

although the β -subunit of AP-1 was recently found in a proteomic-based search for Numb interaction partners [19]. In any case, the new findings reported in this issue extend the multiple roles that have been assigned to the Numb protein.

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Animal Communication: Sniffing Is About More Than Just Smell

A recent study shows that subordinate rats reduce their rate of sniffing while dominants explore their faces thus delaying dominants' subsequent aggression. Sniffing not only facilitates acquisition of olfactory information, but unexpectedly, also serves as a medium for communication.

Bennett G. Galef

When two Norway rats meet for the first time, they engage in lengthy bouts of mutual olfactory exploration, sniffing one another's faces, flanks and anogenital areas. Such intense olfactory activity promotes acquisition of information regarding the identity, sex, reproductive condition and dominance status of interacting individuals [1] and permits exchange of information as to the foods two interacting individuals have recently eaten [2]. Unexpectedly, such mutual olfactory exploratory behavior, studied for decades in one of mankind's most closely observed experimental animals (*Rattus norvegicus*), still contains secrets awaiting discovery. In this issue of *Current Biology*, Wesson [3] reports evidence that the duration and frequency of face sniffing between rats interacting

for the first time (Figure 1) plays an important role in mediating the aggressive behavior of pair members.

To explore the details of sniffing in freely moving, socially interacting animals, Wesson [3] devised head-mounted, wireless, radio transmitters linked to thermocouples implanted in the nasal cavity of subjects. These contrivances allowed him to simultaneously record on video both the behavior of interacting rats and the frequency and amplitude of the sniffing of each member of pairs of rats meeting for the first time.

Wesson [3] found that when one rat investigated the face of another, some recipients of facial investigation significantly decreased the frequency with which they sniffed their partners' faces. In particular, when large male rats were paired with potentially

subordinate individuals — either smaller males or females ovariectomized to increase the probability that they would behave submissively [4] — the subordinate member of many pairs significantly decreased its sniffing rate while the dominant individual examined its face. In contrast, the larger, presumably dominant member of such a pair showed either no change or an increase in sniffing while subordinates investigated their faces.

Subordinates' reduction in sniffing frequency while dominant individuals explore their faces plays a significant role in mediating agonistic interactions between pair members. The latency with which a dominant rat exhibited aggressive behavior following a bout of sniffing at the face of a subordinate was significantly correlated with the magnitude of the subordinate's decrease in sniffing frequency. The greater a smaller animal's decrease in sniffing rate (relative to baseline), the longer the latency to its larger partner's next expression of dominance asserting behaviors (boxing, kicking, standing over, and so on). Thus, rate of sniffing by submissive rats in social situations acts as a submissive or



Figure 1. Rats engaged in mutual facial exploration, a situation that results in a reduced rate of sniffing by the subordinate member of a pair and no change in the sniffing rate of the dominant.

The magnitude of the subordinate individual's reduction in rate of sniffing is correlated with an increase in latency to first subsequent aggressive behavior by its dominant pair mate.

appeasement behavior [5] modulating the aggressive tendencies of their more dominant partners.

Olfactory information passing between pair members does not mediate the reduced rate of sniffing exhibited by subordinate animals when face to face with dominants. Treating the nasal epithelia of both members of pairs of rats with $ZnSO_4$ (to produce a transient anosmia [6,7]) before allowing pair members to interact has no effect on the sniffing behavior of either dominant or submissive individuals during periods of face-to-face investigation. Just as in intact pairs, anosmic dominant individuals continue to sniff at a high rate, and anosmic subordinate individuals reduce their rate of sniffing while being investigated.

Using a within-subject experimental design, Wesson [3] further examined the effects on sniffing frequency of prior treatment of both members of an interacting pair with oxytocin (to reduce aggressive behavior [6]). He found, as expected, that oxytocin decreased dominant animals' frequency, relative to baseline, of engaging in aggressive behaviors. Treatment of pair members with oxytocin also caused subordinate individuals to show significantly less reduction in sniffing frequency during bouts of facial investigation by dominants than when the same pairs of animals were treated with saline, suggesting that reduced sniffing in subordinates is a response to the expression of dominance by larger animals.

As is the case with any interesting finding, Wesson's [3] discovery of a

communicative function of rats' sniffing rate during periods of face-to-face interaction raises at least as many questions as it answers. For example, although the present data exclude olfaction as the modality mediating detection of sniffing rate, sniffing involves changes in both auditory cues and movement of the vibrissae and anterior portions of the face. Either might provide the channel via which information is being communicated between pairs of unfamiliar, potentially antagonistic individuals.

During aggressive and affiliative social interactions, rats emit 22 khz and 50 khz ultrasonic vocalizations that modulate social behavior [7]. If sniffing results in production of ultrasounds, then the changes in subordinates' sniffing rate during face-to-face interaction with dominants might simply contribute to the ultrasonic repertoire of rats. Alternatively, the rapid movements of vibrissae of rats while sniffing might provide either somatosensory or visual cues to dominant individuals during periods of facial investigation of subordinates and serve as the medium for communication.

The new investigations focussed on the effects of changes in the sniffing rate of subordinate individuals and the role of such changes in sniffing frequency in modulating dominants' aggressive behavior. Possibly, failure of dominant individuals to reduce their rate of sniffing also serves as a signal mediating social interaction. Further, given that sniffing rate has been demonstrated by Wesson [3] to serve as a medium for rats' social

communication, then sniffing rate is likely also to be involved in mediating other social interactions of Norway rats such as those between sexual partners or parents and their offspring.

Most challenging will be to understand how rats integrate the information available in the auditory, tactile, visual and olfactory social signals emitted by conspecifics to produce behaviors appropriate to the diverse social circumstances they encounter throughout life.

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DNA Replication: Polymerase Epsilon as a Non-catalytic Converter of the Helicase

In eukaryotes DNA polymerase epsilon (ϵ) synthesises the leading DNA strand during replication. A new study provides insight into how this polymerase also functions independently of its enzyme activity to assemble and activate the replicative helicase.

Philip Zegerman

Although it is over 50 years since the purification of the first DNA

polymerase, how cells from all domains of life manage the perfect duplication of the genome before division remains a subject of intense