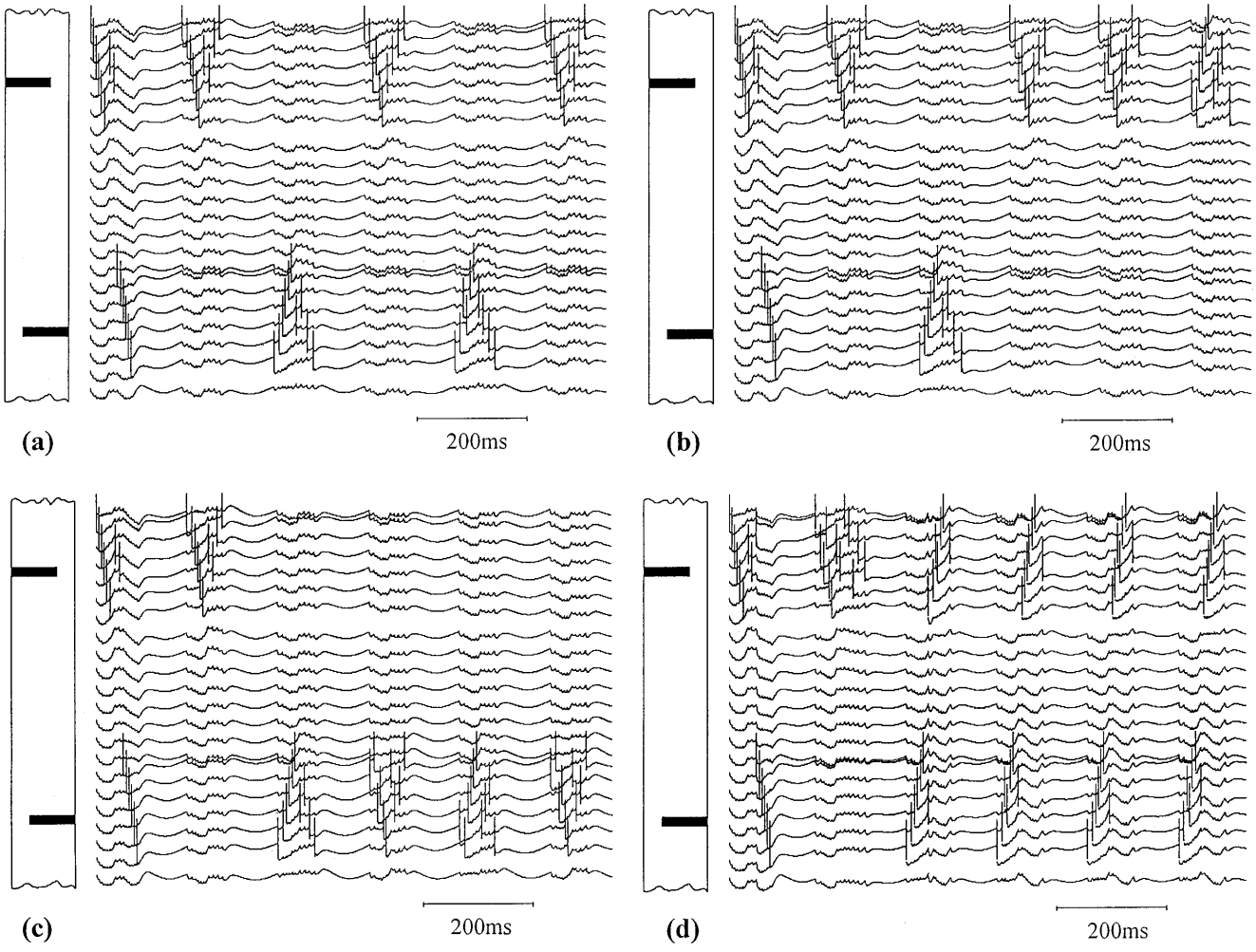

Fig. 4a–d. The firing patterns of network (1) with two input stimuli. Same parameters are used in the four panels except A^{ADP}. **a** $A^{\text{ADP}} = 10.0$ mV. **b** $A^{\text{ADP}} = 9.7$ mV. **c** $A^{\text{ADP}} = 10.5$ mV. **d** $A^{\text{ADP}} = 12.1$ mV. Other parameters are given in context

investigation of this problem will be done in our future work.

