

## The conditioned response: More than a knee-jerk in the ontogeny of behavior

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In experimental studies of conditioning in adult vertebrates, it is implicit that the behavioral repertoire will change little between the time of conditioning and the time of testing. In developing organisms, however, patterns of response to the CS, the US and their pairing are superimposed on rapidly developing neural, motor, and behavioral systems. Thus, the conditioned response (CR) may be affected by (a) the age at which conditioning takes place; (b) the age at which testing takes place; or (c) the delay between conditioning and testing. The same confounds exist in studies of invertebrate species with brief lifespans, as suggested in Turkkan's target article. One approach to dealing with these confounds is to attend to details of the UR and the CR at the ages of both conditioning and testing (Smotherman & Robinson 1985). We believe that understanding the behavioral repertoire of immature organisms at all relevant times is underappreciated in studies of learning, both ontogenetically and phylogenetically.

To clarify a point mentioned by Turkkan, the evidence for conditioning in 19-day-old rat fetuses includes a "suppression of total activity (which is) generally similar to LiCl-generated suppression of activity." More important, the suppression of movement exhibited on day 19 of gestation is not evident across all categories of behavior. For example, lateral flexions of the trunk increase in frequency as one component of the CR. This is noteworthy, because trunk flexions are ordinarily infrequent on day 19 and are not part of the fetal response to ip injection of LiCl at this age. On day 17, though, trunk flexions are the predominant behavioral response to the US. Thus, not only is the magnitude of the CR very similar to the UR (overall suppression of activity), but it is similar in details of form as well. It is evident that specific components of the response to LiCl on the day of conditioning (day 17) are retained and expressed on the day of testing (day 19).

The behavioral repertoire of the immature organism clearly develops within a niche that often places physical and sensory demands upon the organism. To illustrate, one component of the behavioral response of adult rats that encounter novel/aversive chemosensory stimuli is stereotypic facial wiping behavior. Ontogenetic investigation of this species-typical action pattern has suggested that it emerges late during the second postnatal week and is absent in neonatal rats. However, we have demonstrated that 20–21 day old rat fetuses reliably (100% of subjects) perform facial wiping behavior in response to intraoral infusion of novel fluids (Smotherman & Robinson 1987). This paradoxical discontinuity appears to be due to environmental constraints on the wiping response in young rat pups. On the day of birth, before the righting reflex is well developed, the infusion is accompanied by an increase in pup activity, which often results in pups rolling to their backs. In a supine posture, the forelimbs are freed from a support function, which permits the performance of facial wiping (observed in 50% of subjects). Twenty-four hours later, although behaviorally active pups rarely (20% of subjects) express facial wiping when tested on a solid substrate, they reliably (90% of subjects) exhibit the facial wiping response to infusion when suspended in a fluid medium, freeing the forelimbs from a support function (Smotherman & Robinson, *in press*). These findings argue that an element of the behavioral repertoire that is commonly expressed at one age may not be expressed at all subsequent ages because of temporary constraint by environmental or behavioral conditions.

A standard research strategy of developmentalists is to identify a focal behavior (such as a manifestation of conditioning) in the adult of the species, then to apply the behavioral testing para-

digim in an iterative fashion to successively younger animals until the focal behavior is no longer present. Unless environmental and behavioral constraints on the expression of the focal behavior are considered, this general approach to identifying behavioral origins may yield erroneous conclusions. Given the appropriate attention to details of the behavioral repertoire as it changes during ontogeny and features of the immediate environment that may facilitate or constrain particular elements of the repertoire, classical conditioning in the acquisition of early behavior may be more ubiquitous even than suggested by the "new hegemony" described by Turkkan.

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