

electronic circuits is often characterized for small-signal and large-signal behavior. For small signals, input-output relationships are approximately linear. For large signals, nonlinearities, such as thresholds and saturation, become apparent. Electronic filters and amplifiers are often designed so that the circuit operates mostly in the linear, small-signal range. Combinatorial switching circuits are designed to operate exclusively in the large-signal domain. The (small-signal) spectrum analyzer model of auditory processing has been fruitful. Garcia-Lazaro *et al.*'s [3] data suggest that it is time to explore auditory models that combine small and large-signal dynamics.

We understand that the dynamics of the auditory forebrain are complex. Serial context effects can extend over long time intervals [8,9]. There are circumstances in which neurons can shift from apparent event or feature coding, to rate coding without a precise temporal relationship to the stimulus [10,11]. We do not understand the circumstances that favor different dynamical modes, the transitions between modes, or the extent of the neuronal assemblies which may have their activity constrained in different ways as a sound sequence unfolds [12–14]. As studies of plasticity have also been chiefly aimed at the spectrum-analyzer model of the auditory system [15,16], we also know very little about how experience and behavioral training affect forebrain dynamics. These issues pervade studies of how the auditory cortex responds to animal vocalizations and speech sounds [17–20]. Garcia-Lazaro *et al.*'s [3] analytical framework is a step beyond the strictly empirical, towards a more hypothesis driven understanding.

Perhaps most telling is that Garcia-Lazaro *et al.*'s [3] optimal stimuli sound biological, rather like a howling cat, while their other stimuli sound mechanical. This is not likely to be an accident.

References

1. Friederici, A.D. (2002). Towards a neural basis of auditory sentence processing. *Trends Cogn. Sci.* 6, 78–84.

2. Escabi, M.A., and Read, H.L. (2003). Representation of spectrotemporal sound information in the ascending auditory pathway. *Biol. Cybern.* 89, 350–362.
3. Garcia-Lazaro, J.A., Ahmed, B., and Schnupp, J.W.H. (2006). Tuning to natural stimulus dynamics in primary auditory cortex. *Curr. Biol.* 16, 264–271.
4. Miller, L.M., Escabi, M.A., Read, H.L., and Schreiner, C.E. (2002). Spectrotemporal receptive fields in the lemniscal auditory thalamus and cortex. *J. Neurophysiol.* 87, 516–527.
5. Voss, R.F., and Clarke, J. (1975). 1/F noise in music and speech. *Nature* 258, 317–318.
6. Attias, H., and Schreiner, C.E. (1997). Temporal low-order statistics of natural sounds. *Adv. Neural Inf. Proc. Syst.* 9, 27–33.
7. Nelson, P.C., and Carney, L.H. (2004). A phenomenological model of peripheral and central neural responses to amplitude-modulated tones. *J. Acoust. Soc. Am.* 116, 2173–2186.
8. Ulanovsky, N., Las, L., Farkas, D., and Nelken, I. (2004). Multiple time scales of adaptation in auditory cortex neurons. *J. Neurosci.* 24, 10440–10453.
9. Bartlett, E.L., and Wang, X. (2005). Long-lasting modulation by stimulus context in primate auditory cortex. *J. Neurophysiol.* 94, 83–104.
10. Lu, T., Liang, L., and Wang, X. (2001). Temporal and rate representations of time-varying signals in the auditory cortex of awake primates. *Nat. Neurosci.* 4, 1131–1138.
11. Wang, X., Lu, T., Snider, R.K., and Liang, L. (2005). Sustained firing in auditory cortex evoked by preferred stimuli. *Nature* 435, 341–346.
12. Elhilali, M., Fritz, J.B., Klein, D.J., Simon, J.Z., and Shamma, S.A. (2004). Dynamics of precise spike timing in primary auditory cortex. *J. Neurosci.* 24, 1159–1172.
13. Martin, E.M., West, M.F., and Bedenbaugh, P.H. (2004). Masking and scrambling in the auditory thalamus of awake rats by Gaussian and modulated noises. *Proc. Natl. Acad. Sci. USA* 101, 14961–14965.
14. Mäkinen, V., Tiitinen, H., and May, P. (2005). Auditory event-related responses are generated independently of ongoing brain activity. *Neuroimage* 24, 961–968.
15. Kilgard, M.P., and Merzenich, M. (1998). Cortical map reorganization enabled by nucleus basalis activity. *Science* 279, 1714–1718.
16. Fritz, J.B., Elhilali, M., and Shamma, S.A. (2005). Differential dynamic plasticity of A1 receptive fields during multiple spectral tasks. *J. Neurosci.* 25, 7623–7635.
17. Eggermont, J.J. (1995). Representation of a voice onset time continuum in primary auditory cortex of the cat. *J. Acoust. Soc. Am.* 98, 911–920.
18. Versnel, H., and Shamma, S. (1998). Representation of natural and synthetic vowels in the primary auditory cortex. *J. Acoust. Soc. Am.* 103, 2502–2514.
19. Cheung, S.W., Nagarajan, S.S., Schreiner, C.E., Bedenbaugh, P.H., and Wong, A. (2005). Plasticity in primary auditory cortex of monkeys with altered vocal production. *J. Neurosci.* 25, 2490–2503.
20. Steinschneider, M., Volkov, I.O., Fishman, Y.I., Oya, H., Arezzo, J.C., and Howard, M.A. (2005). Intracortical responses in human and monkey primary auditory cortex support a temporal processing mechanism for encoding of the voice onset time phonetic parameter. *Cereb. Cortex* 15, 170–186.