Decreasing this parameter to $A^{\mathrm{ADP}} = 9.7$ mV, the network displays a different firing pattern in which only the upper assembly is active and the activity of the lower assembly is totally suppressed (Fig. 4b). It is supposed that this result simulates the attention patterns given in Fig. 2c and d. Changing $A^{\mathrm{ADP}} = 10.5$ mV, the opposite situation occurs in which the lower assembly is active and the upper assembly's activity is totally suppressed (Fig. 4c). In corresponding behavior results, the lower bar enters the focus of attention (not shown). An interesting phenomenon occurs when parameter A^{ADP} is adjusted to $A^{\mathrm{ADP}} = 12.1$ mV; both the upper and lower assemblies fire simultaneously at the same cycle of intrinsic oscillation (Fig. 4d). This result simulates the situation in which the test fly does not focus attention on either of the two bars, but fixates other segments of the panorama, as shown by the many peaks in Fig. 2b and c whose locations are not related to the two bars.

In accordance with the above simulation results, we propose that a natural selective process may exist in the brain. At any given time, the visual stimulus encoded by the only active cell assembly naturally enters the focus of attention. More interesting is that such an active cell assembly spontaneously emerges during the dynamical development of the network. This attention mechanism differs in essence from the spotlight metaphor (Crick 1984), in which scenes are searched item by item by a spotlight of attention which enhances information within a selected region in the scene and filters out information outside of it. The feasibility of this emergent selective mechanism can be strengthened by the following simulation and behavior experiments in mutants.

4 Selective visual attention in learning and memory mutants

In *Drosophila*, we are interested in how the selective attention and the encoding of sensory information are influenced by mutation. Many approaches have established that, due to defects in cAMP metabolism, *dunce* and *rutabaga* mutations affect learning behavior. However, little is known about how their central neurons are affected. Most recently, using the *Drosophila* "giant" neuron culture, aberrant spontaneous spikes and altered firing patterns in *dunce* and *rutabaga* neurons were demonstrated (Zhao and Wu 1997). These electrophysiological experimental results provide us with a unique opportunity to discuss the mutational effects on the electrical activity of a neural network.

4.1 Simulation results

An immediate hallmark of the mutant neurons was the spontaneous firing activities observed in subsets of neurons. In contrast, wild-type neurons remained quiescent unless step current stimulation was applied (Zhao and Wu 1997). From examples given in Zhao and Wu (1997), spontaneous spikes obtained in the absence of application of current in isolated "giant" neurons from *dnc*^{2}, *rut*^{1}, and *dnc*^{M11}*rut*^{2} seem to have random interspike intervals. Figure 5a (Zhao and Wu 1997) shows such an example; the 11 interspike intervals randomly distribute in the range (150 ms, 550 ms) with a mean value of 316 ms. To simulate the mutant neurons, it is principal to know the statistical properties of these spontaneous spikes. However, the number of spikes in mutant neurons published in Zhao and Wu (1997) is so limited that their interspike interval distributions, correlation functions and other statistical properties cannot be analyzed in detail. The important difference between the mutant neurons and the wild-type neurons is the existence of spontaneous firing in subsets of mutant neurons in the absence of current application. Therefore, in this paper, we discuss the most simple situation in which a random spontaneous firing with a uniform distribution is used to simulate mutant neurons. Other situations, in which more complex statistical properties of spotaneous firing are involved, require deeper investigation in future work.

