nation of the high eccentricities is that they are produced by strong dynamical interactions occurring as a result of mutual gravitational interactions once the gas has been, or is in the process of being, removed (*11*).

The construction of planetary systems involves many physical processes and many bodies gravitationally interacting on long time scales. For example, the core accumulation scenario starts from the sticking together of submicrometer dust grains to produce larger particles, which then produce a swarm of planetesimals with sizes on the order of 1 km (*4*). In turn, these form the building blocks of cores large enough to accrete gas and to have a strong enough interaction with the gas disk to produce orbital migration. Many aspects of these processes, however, remain uncertain. Although individual aspects may be studied in depth by computer simulation, including all of them—together with the gravitational interactions of many planetary embryos and realistic protoplanetary disk modeling—is not yet feasible.

An ad hoc procedure has therefore been adopted for synthesizing planetary systems (*9*), which focuses on the late stages of formation and considers the evolution and gravitational interactions of a few protoplanetary bodies. Simplified prescriptions extracted from more detailed computations are used to describe how these objects accrete gas and solids from, and interact gravitationally with, the protoplanetary disk. An evolutionary model for the protoplanetary disk is an important determinant of the final outcome. At present this must be a somewhat uncertain procedure, hence the modeling has some explanatory power but does not yet have real predictive power.

Such modeling is able to produce giant planets that can migrate over the protoplanetary disk lifetime, thereby accounting for the close-in giants (hot Jupiters) when the migration stops. When several protoplanets are involved, pairs with commensurable orbital periods may be formed, several examples of which have already been observed (*10*). However, these may also involve super-Earths. For example, a system of three short-period planets having orbital periods in the approximate ratios 1:2:4 was recently announced (*12*). A possibility yet to be fully investigated is that these migrated inward, with a pair of strict 2:1 commensurabilities, until they entered a central magnetospheric cavity, a region where the disk has been expelled through interaction with the magnetic field of the central star (*13*). Later orbital evolution resulting from tidal interaction with the central star then caused the strict commensurabilities to be lost (*14*).

The number of planets that form and the amount of migration and dynamical evolution they undergo depend on the mass of the protoplanetary disk and its lifetime. Because disk lifetimes are comparable to planetary accumulation times and the latter tend to be shorter for the more massive disks, short- lived low-mass disks tend to produce few giant planets undergoing limited orbital migration, such as in our solar system. In contrast, more massive disks would produce more giant planets that undergo large-scale migration and appreciable dynamical interactions. Thus, Thommes *et al.* relate the architecture of the final planetary system to the properties of the original protoplanetary disk.

The idea investigated by Thommes *et al.* that some period of strong dynamical interactions or gravitational scattering takes place in systems containing giant planets with high orbital eccentricity is compelling. It has been shown to have reasonable success at reproducing the observed eccentricity distribution (*11*). However, it would tend to produce planetary orbits that are to some extent misaligned with the stellar equatorial plane defined by its rotation axis. Such a misalignment is now measurable through its effects on the spectrum of the central star, in systems with transiting planets. At present the indications are that several systems with close-in giant planets are consistent, with no misalignment between the orbital and stellar equatorial planes (*15*). However, the available sample is too small to either support or rule out any theory at this point. But with new planets being discovered at an accelerating pace, this situation may change in the near future.

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PSYCHOLOGY

# Trust Me on This

**Andreas Meyer-Lindenberg**

Borderline personality disorder is associated with abnormal activity in a brain region associated with monitoring trust in relationships.

Unstable interpersonal relationships, reduced impulse control, and difficulty regulating emotions characterize borderline personality disorder, a severe mental illness that accounts for up to 20% of psychiatric inpatients and exerts a tremendous toll on those afflicted, their social network, and the health-care system (*1*). Close relationships of patients are often tumultuous, spiraling out of control through highly emotional and unpredictable behavior that can leave others baffled, angry, and frightened. On page 806 in this issue, King-Casas *et al.* (*2*) use an economic exchange game and neuroimaging to provide a glimpse into the neural mechanisms underlying the breakdown of cooperation in individuals with borderline personality disorder. The study also establishes a game theory paradigm that holds promise for investigating social interactions, particularly psychiatrically relevant disturbances of social behavior.

