Modelling Multi-modal Learning in a Hawkmoth

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Abstract. The moth *Macroglossum stellatarum* can learn the colour and sometimes the odour of a rewarding food source. We present data from 20 different experiments with different combinations of blue and yellow artificial flowers and the two odours honeysuckle and lavender. The experiments show that learning about the odours depends on the colour used. By training on different colour-odour combinations and testing on others, it becomes possible to investigate the exact relation between the two modalities during learning. Three computational models were tested in the same experimental situations as the real moths and their predictions were compared to the experimental data. The average error over all experiments as well as the largest deviation from the experimental data were calculated. Neither the Rescorla-Wagner model or a learning model with independent learning for each stimulus component were able to explain the experimental data. We present the new categorisation model, which assumes that the moth learns a template for the sensory attributes of the rewarding stimulus. This model produces behaviour that closely matches that of the real moth in all 20 experiments.

1 Introduction

Flowers attract pollinators mainly by colour and odour stimuli. For newly eclosed moths and butterflies, it is important to quickly recognise a rewarding flower, and innate colour and odour preferences contribute to this ability [10,33]. By their innate preference for blue, naive honeybees are guided to flowers with a large amount of nectar [15]. A preference for blue is shared by other insects but innate colour preferences can differ between species [34]. Rapid and flexible learning to associate colour or odour with a reward has been demonstrated in honeybees, butterflies and moths [1,32,31,20,24,30,33].

The diurnal hummingbird hawkmoth, *Macroglossum stellatarum*, uses colour vision in food-searching, and spontaneously forages from coloured artificial flowers without any odour [19,18]. *M. stellatarum* has a strong innate preference for

S. Nolfi et al. (Eds.): SAB 2006, LNAI 4095, pp. 422–433, 2006.

blue flowers as a food-source and a weaker preference for yellow [18], but it can easily and equally fast learn other colours including green which is not a colour of a typical flower [2,18].

M. stellatarum has most probably evolved from a nocturnal ancestor, and in nocturnal hawkmoths, odour is very important in food-searching [6,28]. It has recently been shown that the ability of *M. stellatarum* to learn an odour that accompanies a colour depends on the choice of colour [3]. When an innately preferred blue colour is learned together with an odour, the moth will not learn the odour. On the other hand, if the less preferred colour yellow is used in, the moths can readily learn the odour.

Stimuli of one sensory modality can influence learning of stimuli of another modality in different ways. In most cases, two stimuli are more effective than one and the advantages of multi-sensory integration are of great importance in many animals [22]. In honeybees, colours attract attention before odour, while odour attracts attention when the bees are very close to the food source [32,14]. There is also evidence for increased learning when two stimulus types are combined [29]. In bumblebees, it has been shown that the presence of odour enhances colour discrimination, and increases attention and memory formation [21]. In honeybees, the similarity between colours modulate odour learning [32,14]. The similarity between colours has also been shown to modulate place learning in a hawkmoth [4].

A special case of multi-modal learning is configural learning where an animal learns to respond to a configuration of stimuli, but not to the single stimulus modalities themselves [23]. The hawkmoth *Manduca sexta* needs both an odour and a visual stimulus to unroll the proboscis for feeding [28], which also might be a preference for a configuration of both cues.

In contrast, two different situations have been found where learning of one stimulus prevents the learning of another stimulus. First, animals trained to a stimulus compound consisting of, for instance, a colour and an odour, sometimes only learn one of the components. For example, they learn the colour but not the odour. This effect is called overshadowing [25]. Second, when animals are first trained to one stimulus component and later to the compound they will not learn the stimulus component that was initially absent. The first component already predicts the reward and blocks learning of the second component [17]. Blocking and overshadowing were originally defined for classical conditioning but have also been found in instrumental conditioning [8,9,23]. A possible reason for the lack of learning of the second stimulus may be that the animal directs its attention only to the first stimulus [35]. The existence of blocking and overshadowing in insects is controversial and experiments have given mixed results [8,9,7,11,13]. In particular, it has been disputed whether the learning of one stimulus modality depends on the other.

To test this, we collected data from 20 different learning experiments with *M. stellatarum* where multi-modal stimuli were used. Most of the animal data has been previously published [3], but experiments 8-12 are reported here for the first time. We also tested a number of learning models on these experiments using