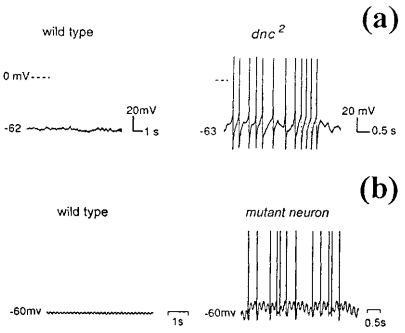

Fig. 5a,b. Spontaneous firing in isolated mutant neurons. **a** Regenerative spikes in the absence of current injection in an isolated "giant" neuron from *dnc*^{2} (from Zhao and Wu, 1997). **b** Random firing of a simulated mutant neuron in the absence of information inputs and other inputs (e.g. V_i^{exc} and $V^{\mathrm{inh}}(t)$) from neurons in network

To develop a mutant network, we attach a random firing feature to a subset of the normal spiking neurons in this network. No matter whether the network receives the information input or not, random firing with a uniform distribution is added to part of the spiking neurons; these neurons are called simulated mutant neurons and the membrane potential for each of them can be modeled by the following equation:

$$V_i(t) = V^{\mathrm{rest}}(t) + V^{\mathrm{osc}}(t) + V_i^{\mathrm{ADP}}(t) + V^{\mathrm{inh}}(t) + V_i^{\mathrm{exc}}(t) + V_i^{\mathrm{ran}}(t) \ , \qquad (2)$$

where function $V_i^{\mathrm{ran}}(t)$ describes the spontaneous firing property. Besides a subset of simulated mutant neurons, the mutant network is supposed to include a good many normal neurons whose membrane potentials are described by Eq. (1).

In our simulation, it is assumed that when $t = t_i^{\mathrm{old}} + \Delta\tau^i, V_i^{\mathrm{ran}}(t) = V^{\mathrm{super}}$; otherwise, $V_i^{\mathrm{ran}}(t) = 0$.

Here, t_i^{old} is the time for the last spontaneous firing event in simulated mutant neuron i. $\Delta\tau^i = 16 \times [1+ \text{random}(N)]$ ms, where the function random(N) creates a random integer between 0 and $N-1$ according to a uniform distribution. We choose $N = 51$. To induce spontaneous firing, a large enough superthreshold stimulus V^{super} is needed; thus we set $V^{\text{super}} = 40$ mV. Other parameters in Eq. (2) are set to be the same as in Eq. (1). Numerical experiments show that under the effect of function $V_i^{\text{ran}}(t)$, simulated mutant neurons are able to fire spontaneously and randomly in the absence of informational input to the network. According to the expression of $\Delta\tau^i$, simulated interspike intervals range within (16 ms, 800 ms) with a mean value of 392 ms. Figure 5b displays the spontaneous firing of an isolated simulated mutant neuron, for comparison with an isolated real "giant" neuron (Fig. 5a).

Simulations show that when the proportion of the mutant neurons to the total neurons in the network is increased to a critical value (denoted by α%), random firing appears in the network and leads to an incapability of selective attention. It is found that the mutant neurons, being far away from the incident location of information input to this network, have less effect on the dynamics of this network than those directly receiving information inputs. In two situations, the critical values α% are 23% and 13%. An example with $\alpha = 18$ is given in Fig. 6, in which random firing dominates the developing dynamics of the network and no obvious assemblies relating to the input stimuli can be distinguished. Results show that only a subset of simulated mutant neurons are enough to cause poor attention performance in the network. This is in accord with the electrophysiological fact that aberrant spontaneous firing only exists in subsets of mutant neurons (Zhao and Wu 1997).