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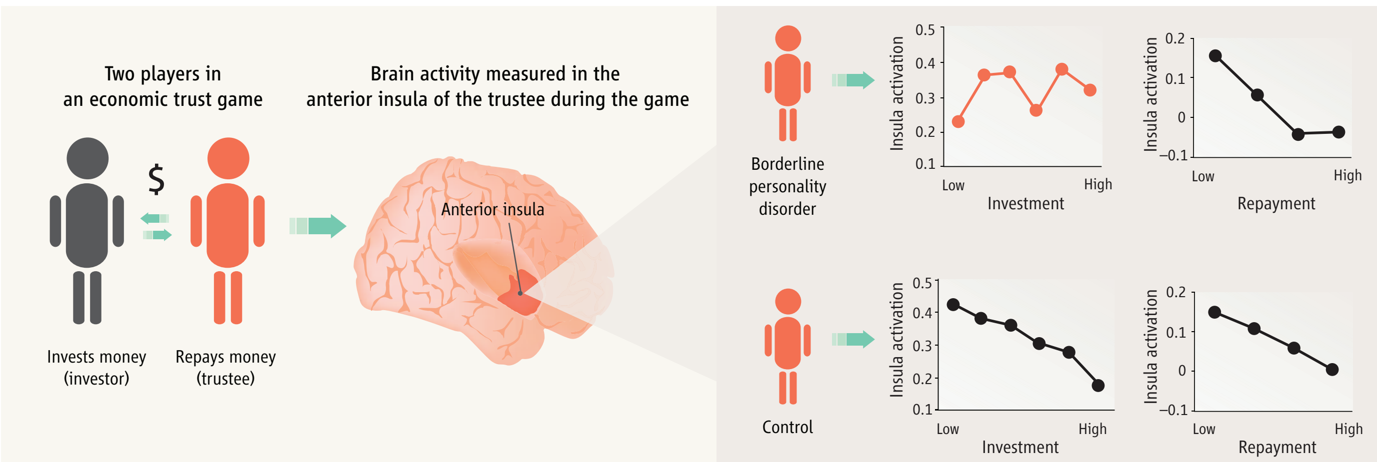
In the multiround economic trust game, money is exchanged between an investor, who decides how much money to commit, and a trustee, who decides how much of the investment (which is tripled during the transfer) to repay the investor. If both cooperate, both benefit from the exchange, much more so than if the investor keeps most of the money. However, this requires a degree of trust between the players, which is built up through repeated fair offers. An investor who does not trust will not invest much money. This is exactly what happened at the end of games with trustees who suffered from borderline personality disorder, indicating that they were less likely to establish or maintain a cooperative relationship. By contrast, healthy trustees were successful at doing so (thus, investment remained high at the end of the game). The better outcome was accomplished through a coaxing strategy, in which wary investors transferring small amounts of money were encouraged by generous returns, which signaled trustworthiness. Healthy players used this strategy twice as often as borderline personality disorder subjects. Why?




**Just can't cooperate.** Activation of the anterior insula is observed during an economic trust game in individuals with borderline personality disorder and healthy controls. Both groups show higher activation in response to stingy repayments they are about to make. However, only players with the disorder have no differential response to low offers from an investor (upper left graph), indicating that they lack the "gut feeling" that the relationship (cooperation) is in jeopardy.

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To find out, King-Casas *et al*. used neuroimaging to study brain activation of trustees confronted with a small investment (a signal of the investor's lack of trust). Individuals with borderline personality disorder and healthy players differed in the activity of one brain area—the anterior insula (see the figure). In healthy trustees, small investments corresponded to large activations and large investments corresponded to small activations. By contrast, in players with borderline personality disorder, the anterior insula did not distinguish between offer sizes. As expected from previous work (*3*), the same brain area was also reactive to the amount trustees were about to repay the investor, but this was now found in both patients and healthy controls. In healthy controls, the anterior insula was activated in response both to distrustful offers from investors and stingy repayments they were about to make, whereas in trustees with the personality disorder, differential neural activity was observed only when they were repaying. Thus, their impairment selectively affected representation of the other player in the pair.

The anterior insula is traditionally associated with sensing the physiological state of the body, but strongly reacts to adverse or uncomfortable occurrences in social interactions, such as unfairness (*4*), risky choices, frustration, or impending loss of social status (*5*). This brain region also responds to the intentions and emotional state of others (*6*, *7*), and imbues them with feeling (*8*). Because rewarding aspects of social interactions have been mapped to the ventral striatum in the brain (*9*), the present results suggest that activation of the anterior insula in a social context represents a negative/aversive evaluation of perceived or planned action, perhaps associated with a feeling of discomfort. If true, this implies that individuals with borderline personality disorder may have difficulty cooperating because they lack the "gut feeling" (corresponding to the anterior insula signal) that the relationship is in jeopardy and/or expect such behavior from the outset. The correspondence of these brain findings to current psychotherapeutic practice is remarkable. The most effective treatment of borderline personality disorder (*1*), dialectical behavior therapy, is based on the assumption that patients lack skills in interpersonal self-regulation, and attempts to build these abilities.

