The incentive circuit of the fruit fly brain: a computational perspective

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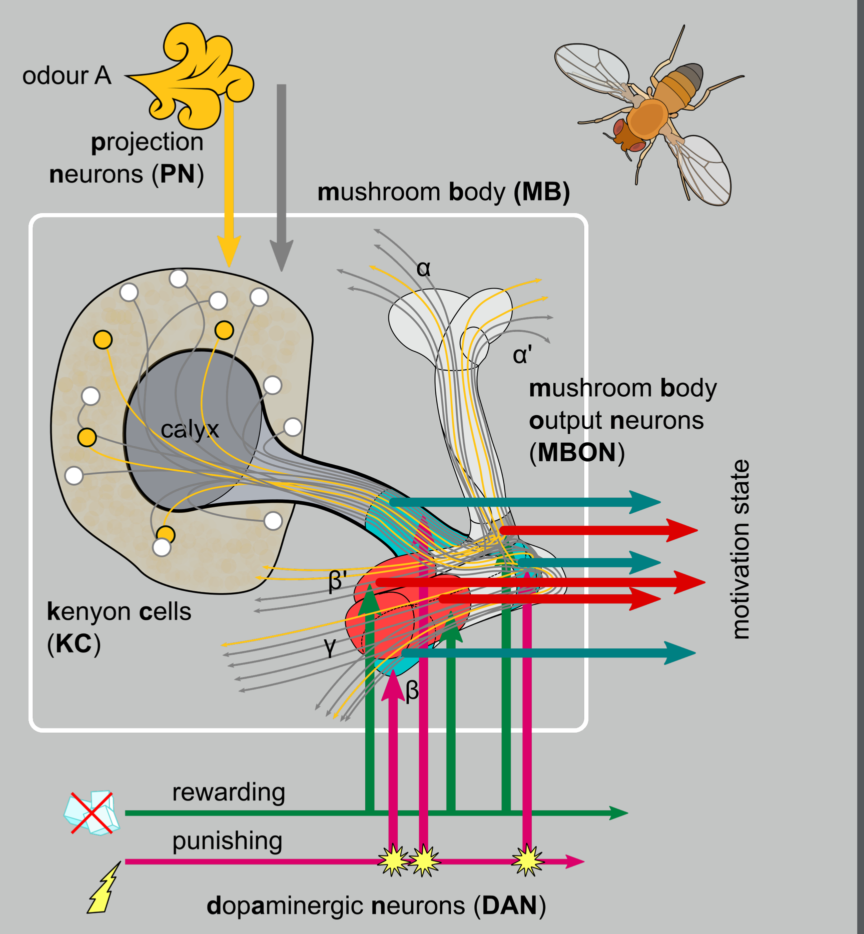
Abstract

1. Key circuits for associative and reinforcement learning have been identified in the mushroom body neuropils of the insect brain [1, 2].
2. Detailed imaging, electrophysiological and structural data about the mushroom bodies in *Drosophila melanogaster* has led to the identification of a variety of microcircuits involved in memory.
3. In [3], we propose a comprehensive scheme, based on the connectivity and the responses of identified neurons in the mushroom bodies.
   - ▷ We link these known microcircuits together as an incentive circuit that acquires, forgets and assimilates associative memories over different timescales.
   - ▷ We suggest that our novel dopaminergic learning rule increases the adaptation capabilities of the overall circuit.

About the mushroom bodies



- Sensory input is projected onto the calyxes, from where the numerous kenyon cells (KCs) distribute it to the much fewer output neurons (MBONs).
- Dopaminergic neurons (DANs) deliver multi-dimensional reinforcement signals and modulate the KC-to-MBON synaptic weights.

Mapped neurons and synapses

- The model has been validated by mapping all its connections to their equivalent in flies:

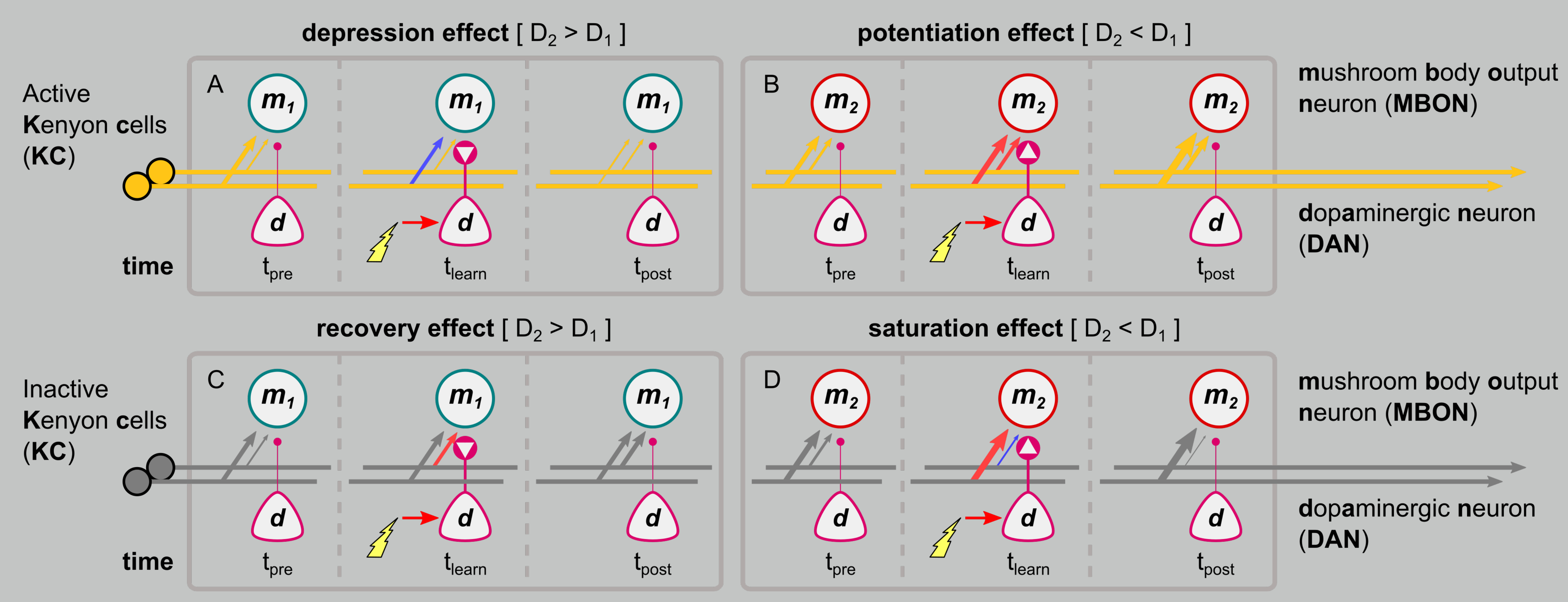
fruit fly data	model	Source
PPL1-01 $\multimap$ MBON-11	$d_{av} \multimap s_{at}$	[4]
PAM-07 $\multimap$ MBON-05	$d_{at} \multimap s_{av}$	[1]
MBON-11 $\dashv$ PPL1-01	$s_{at} \dashv d_{av}$	[4]
MBON-05 $\dashv$ PAM-07	$s_{av} \dashv d_{at}$	[1]
MBON-11 $\dashv$ MBON-01	$s_{at} \dashv r_{av}$	[5]
MBON-05 $\dashv$ MBON-12	$s_{av} \dashv r_{at}$	[1]
PPL1-03$_2$ $\multimap$ MBON-12	$c_{av} \multimap r_{at}$	[1, 6]
PAM-02 $\multimap$ MBON-01	$c_{at} \multimap r_{av}$	[1, 6]
MBON-12 $\rightarrow$ PAM-02	$r_{at} \rightarrow c_{at}$	[6]
MBON-01 $\rightarrow$ PPL1-03$_2$	$r_{av} \rightarrow c_{av}$	[2]
PPL1-03$_2$ $\multimap$ MBON-15	$c_{av} \multimap m_{av}$	[1]
PAM-02 $\multimap$ MBON-02	$c_{at} \multimap m_{at}$	[1]
MBON-15 $\rightarrow$ PPL1-03$_2$	$m_{av} \rightarrow c_{av}$	[1, 2]
MBON-02 $\rightarrow$ PAM-02	$m_{at} \rightarrow c_{at}$	[1, 2]
PPL1-03$_1$ $\multimap$ MBON-15	$f_{at} \multimap m_{av}$	[1]
PAM-04 $\multimap$ MBON-02	$f_{av} \multimap m_{at}$	[1]
MBON-15 $\rightarrow$ PAM-04	$m_{av} \rightarrow f_{av}$	[2]
MBON-02 $\rightarrow$ PPL1-03$_1$	$m_{at} \rightarrow f_{at}$	[2]
PPL1-03$_1$ $\multimap$ MBON-12	$f_{at} \multimap r_{at}$	[1]
PAM-04 $\multimap$ MBON-01	$f_{av} \multimap r_{av}$	[1]

Dopaminergic learning rule

- Update of the KC-to-MBON synaptic weights:

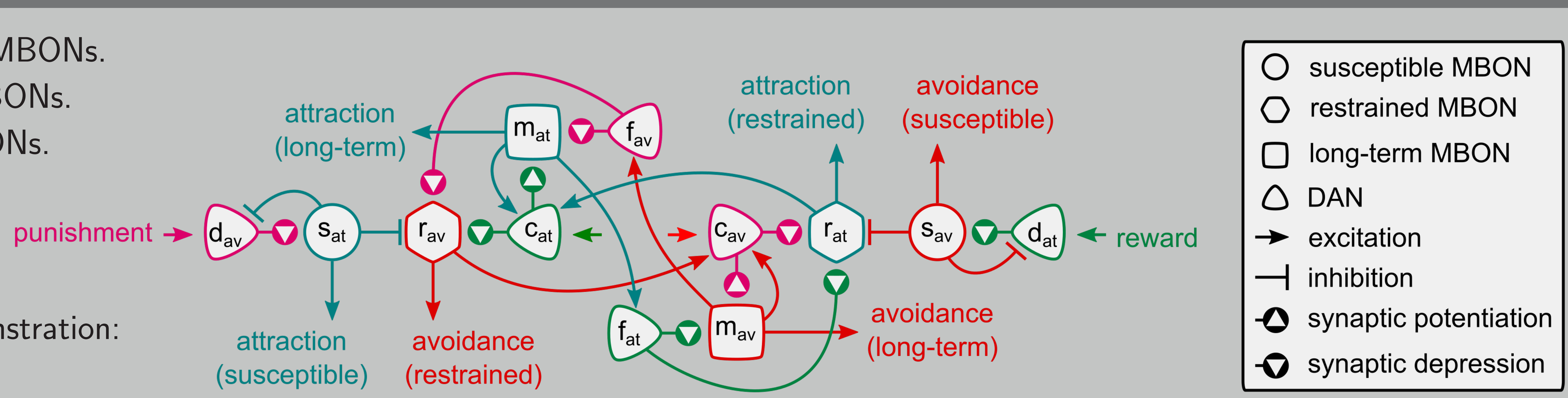
$$\Delta W^{ij}_{k2m}(t) = \delta^{ij}(t)[k^i(t) + W^{ij}_{k2m}(t) - w_{rest}]$$

- $\delta^{ij}(t) = D^{ij}_2(t) - D^{ij}_1(t)$ controls the learning at the KC^i-to-MBON^j synapse.
- $k^i(t)$ is the KC activity.
- $w_{rest} = 1$ is the resting value.
- $D^{ij}_1(t)$ and $D^{ij}_2(t)$ are components of the dopaminergic signal, with a short and a long time-constant respectively, that are key for explaining backward learning [7].
- Depending on conditions, this synaptic modulation causes weights to stabilise or to increase with positive feedback
  - ▷ We exploit these properties to enable short- and long-term memories, respectively, to be formed and forgotten in parallel for different contexts.