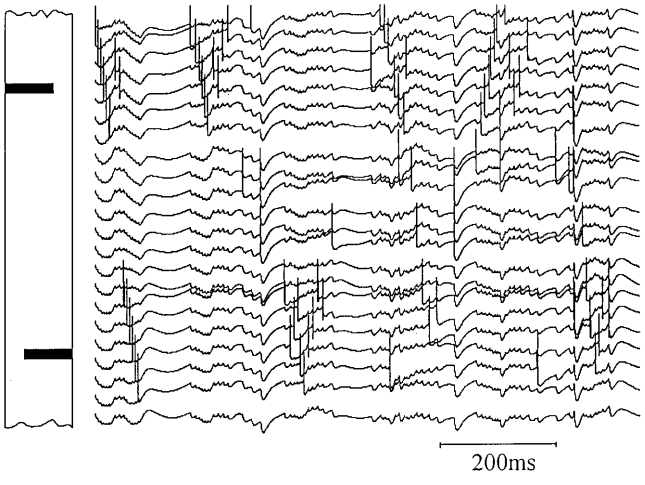

Fig. 6. Mutation in a subset of neurons results in the incapability of the network to perform selective attention. The parameters of the network and the information inputs are the same as in Fig. 3c except 18% spiking neurons are replaced by abnormal neurons having random spontaneous firing

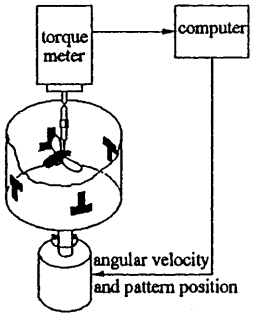

Fig. 7. *Drosophila* flight simulator. Flies were attached to a torque meter with their heads immobilized, and allowed to control with their yaw torque the angular velocity of a vertical drum surrounding them. The internal surface of the drum was covered with four regularly spaced figures to stimulate the fly visually

4.2 Behavior experimental results

From simulations with the two stimuli given above, we infer that *dunce* and *rutabaga* cannot correctly focus attention under other visual inputs either. To verify this inference, other behavior experiments were carried out; the simulator is shown in Fig. 7. A visual stimulus consists of four regularly spaced figures; two upright and two inverted T-shaped figures are located in the four quadrants of a brightly illuminated arena, with identical patterns facing each other. Each 2-day-old or 3-day-old female fly of the wild-type Canton-S, mutants *dunce* and *amnesiac* is allowed to have a 6-min flight. For each strain of *Drosophila*, the performances of six individual flies are displayed in the form of histograms in Fig. 8.

Results show that the attention patterns of the mutants are very different from that of the wild type. In detail, mutants *dunce* and *amnesiac* have limited abilities to focus attention on the specific visual figures, but wild-type flies are strongly attracted by the same visual figures. The possible cause can be attributed to the abnormal spontaneous spikes and altered firing patterns (Zhao and Wu 1997), although electrophysiological results on the activity of the central neurons in mutant *amnesiac* are still lacking.

5 Summary and discussion

In summary, a possible link between the activity of cell assemblies, the encoding of sensory information, and the selective attention in *Drosophila* is proposed. Our results suggest that selective attention is an emergent behavior of the dynamic cell assemblies in the central neural system of the *Drosophila* brain.

So far some questions concerning attention in *Drosophila* appear controversial and remain to be unanswered, both experimentally and at a deeper explanatory level (Taylor 1998). For example, what happens to unattended stimuli? Are we only conscious of what we attend to? Are we fleetingly aware of things but then forget them or are we not aware of them at all? If neural systems of other animals including human beings have