King-Casas *et al*. interpret their observations with regard to social norms: Lack of cooperativity violates social expectations, corresponding to the insula signal, and individuals with borderline personality disorder then have atypical social norms because they fail to react to norm violations from others. This may be so. However, humans in general prefer prosocial, altruistic, fair, and trusting behaviors, which have a genetic basis (*10*). Although the neural circuitry underlying these behaviors has been studied mainly with regard to pleasure-seeking actions linked to reward (*9*), negative signals indicating lack of cooperativity or trust could also contribute to the hard-wiring of prosocial behavior in the human brain.

What causes these intriguing changes in borderline personality disorder? Despite the slim evidence, it is very likely that it arises from a combination of genetic predisposition (*11*) and severe early childhood trauma (*12*). Early traumatization has been associated with enduring dysregulation of stress responses in adults (*13*). Moreover, gene variants have been identified that modify the impact of early trauma (such as child abuse) on adult symptoms of stress (*14*). It will be of interest to determine whether such genetic variants affect insula structure and function by "genetic imaging"—that is, using neuroimaging to investigate neural mechanisms linked to genetic variation (*15*). It will also be relevant to clarify the regulatory functions of the insula in borderline personality disorder, because this brain region functionally interacts with other limbic brain regions (such as the amygdala) that are implicated in this condition (*16*).

The use of a game theoretic approach to investigate personality disorders may be useful for studying other mental illnesses where social dysfunction is a prominent source of disability and distress, such as schizophrenia or autism. Game theory originated as an instrument of neuroeconomic analyses that assume perfect rationality of the players, and at first it came as a surprise that economic choices were in fact strongly impacted by emotional and reward-related brain processes. As King-Casas *et al.* show, it has now evolved into a tool for investigating psychopathological impairment of social interactions. Such advances are needed for patients, therapists, and researchers to grapple with social dysfunction, which is among the most impairing and least treatable components of severe illnesses such as schizophrenia.

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ECOLOGY

# The Coming Arctic Invasion

**In a future warmer climate, molluscs and other species are likely to migrate from the Pacific to the Atlantic via the Bering Strait.**

**Geerat J. Vermeij[1] and Peter D. Roopnarine[2]**

The current episode of climate warming is having drastic consequences for animal and plant life worldwide. Besides the expected poleward expansion of temperate and tropical species and the latitudinal contraction of cold-adapted ones, an even more dramatic interoceanic invasion will ensue in the Arctic: North Pacific lineages will resume spreading through the Bering Strait into a warmer Arctic Ocean and eventually into the temperate North Atlantic.

Trans-Arctic invasion began about 3.5 million years ago during the warm mid-Pliocene epoch (*1*). A combination of northward flow through the Bering Strait, high productivity in the Bering Sea (the geographic source of trans-Arctic invaders) (*2*), favorable conditions for rapid growth and dispersal in the Arctic Ocean, and the removal through extinction of many species during the mid-Pliocene in the North Atlantic (*1*) enabled hundreds of marine lineages to colonize and enrich the biotas of the Arctic and North Atlantic. Although geochemical evidence from a core drilled near the North Pole points to perennial sea-ice cover in the Arctic beginning in the middle Miocene (14 million years ago) (*3*), the presence of mid-Pliocene temperate marine molluscs in northern Alaska and Greenland (*4*) indicates that coastal sectors of the Arctic Ocean were seasonally or perennially ice-free at that time.


**Source regions of potential trans-Arctic invaders.** Fifty-six molluscan lineages present in the Bering and Chukchi seas (light-blue region) have not yet participated in trans-Arctic expansion but have the potential to do so; 28 of these species extend as far north as the Pribilof Islands and Anadyrski Gulf. Another 19 mollusk species are separated from related temperate Atlantic relatives by a genetic and geographic gap. These numbers exclude North Pacific lineages whose participation in the trans-Arctic interchange during the Pliocene led to the formation of species still living in the high Arctic.

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In much of today's ice-bound nearshore Arctic Ocean, annual phytoplankton production is a factor of 8 to 30 lower than in the Bering Sea (*2*), with production beneath the ice accounting for 1 to 33% of annual Arctic production of phytoplankton (*5*). In the relatively ice-free mid-Pliocene Arctic Ocean, food for suspension-feeding animals would have been much more abundant, allowing many planktonically dispersing, large-bodied, fast-growing species that require high productivity to survive in that ocean and to seed populations in the temperate Atlantic. Most trans-Arctic lineages with temperate Atlantic members show genetic and geographic gaps between Pacific and Atlantic populations, indicating that post-Pliocene sea-ice expansion in the coastal Arctic Ocean ended trans-Arctic dispersals in these lineages.

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