

# Comparative Cognition: Rats Pay Back *Quid Pro Quo*

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**Humans engage in exchanges of commodities or services, often paying back a commodity with a different service. New research suggests that rats can reciprocally trade food for allogrooming, and *vice versa*.**

A key feature of human interactions is the *quid pro quo*: you do something for me, and in exchange I do something for you. Such exchanges of ‘something for something’ are typically not limited to a trade of the very same *something*; rather, you provide one type of commodity or service, and in the future, I will pay it back with a different commodity or service. As reported in this issue of *Current Biology*, Schweinfurth and Taborsky [1] show that rats also reciprocally trade different commodities.

## Rats Pay Back *Quid Pro Quo*

In the new study by Schweinfurth and Taborsky [1], a *focal* rat received an experience phase followed by a test phase. In the experience phase, the focal rat experienced a *partner* rat cooperating or non-cooperating with one of the commodities. In the test phase, the focal rat was allowed to return the service to the same partner by using the opposite commodity to that provided in the experience phase. For example, Figure 1A shows a focal rat receiving food from a cooperating partner (the cooperating partner had been trained to pull a stick connected to a movable platform, which moved into position to provide food only to the focal rat, not to the puller).

Figure 1B shows the focal rat now engaged in grooming of the partner (grooming was induced by applying salty water to the neck of the focal rat). Schweinfurth and Taborsky [1] observed that focal rats groomed previously cooperative food providers more often than previously non-cooperative rats. Similarly, they found that focal rats provided more food to previously cooperating high groomers than to low groomers.

## Do Rats Remember Cooperative Exchanges Using Episodic Memory?

In this work [1], the test phase began immediately after the experience phase. Thus, memory of cooperative exchanges may have been minimal. In natural situations, however, *quid pro quo* exchanges typically occur after a delay. Payback in the future would require memory about earlier cooperative experiences. An interesting area for future research would include inserting a substantial delay between experience with a cooperater and the opportunity to pay it back. Do rats remember earlier cooperative bouts? How long does this memory survive? What types of memory processes are implicated in these exchanges?

Episodic memory is an intriguing possibility for tracking social exchanges in rats. Episodic memory involves our memories for unique personal past events, which makes episodic memory a candidate for memory of social exchanges. Evidence for episodic memory of individual social exchanges would require careful elimination of non-episodic alternative hypotheses [2]. Episodic memory typically focuses on the origin of previous events, an aspect of memory called *source memory*. We recently developed an animal model of source memory [3–7], which could be adapted to study social exchanges.

In our approach [3–7], rats foraged for distinctive flavors of food that replenished or failed to replenish at its recently encountered location according to a source-information rule in an eight-arm radial maze. The source memory of eating chocolate pellets was manipulated by the experimenter placing the rat at the food trough of an arm which dispensed chocolate (which we refer to as an experimenter-generated event),

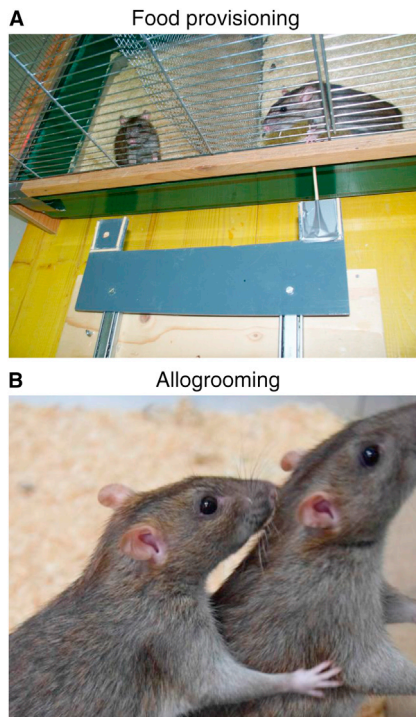
whereas the rat encountered chocolate on its own at a food trough on a different arm (referred to as a self-generated event). These arms were randomly selected and rats discovered chow-flavored pellets at two other randomly selected arms.

After a retention interval, the rats discovered chow-flavored pellets at the other four arms. The arm where the rat discovered chocolate on its own provided additional chocolate at the test (replenishment), whereas the arm where the rat was placed by the experimenter did not provide additional chocolate (nonreplenishment). Chow-baited locations never replenished. Thus, the rat needed to remember the source of chocolate (self-generated *versus* experimenter-generated information). Rats revisited the replenishment location at a higher rate than the nonreplenishment location while avoiding revisits to chow locations, which is consistent with the hypothesis that rats remember the source of encoded information. It was recently shown that monkeys also have source memory [8].

## Do Rats Remember Multiple Episodes of Cooperative Exchange?

A social exchange of services is a plausible candidate for the content of a source memory, but experiments would be needed to show that memory of a social exchange survives a delay and that it is based on memory of a specific social episode. Another aspect of social exchanges focuses on the large number of potential partners that might engage in cooperative and non-cooperative interactions. Could many such exchanges be tracked by episodic memories? Recent work suggests that rats remember multiple events and the contexts in which those events occurred, raising the possibility that many social exchanges





**Figure 1. Rats reciprocally trade food for allogrooming, and vice versa.**

A partner was cooperative, providing food (A) or allogrooming (B), for the focal rat, or it was non-cooperative. Next, the focal rat could provide the partner with the alternative service. (Photos from Schweinfurth and Taborsky [1].)

could be tracked using episodic memories.