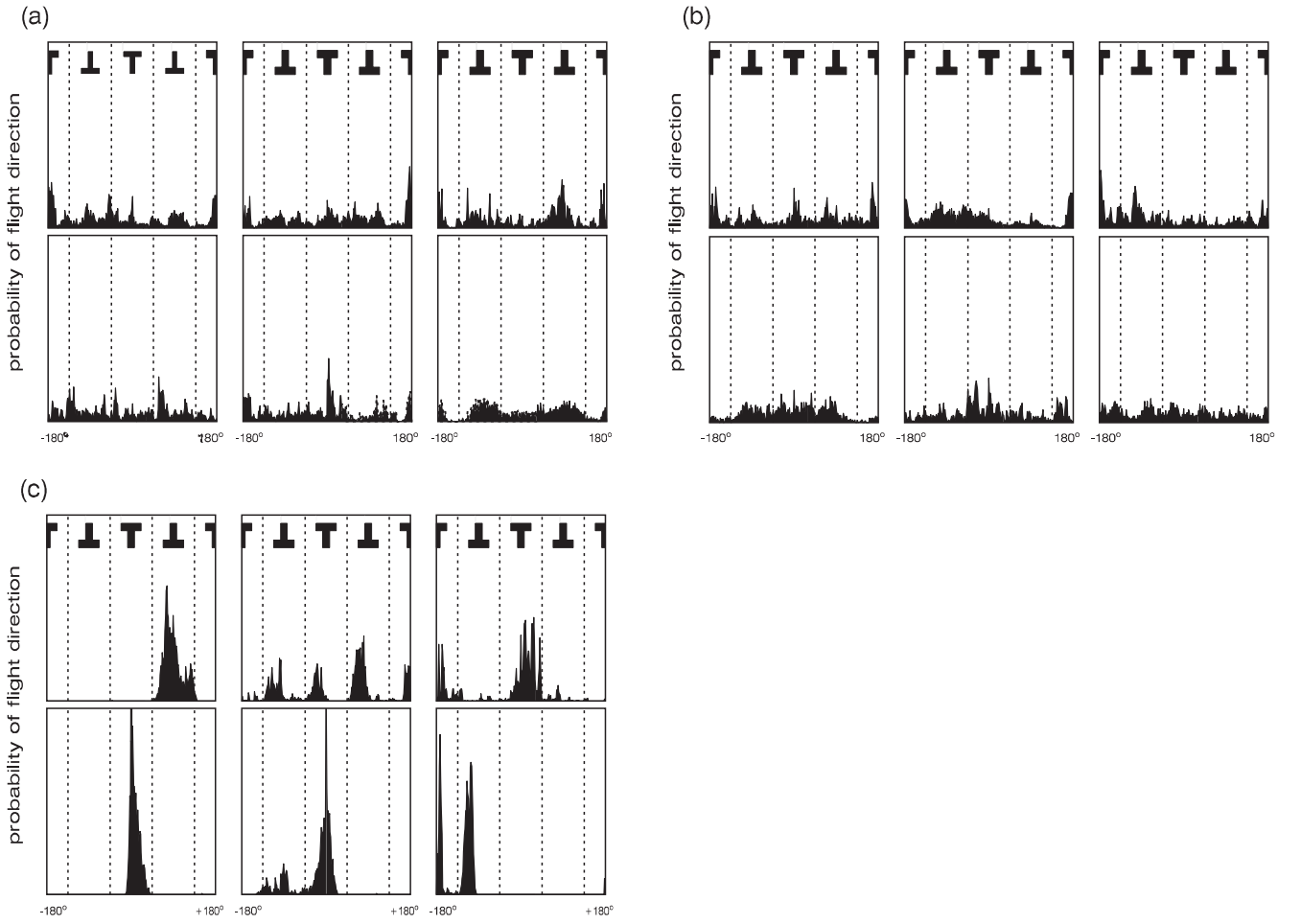

Fig. 8a–c. Histograms of a 6-min flight. **a** Six individual *dunce* mutant flies show a poor attention ability. **b** Six individual *amnesiac* mutant flies show a poor attention ability. **c** Six individual wild-type flies display different patterns of selective attention for the same visual figures

similar attention mechanisms to that in the *Drosophila* brain, the idea proposed in this work may provide possible answers to the above questions. According to the emergent mechanism of attention supported in this work, not all visual stimuli presented on the retinae enter higher brain areas, although they are processed in parallel at an early stage of visual input. Some stimuli will not be acknowledged at higher levels in the sense that the neural activity encoding these stimuli will be suppressed in competition for a limited information processing capacity. For a neural system, such an attention manner may be one of the optimal ways of working.

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