Learning and Memory without a Brain
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Over the last 40 years, the study of animal learning has gone through a radical metamorphosis. Animal learning of the 1960s variety was largely dominated by researchers who took Watson's behaviorist dictates as scripture. They hoped to explain complex behavior in simple S-R terms while avoiding reference to unobservable constructs. They were, in retrospect, the killjoys of creativity, always suspicious of anything new and wary of most internal/theoretical constructs. Against this backdrop, came the cognitive approach, opening the doors to a new faith that promised greater tolerance for internal constructs.

Today, we often take for granted that all higher vertebrates process information in a limited capacity device (short-term memory [STM]) (Wagner et al. 1973), that attention guides the learning process (Mackintosh 1975), and that the organism can abstract the contingency between its behavior and an environmental outcome (Maier and Seligman 1976). Yet 30-40 years ago, each of these claims was greeted with skepticism, with many questioning whether explanations of animal behavior require such cognitive constructs.

I began my research career well indoctrinated into the cognitive approach and I championed its benefits (e.g., Moye et al. 1981; Rescorla et al. 1985; Grau 1987a). But in recent years, my collaborators have led me down an alternative path that I initially thought led in an incomprehensible direction, a course that sought evidence of learning and memory within a vertebrate that effectively lacks a brain. As we will see, this path led to a new vista, one that has forced me to question my cognitive faith. It seems that many of the behavioral effects I thought were best described in cognitive terms can be observed in the absence of a brain. I now find myself in the unfortunate position of the killjoy, questioning the application of cognitive constructs to infrahuman species.

Memory within the Spinal Cord

The starting point for this work was a series of studies that explored how the body (and mind) regulate pain. I had shown that exposure to a mildly painful stimulus engages an inhibitory mechanism that reduces behavioral reactivity to subsequent noxious stimuli, a phenomenon known as antinociception. For example, in rats, exposure to a few brief tailshocks inhibits tail-withdrawal from radiant heat (the tail-flick test). This response is mediated by a nociceptive (pain signal) reflex that is organized within the spinal cord; it is a spinal reflex that can be readily elicited after the lower spinal cord has been surgically disconnected from the brain. Exposure to moderate shock appears to inhibit nociceptive reactivity (antinociception) by engaging neural mechanisms within the brain that, through a descending pathway, inhibit spinal nociceptive reflexes. I argued that the memory of the aversive event helped maintain the antinociception after shock exposure. Specifically, that the central representation of the aversive event in short-term memory (STM) continues to drive the antinociceptive systems after shock exposure, producing an antinociception that lasts 10 min or more.

STM is generally envisioned as a kind of rehearsal buffer where information can be temporarily maintained (e.g., Atkinson and Shiffrin 1968). Because it is thought to have a limited capacity, it is subject to distraction -- new information can disrupt the rehearsal of items already in STM, causing their memory to rapidly decay. Interestingly, a distracting stimulus also disrupts memory in other animals, which suggests that rats too process information in a STM-like device (Wagner 1981). Assuming this perspective, I reasoned that if the central representation of an aversive event in STM maintains the activation of the antinociceptive systems, then displacing this memory with a distractor should cause the antinociception to decay more rapidly. As predicted, presenting a visual distractor (a flashing light) after shock decreased the duration of the subsequent antinociception (Figure 1A) (Grau 1987a).

To derive predictions from this memory-oriented perspective, I had to assume that the