In our approach to documenting multiple episodic memories [9,10], rats were presented with odor-infused lids. Selecting a novel odor was rewarded whereas old (familiar) odors were not rewarded. To dissociate episodic memory from judgments of relative familiarity (a non-episodic memory), we presented all of the odors in each of two distinctive contexts (arenas that differed in size, pattern, extra-arena cues, and so on). Importantly, rewards were given whenever the item was new to each context. Rats could use episodic memory to remember the presentation of each item and the context in which it had been previously presented [11]. Alternatively, the rats could choose new items by avoiding the familiar odors. To dissociate item-in-context and familiarity hypotheses, we unexpectedly transitioned between the two contexts. Critically, we identified sequences of odor

presentations across the unexpected context transitions that predict above chance performance for item-in-context memory and below chance performance for selecting the least familiar item.

To dissociate episodic memory from familiarity judgments, we identified sequences of odors that put familiarity cues and item-in-context memory in conflict. For a particular pair of odors (for example, cinnamon and basil), we presented one item (cinnamon) but not the other (basil) in the first context. Next, both items were presented in the second context (notably cinnamon followed by basil). Finally, the memory assessment occurred upon return to the first context, and the choice was between cinnamon and basil. Basil is the correct choice based on item in context because it has not yet been presented in the first context; basil is rewarded when chosen in this test, and our measure of accuracy is the proportion of choices of the rewarded item.

Critically, prior to the memory assessment, basil was presented more recently than cinnamon. Because cinnamon would be *less familiar* relative to basil in the memory assessment, an animal that relied on judgments of relative familiarity would choose the cinnamon (following the rule *avoid familiar items*). Such a choice would result in accuracy *below chance*. By contrast, an animal that relied on item-in-context memory would choose basil in the memory assessment, which would in turn result in *above chance* accuracy. Importantly, this memory assessment dissociates item-in-context memory (above chance) from judgments of relative familiarity (below chance).

To test whether the rats were relying on item-in-context episodic memory or non-episodic judgments of familiarity, we examined the rats' accuracy in the initial memory assessments (before receiving feedback from rewards in the novel condition). When the identity of items in context was put in conflict with familiarity cues, initial performance was above chance using 32 odors and context transitions that ranged from 2 to 15. High accuracy provides compelling evidence that rats relied on episodic item-in-context memory for

many items rather than judgments of familiarity.

How many social exchanges can rats remember? The observation that rats remember many items in context using episodic memories raises the possibility that rats may track many social exchanges, but experiments are needed to show that these social exchanges are remembered episodically.

### Do Rats Plan for the Future Using Cooperative Exchanges?

A final intriguing possibility raised by the work of Schweinfurth and Taborsky [1] is the potential for future planning in social exchanges. Relatively little is known about the future planning abilities of rats [12–16], and there are challenging standards to rule out non-prospective alternative strategies [17]. However, the observation that rats reciprocally trade commodities and services raises the intriguing possibility that a cooperative rat may anticipate reciprocity in the future. New experiments would be needed to determine if rats act now for one commodity in anticipation of a different commodity or service in the future, an ability that has been documented with food-storing scrub jays [18,19].

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## Immunology: Is Actin at the Lytic Synapse a Friend or a Foe?

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**Cytotoxic T cells and natural killer cells defend us against disease by secreting lytic granules. Whether actin facilitates or thwarts lytic granule secretion has been an open question. Recent results now indicate that the answer depends on the maturation stage of the immune cell–target cell contact.**

Cytotoxic T cells and their close brethren natural killer (NK) cells lyse virally infected cells and tumor cells by first forming a specialized contact with the target cell known as the immunological synapse [1]. The formation of this synapse is driven in large part by the creation of a radially symmetrical inward flow of actin in the cortex of the T or NK cell at its site of apposition with the target cell [2]. This centripetal actin flow has been shown in T cells to be generated by a combination of Arp2/3-complex-dependent actin polymerization in the outer portion of the immunological synapse, and the contraction of myosin-2-decorated, formin-generated actin arcs in the medial portion [3–6]. Actin assembly and flow are required for the formation and sustained signaling of receptor microclusters, the activation of integrins, and the correct spatial distribution of these and other key components of the mature immunological synapse [7,8].

Concomitant with this large-scale remodeling of the actomyosin cortex, T cells and NK cells rapidly reposition their centrosome, placing it just under their plasma membrane at the center of the synapse [9]. This serves to aim their microtubule-based secretory machinery in the direction of the target cell to support the polarized secretion of lytic granules, whose contents kill the target cell without incurring collateral damage.

A new paper by Carisey *et al.* [10], in this issue of *Current Biology*, addresses the question of actin’s role in the secretion of lytic granules from the center of the immunological synapse. Traditionally, cortical F-actin has been regarded as a barrier to vesicle secretion, such that cells must first clear it before vesicles can dock and fuse [11]. Consistent with this view, recent lattice light-sheet microscopy images of T-cell–target-cell conjugates [12] showed that an initial dense mat of actin in the cortex

of the T cell at its site of contact with the target cell is largely if not entirely cleared from the center of the synapse as it matures (Figure 1A,B). Similarly, the center of mature synapses in lipid-bilayer-engaged T cells typically appears ‘actin-poor’ in confocal micrographs, especially when compared with the outer portions of the synapse described above [3–6]. But is F-actin really eradicated from the center of the immunological synapse from where lytic granules are soon to be secreted?

Two seminal papers that addressed this question were published in 2011 by the groups of Dan Davis [13] and Jordan Orange [14]. Using super-resolution microscopy (specifically, 3D structured illumination microscopy or 3D SIM, and stimulated emission depletion microscopy or STED) of fixed NK cells engaged with an activating surface, these groups showed that the center of the NK cell immunological synapse contains a pervasive meshwork of actin