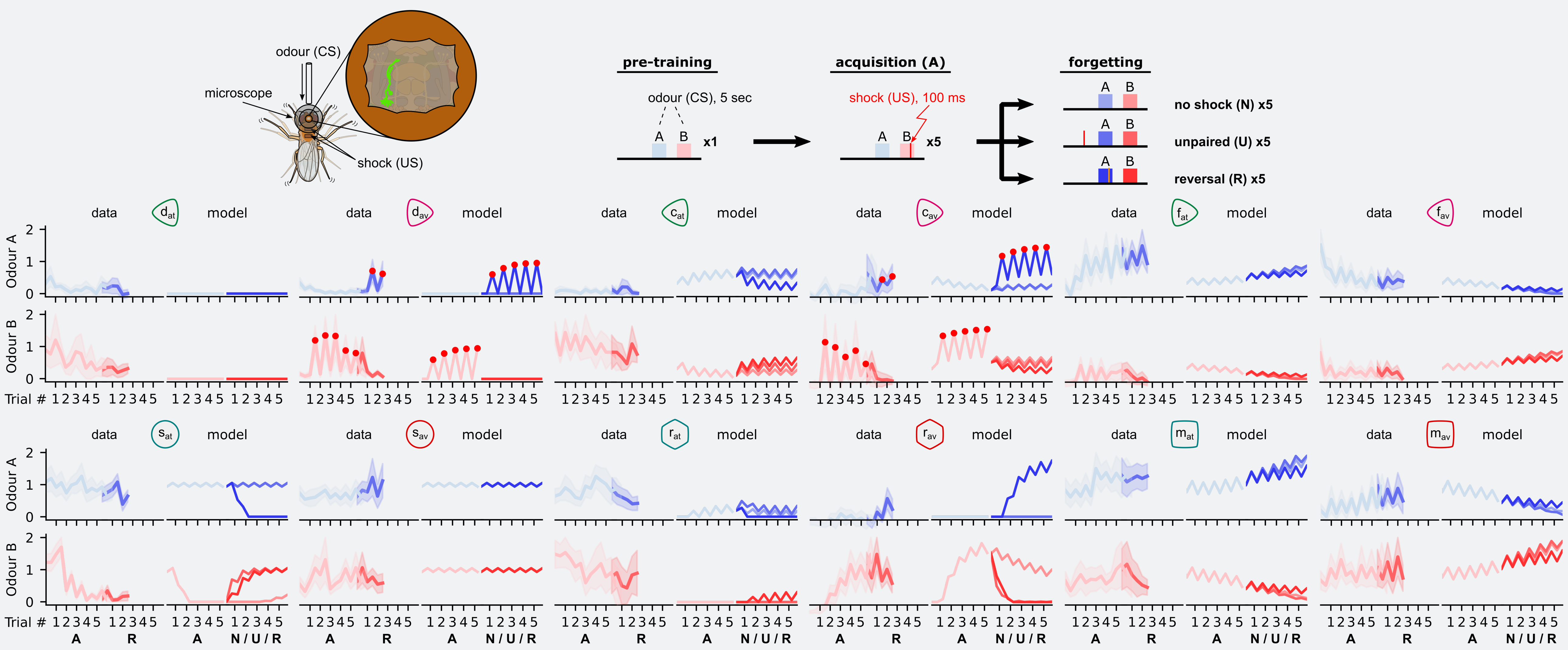


Computational model of the incentive circuit

- Primitive $\rightarrow$ susceptible (s) MBONs.
- Flexible $\rightarrow$ restrained (r) MBONs.
- Long-term memory (m) MBONs.
- Discharging (d) DANs.
- Charging (c) DANs.
- Forgetting (f) DANs.
- Step-by-step functional demonstration: link to video

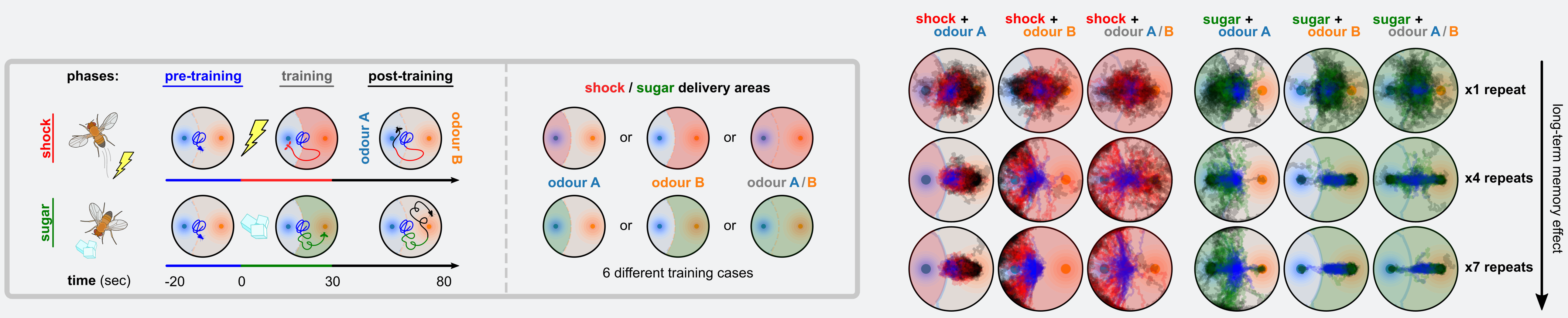


Modelling the neural responses



- We show that the incentive circuit combined with the DLR can replicate experimental observations of the response dynamics of specific neurons during acquisition and a variety of forgetting stages of odour-shock association.

Modelling the behaviour



- We further verify the function of the incentive circuit by demonstrating how the reproduced responses of the output neurons could drive the behaviour of a virtual fruit fly, creating similar odour preferences to the real flies.

Conclusion

- The dopaminergic learning rule is an alternative to prediction error learning rules, and within the incentive circuit can support acquisition, forgetting and assimilation of memories.
- Different MBONs hold primitive, flexible or long-term memories, supporting flexible exploration/exploitation trade-off in an olfactory conditioning task.

EPSRC Engineering and Physical Sciences Research Council

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