



Spontaneous decisions and operant conditioning in fruit flies

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ABSTRACT

Already in the 1930s Skinner, Konorski and colleagues debated the commonalities, differences and interactions among the processes underlying what was then known as “conditioned reflexes type I and II”, but which is today more well-known as classical (Pavlovian) and operant (instrumental) conditioning. Subsequent decades of research have confirmed that the interactions between the various learning systems engaged during operant conditioning are complex and difficult to disentangle. Today, modern neurobiological tools allow us to dissect the biological processes underlying operant conditioning and study their interactions. These processes include initiating spontaneous behavioral variability, world-learning and self-learning. The data suggest that behavioral variability is generated actively by the brain, rather than as a by-product of a complex, noisy input–output system. The function of this variability, in part, is to detect how the environment responds to such actions. World-learning denotes the biological process by which value is assigned to environmental stimuli. Self-learning is the biological process which assigns value to a specific action or movement. In an operant learning situation using visual stimuli for flies, world-learning inhibits self-learning via a prominent neuropil region, the mushroom-bodies. Only extended training can overcome this inhibition and lead to habit formation by engaging the self-learning mechanism. Self-learning transforms spontaneous, flexible actions into stereotyped, habitual responses.

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1. Introduction: operant and classical conditioning

Evolution is a competitive business. This competition has shaped the behavior of all ambulatory organisms to provide them with much more flexibility and creativity than the common stimulus–response cliché would allow them (Brembs, 2009a). In the wild, animals face a world that constantly challenges them with physically superior competitors, ever faster prey, ever more cunning predators, unpredictable weather, foreign habitats and a myriad of other, potentially life-threatening problems. In order to survive and procreate, animals have evolved not only to learn about the relationships between objects and events in this world (often studied experimentally using classical or Pavlovian conditioning), but also about how the world responds to their actions (often studied experimentally using operant or instrumental conditioning). Traditionally, both learning processes have been conceptualized as the detection and memorization of temporal contingencies, in the former case among external stimuli and in the latter between actions and external stimuli. However, most learning situations comprise both contingencies in an inextricable loop: the behaving

animal constantly receives a stream of sensory input that is both dependent and independent of its own behavior. It was the genius of Pavlov to prevent his dogs from entering this loop with the world, isolating the conditioned and the unconditioned stimulus from the control of the animal. On the face of it, Skinner’s analogous genius was to isolate the instrumental action and study the rules by which it controls its consequences. However, as the scholars at the time were well aware, the levers in Skinner’s boxes signaled food for the rats pressing them just as accurately as Pavlov’s bell signaled food for his dogs. Therefore, a recurrent concern in learning and memory research has been the question whether a common formalism can be derived for operant and classical conditioning or whether they constitute an amalgamation of fundamentally different processes (Skinner, 1935, 1937; Konorski and Miller, 1937a,b; Guthrie, 1952; Sheffield, 1965; Rescorla and Solomon, 1967; Trapold and Winokur, 1967; Trapold and Overmier, 1972; Hellige and Grant, 1974; Gormezano and Tait, 1976; Donahoe et al., 1993; Donahoe, 1997; Brembs and Heisenberg, 2000; Brembs et al., 2002; Balleine and Ostlund, 2007).

In this article I would like to review some of the new evidence for and against a hypothesis that there may be two fundamental mechanisms of plasticity, one which modifies specific synapses and is engaged by learning about the world, and one which modifies entire neurons and is engaged whenever neural circuits controlling behavior need to be adjusted. Both of these mechanisms appear to

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be deeply conserved on the genetic level among all bilaterian animals. I will refer to these mechanisms as world- and self-learning, respectively, when presenting some of this evidence. It is important to emphasize that while these biological processes may to some extent be differentially recruited during certain, specific operant and classical conditioning experiments in the laboratory, they probably are engaged, to varying degrees, in many different conditioning situations. Thus, while the terms 'classical' and 'operant' are procedural definitions denoting how animals learn, self- and world-learning denote the biological processes underlying what is being learned during operant, classical or other learning situations (Colomb and Brembs, 2010).

