

# Social cognition in the rodent: nothing to be sniffed at

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**The rat is emerging as a powerful model for studying cognition and its neural bases. Extending this work to the social domain requires understanding better how rats transmit and interpret social information. A recent study highlights a novel role for sniffing as a channel for such social communication.**

Social interactions are among the most challenging situations that animals face and therefore an important context in which to investigate cognitive brain functions. Rats are social animals that live in large colonies with a hierarchical structure, where they engage in a wide range of social behaviours, including mutual grooming, social exploration, vocalization, play, aggression, and sexual behaviour [1]. Recent work indicates that rats also exhibit forms of pro-social behaviour commonly considered the domain of primates, including engaging in reciprocal interactions with conspecifics [2] and responding to the distress of a restrained conspecific by working to release it [3]. Rats may therefore serve as good models for investigating the neural mechanisms of social behaviour.

A critical step toward comprehending rodent social behaviour is to better understand the channels of communication through which they transmit, interpret, and respond to social information. Now, a recently published study [4] provides evidence that sniffing plays a heretofore unsuspected role in communication between rats.

Olfaction is known to be critical to rat behaviour both in general and in social contexts. Rats can recognize one another by their olfactory signatures [5]. When rats encounter conspecifics, they engage in vigorous investigation and exchange of chemical signals, which include sniffing of the face, flank, and ano-genital regions. Wesson [4] monitored sniffing during such encounters using a small implanted thermocouple (a temperature sensitive bi-metallic wire) connected to a wireless transmitter. This technique allows nasal respiration to be monitored because the changes in air flow associated with inhalation and exhalation cool and warm the thermocouple. Surprisingly, he observed that subordinate males and ovariectomized females decreased their sniffing rate specifically when engaged in face-to-face interactions (and not flank or ano-genital investigation) with a dominant conspecific.

To understand what this might mean, let us first consider other forms of social communication in the rat. A well-studied example is the 'social transmission of food preference', in which the safety of a given food is signalled to a naïve conspecific. The signal is mediated by the conjunction of carbon disulfide (CS<sub>2</sub>) and the odour of recently eaten food in the demonstrator's breath [6].

Because both of these chemical signals are incidental by-products of eating, this phenomenon can be considered a passive form of communication. Social transmission of fear is another example of passive communication. The signal underlying this recently described phenomenon is the cessation of movement-evoked sound that occurs when animals freeze in response to a perceived threat. This cessation of sound, again an incidental or passive cue, is sufficient to elicit defence responses, but only in those rats that have prior experience of the threat [7].

Demonstration of active social communication in rats is more challenging. To be an active cue, the sending animal should have the option to transmit the signal or not. Ultrasonic vocalizations may represent an important channel for active social communication in the rat, given that they are likely emitted specifically for the purpose of communication. Although the precise use of ultrasonic vocalizations in adult rats is a matter of on-going debate, it is well-established that rat pups, when distressed, emit ultrasonic vocalizations that prompt the dam to retrieve them to the nest [8]. Postural cues also play an important role in the active transmission of social information in rats, as well as many other species. In agonistic encounters, subordinate rats display a belly-up posture, risking injury, but decreasing the likelihood of further aggression from the dominant rat [9].

Is the drop in sniffing frequency recorded by Wesson an active attempt by the submissive animal to reduce the cost of a status-divergent encounter or an incidental by-product of some other process?

Rats are known to modulate their sniffing rhythms during encounters with odours and the observed drop in sniffing frequency might simply reflect a change in acquisition of olfactory information [10]. However, the change in sniffing appeared to persist in animals rendered anosmic by chemical ablation of the olfactory epithelium [4]. This suggests that the drop in frequency had another function. Consistent with that idea, the amount of decrease in sniffing frequency correlated with the latency for the dominant conspecific to initiate aggressive behaviours. Thus, the drop in sniffing frequency appeared to serve as a submissive cue, similar to a belly-up posture, that might help to reduce the cost of an encounter with a dominant conspecific.

However, it is important to consider that sniffing rate has also been shown to reflect important aspects of the physiological state of the animal, much as heart and respiration do. Sniffing is modulated by reward expectation [10], a relationship that might reflect the modulation of respiratory rate by neuromodulators that coordinate physiological responses to salient events, such as an encounter with a dominant conspecific. Thus, it would be important to understand whether the lowering of sniffing frequency is coupled to a general state change induced by a

face-to-face encounter with a dominant conspecific. It will also be important to better understand how a dominant rat senses signals from a subordinate. In addition to sniffing, face-to-face interactions may also be associated with ultrasonic vocalizations, postural cues, whisking changes, and non-volatile chemosignals, any of which could convey redundant or complementary information.

Wesson's study thus illustrates the capacity of sniffing to act as a social cue and highlights the striking ability of rats to transmit social cues, interpret them, and generate appropriate behavioural responses. It also yields a promising new tool to continue exploring rodent social communication in an ethological context.

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# The neural basis of phantom limb pain

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**A recent study suggests that brain changes in amputees may be pain-induced, questioning maladaptive plasticity as a neural basis of phantom pain. These findings add valuable information on cortical reorganization after amputation. We suggest further lines of research to clarify the mechanisms that underlie phantom pain.**

Phantom limb pain (PLP) is still an enigma and a better understanding of its mechanisms is needed. One prominent hypothesis suggests that, following limb amputation, the loss of afferent input allows for invasion of neighboring cortical regions into the former representation zone of the limb in primary sensorimotor cortex. These maladaptive changes have been suggested to be the neural basis of PLP and this view has generated new treatment approaches, such as sensory discrimination or mirror training [1]. In a recent paper, Makin *et al.* [2] argue for an alternative representation hypothesis, where PLP is associated with preserved functional and structural representations in the phantom hand area in sensorimotor cortex. Greater phantom pain in this study was associated with more local activity and more structural integrity in the former hand area, with subjective reports of chronic phantom pain experience accounting for much of the inter-individual variability. PLP was also associated with reduced inter-regional functional connectivity in the primary sensorimotor cortices. Based on these findings, Makin *et al.* [2] suggest that the chronic PLP experience, which may be triggered either by bottom-up nociceptive inputs or

top-down inputs from pain-related brain areas, drives plasticity because it maintains local cortical representations and disrupts inter-regional connectivity.

The study was carefully designed and adds important new findings to the topic of brain plasticity and PLP, but these data also raise new questions.

In the introductory section of their article, the authors state that the cortical plasticity model would suggest less representation of the amputated limb due to remapping of adjacent representations and that the limb representation should be reduced in the cortex of people with PLP. However, somatotopic representations can be viewed as dynamic networks that adapt to changing internal or external demands [3]. Thus, a shift in the representational foci of areas adjacent to that of the amputated limb does not necessarily lead to reduced brain activation in the limb representation, the measure used in this study. It would be interesting to see how activation intensity and activation shifts are related. A continued presence of the limb representation has previously been shown in a somatosensory evoked potential study [4] and the elimination of input from the amputated limb changes both pain and cortical reorganization in some, but not all, amputees [5]. Both animal studies and mathematical modeling have demonstrated that altered input from the limb can even enhance cortical reorganization, seen as a consequence of the deafferentation. Thus, the maladaptive plasticity model also suggests an important role for input from the phantom limb.

Makin *et al.* used phantom movement in most of the traumatic amputees, executed movement in the healthy