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The evolutionary origins of cooperation and trade

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Abstract The neural mechanisms that enable human trade and cooperation are just beginning to be understood. This paper proposes an evolutionary research agenda in rodents that could elucidate how such neural mechanisms arose, and could help scientists understand the variation in them that we find in humans. The evolutionary protocol outlined here is likely to provide deep insights into the human condition.

Keywords Oxytocin · Oxytocin receptor · Experiment · Neuroscience · Evolution

Nearly all microbes engage in trade, sometimes among conspecifics and sometimes across species in a mutualism arrangement. In as similar way, humans cooperate with other humans, often over long periods of time, and in many cases with people who are not closely genetically related. Nonhuman mammals typically do this by using hierarchy to enforce cooperation norms, especially when new animals, often in puberty, join a clan. Humans also enforce cooperation norms via hierarchy, but many of us cooperate with complete strangers absent overt enforcement mechanisms. A key question in biobehavioral studies is how we assess whether a stranger is likely to be a trustworthy trading partner.

Work from my lab in the early 2000s, replicated and extended by many others, showed that the neurochemical oxytocin (OT) is released when we are trusted and motivates reciprocal trustworthy behavior (summarized in Zak 2012). In animal studies, OT is stimulated when encountering familiar or "safe" conspecifics. In over a decade and a half human studies, my lab has documented large variations across indi-

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viduals in endogenous OT responses to social interactions and subsequent cooperative behaviors. For example, women and those who by personality trait are more empathic and agreeable tend to release more OT for a given stimulus. Studies we have done in psychiatric patients have shown that the OT system (OT synthesis and the binding of OT to its receptor) are typically dysregulated in patients whose disorders present with impaired social interactions such as autism and schizophrenia. A key question from our patient studies is hov ealthy individuals the OT system tunes itself to one's social environment to all ople to reap the benefit of social interactions.

Genetic analysis suggests that a mutation perhaps 200,000 years ago resulted in *homo sapiens* who had more OTRs in the frontal cortex than their ancestors and that this adaptation spread quickly through the *homo* line. This produced individuals who were more sens o OT and therefore the social environment. Because modern humans, compa nonhuman primates, appear to have a greater density of OT receptors (OTRs) in frontal cortex, the gregariously social nature of humans may be due, in part, to greater OT synthesis for a given stimulus and/or a larger number of OTRs. The source of these variations, and how quickly this system adapts within an individual and over generations is not unc od, though interesting animal evidence shows epigenetic effects across generati Weaver et al. 2004). While the race is on to create an OTR assay that is safe to use in vivo in humans, evolutionary studies in animals would generate an understanding of foundations of social behaviors in humans as suggested by Burnham et al. 2015). Because only mammals have OTRs, the evolutionary experiments I am proposing are most fruitfully done in fast-breeding mammals, though stu nonmammal vertebrates such as fish or birds, could study the homologous neur de vasotocin though its effects on social behaviors may be more complicated than is oxytocin in mammals (Thompson and Walton 2004).

One experimental approach would use OTR manipulation in rodents to characterize how OTRs respond over generations to a large set of social and environmental stimuli. In particular, studies of social isolation, animal models of autism, schizophrenia, and depression could be fruitfully informed using evolutionary studies. This approach might elucidate the mechanisms through which humans became promiscuously social. Indeed, a number of labs have accelerated this process by using viral vectors to change OTR densities in target animals (Lee et al. 2008) and for the closely related peptide receptor arginine vasopressin (Young et al. 1999). This approach would allow scientists to induce greater variation and to more quickly gain insights into how mutualism depends on trust. What we need to know to establish the evolutionary foundations of economics is how OTRs affect cooperation, trade, and opportunities for mutual gain.

A different experimental approach could use rats that learn via operant conditioning using sucrose rewards to cooperate with each other as in Łopuch and Popik (2011). Adding to this experimental design differential endowments of foods that vary by fructose content, or teams of dyadic rats who can trade in an "island" model, would produce different selection pressures. Breeding such populations for multiple generations, and assessing their behavior and neuroanatomy, could provide deep insights into the biological causes of human prosperity.

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