2. Striving to emulate Pavlov: isolating the operant behavior

Because rats need a lever to press and thus may learn about the food-predicting properties of the lever, this experiment is not ideal for studying the neurobiology underlying operant learning processes. Any memory trace found in the brain cannot be unambiguously attributed to the mechanism engaged when learning about the lever or to the learning about the behavior required to press the lever. Therefore, preparations had to be developed without such 'contamination'. One such preparation is tethered *Drosophila* at the torque meter (Heisenberg and Wolf, 1984; Wolf and Heisenberg, 1986, 1991; Wolf et al., 1992; Heisenberg, 1994; Heisenberg et al., 2001; Brembs, 2009a). For this experiment, the fly is fitted with a small hook, glued between head and thorax (Brembs, 2008). With this hook, the fly is attached to a measuring device that measures the angular momentum the fly exerts when it attempts to rotate around its vertical body axis (yaw torque; Fig. 1)(Götz, 1964; Heisenberg and Wolf, 1984). Even in the absence of any change in their sensory input, flies tethered at the torque meter show a striking variability in their yaw torque behavior (Fig. 1b)(Heisenberg, 1994). On the face of it, one may assume that this variability is mainly due to noise, as there are no cues prompting each change in turning direction. However, a mathematical analysis excluded noise as a primary cause behind the variability and instead revealed a nonlinear signature in the temporal structure of the behavior. If the fly is not changing turning directions at random and given the propensity of nonlinear system to behave random-like, it is straightforward to interpret the data as evidence for a nonlinear decision-making circuit in the fly brain determining in which direction to turn when, and with how much force (Maye et al., 2007; Brembs, 2010). Apparently, even flies are capable of making spontaneous decisions in the absence of any sensory cues eliciting or informing the decision (i.e., initiating activity (Heisenberg, 1983). Conveniently, in this setup many different environmental cues can be made contingent on many different behavioral decisions in order to design experiments exploring the neurobiology of these processes in a genetically tractable model organism (Wolf and Heisenberg, 1991; Wolf et al., 1992; Heisenberg et al., 2001). For instance, the angular speed of a drum rotating around the fly centered within it can be made proportional to the fly's yaw torque, allowing the fly to adjust 'flight direction' with respect to visual patterns on the inside of the drum. One can make different wavelengths of light contingent on the sign (i.e., left or right) of the yaw torque, allowing the animal to control either the coloration (e.g. green or blue) or the temperature (i.e., infrared) of its environment. Various combinations of all these possibilities have been realized and are too numerous to mention here (Wolf and Heisenberg, 1986, 1997; Ernst, 1999; Heisenberg et al., 2001; Brembs and Heisenberg, 2001; Tang et al., 2004; Liu et al., 2006; Brembs and Hempel De Ibarra, 2006; Brembs and Wiener, 2006). Important for the argument made here is the possibility to allow the spontaneous decisions to turn in one direc-

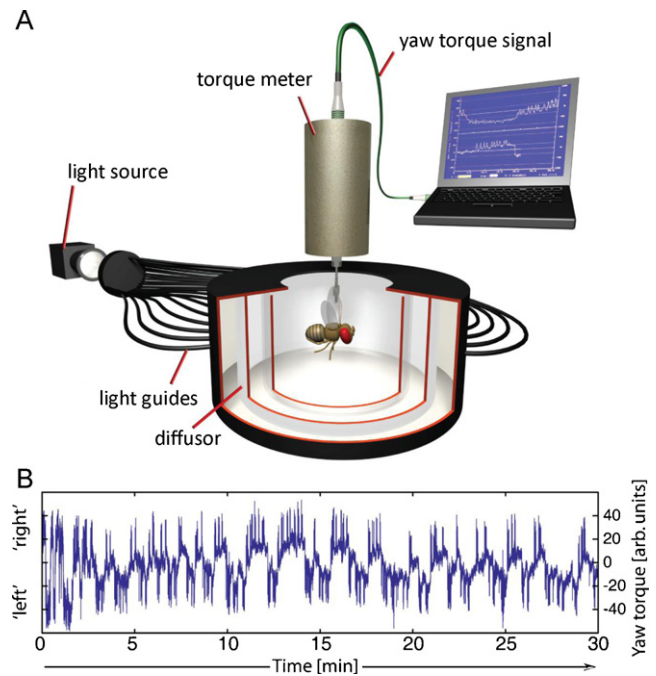


Fig. 1. Suspended at the torque meter, the fruit fly *Drosophila* initiates behavioral activity even in the absence of any change in its stimulus situation. **A** – The tethered fly is surrounded by a cylindrical drum which is illuminated homogeneously from behind (arena). The torque meter is connected to a computer recording the yaw torque traces **B** – Example yaw torque trace showing 30 min of uninterrupted flight in a completely featureless arena. Positive values correspond roughly to turning maneuvers which would rotate the fly to its right in free flight, whereas negative values would turn the fly to its left. The trace exhibits several components contributing to the variability, a slow baseline component and fast, superimposed torque spikes, corresponding to body-saccades in free flight. During the experiment, the fly initiates numerous torque spikes and many changes in turning direction. (Modified from Maye et al., 2007).

tion, say, right turning (positive torque values in Fig. 1b) to switch the environment from one state to another, say from green and hot to blue and cold or vice versa. This simple concept can be simplified even further: positive torque values can be made to lead to hot temperature, without any change in coloration present – the experiment is performed in constant white light: the only thing concomitant with the switch in temperature is the transition of the yaw torque value from one domain to the other, nothing in the environment of the fly changes other than temperature (Fig. 2). Because there are no external cues such as levers indicating which behavior will be rewarded/punished, this is one example of technically isolating the operant behavior to an extent previously unattained.

Parallel developments to isolate the operant behavior have been made in the sea slug *Aplysia* (Nargeot et al., 1997, 1999a,b,d, 2007, 2009; Brembs et al., 2002; Nargeot, 2002; Lorenzetti et al., 2006; Lorenzetti et al., 2008; Nargeot and Simmers, 2010). There, freely moving animals generate feeding movements in the absence of eliciting stimuli. Even the isolated buccal ganglia, which control these feeding movements in the intact animal, generate spontaneous motor patterns in the dish ('fictive feeding'). Implanted electrodes can then be used to provide the animal or the isolated ganglia with a virtual food reward as reinforcement for one class of feeding movements but not others. Analogous to the Pavlovian strategy of isolating the relevant stimuli and then tracing their pathway into the nervous system until the synapse of convergence between conditioned and unconditioned stimulus had been identified, we identified the neuron where spontaneous behavior and reinforcement converge: a neuron called B51 (Plummer and Kirk, 1990; Nargeot et al., 1999b,c; Brembs et al., 2002). Impor-

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