Department of Neuroscience,
Department of Otolaryngology, Evelyn
F. and William L. McKnight Brain
Institute, University of Florida, PO Box
100244, Gainesville, Florida 32610, USA.
E-mail: purvis@mbi.ufl.edu

DOI: 10.1016/j.cub.2006.02.004

Invasive Species: Customs Intercepts Reveal What Makes a Good Ant Stowaway

A recent analysis of decades of US customs intercepts has revealed which ants had an opportunity to become established in the United States, providing insights into the requisite traits that enable an ant species to become a successful invader.

A.S. Mikheyev and U.G. Mueller

Ships inbound from South America have carried agricultural goods into the trans-American trade hub of Mobile, Alabama for several centuries. It appears that these ships inadvertently also delivered fire ant queens in the 1930s when dumping earth ballast in order to receive heavy cargo for the return trip [1,2]. Initially, this fire ant

introduction caused little alarm, as the US already had an endemic fire ant fauna and an earlier fire ant invasion of a different species appeared to do little ecological harm. After a decade of tenuous existence in the vicinity of the port, however, the new invader's range expanded rapidly (Figure 1), with nests virtually blanketing the landscape in some areas. As the number of fire ants increased, so

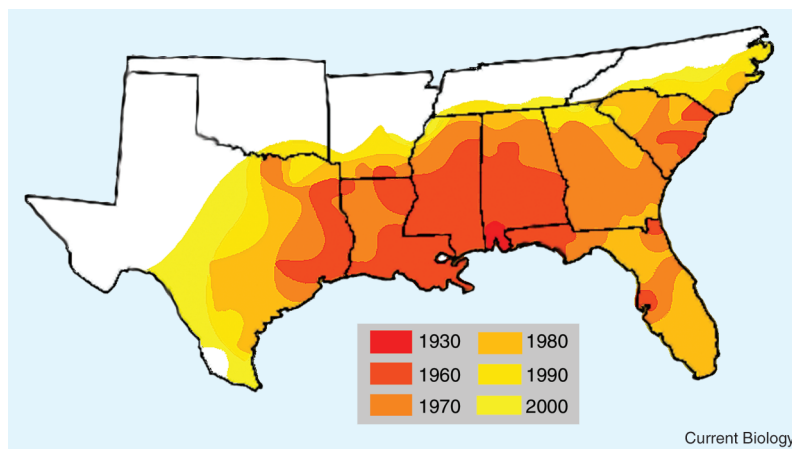


Figure 1. Spread of the fire ant *S. invicta* through the Southern US States (based on USDA infestation maps).

Presently, isolated *S. invicta* populations can be found as far as California. Their range is likely to eventually encompass almost all of the coastal states [14].

did the frequency of their encounters with humans, causing an outcry over ruined lawns, severe allergic reactions to fire ant venom, and short-circuited electrical equipment. The government response, in the spirit of the 'better-living-through-chemistry' ethos prevalent at that time, involved the aerial application of mass quantities of mirex insecticide over the Southern States through the 60s and 70s. Costing in the hundreds of millions of dollars, this treatment likely did irreparable damage to native ecosystems, perhaps even facilitating the fire ants' spread [3], and was abandoned only after mirex was found to be a carcinogen. The fire ants continued their inexorable spread and now occupy over a 100 million hectares from Florida to California, truly earning their scientific name *Solenopsis invicta*.

S. invicta is just one of dozens of ant species that have become established in the US, out of hundreds or even thousands of ant species that may have had an opportunity to do so, when inadvertently brought into the US with cargo. What makes *S. invicta* different from these other ants that failed to invade? Why did *S. invicta* spread so extensively, unlike many other introduced ant species that established footholds in the US but then failed to spread? These questions are central to all invasive species research, but are difficult

to answer because they require an analysis of the intractably large reference set of all other species of potential invaders. Now, Suarez *et al.* [4] have brought us a step closer towards answering these questions by analyzing a list of ants that could have plausibly become established in the US.

The data set, compiled by identifying ant species intercepted at US ports of entry by the US Customs Service from 1927 to 1985 and deposited at the National Museum of Natural History (NMNH), provides not only valuable insights into international ant commerce, but also serves as an invaluable starting point for future investigations of biological invasions. Suarez *et al.* [4] identified 323 ant species that were detected during custom inspections of import goods and that therefore can be considered to have had an opportunity to establish in the US. Even though these arriving species form a fairly representative sub-sample of the total species in their geographic region and taxonomic organization (subfamily), only about twelve percent (28 species) have actually become established in the US. Interestingly, although most of the ant interceptions were associated with imported plant material, arboreal ants were significantly less likely to become established.

Given a list of failed and successful invaders, such as that provided by Suarez *et al.* [4], future

research can directly explore biological differences that enable some species, but not others, to become invasive. A constellation of characteristics common to invasive ants has already been recognized, such as the presence of multiple queens, reduced intraspecific aggressiveness, and small body size [5,6]. Ants provide an excellent phylogenetic framework for rigorously testing correlations between such characteristics and invasiveness, particularly because ants are a diverse group, with many examples of convergent evolution that allow independent comparisons. Unfortunately, we currently lack both natural history and phylogenetic information on exotic ants to carry out these tests. With the help of the dataset compiled by Suarez *et al.* [4], however, we can begin to focus investigations and acquire the requisite information that will eventually provide answers to the most fundamental questions of invasive species biology.

International Needs for Long-Term Monitoring Programs

Suarez *et al.*'s [4] analysis capitalized on an unparalleled dataset accumulated by decades-long collecting, data-basing, and vouchering efforts coordinated between the US Department of Agriculture (USDA) and the NMNH at the Smithsonian Institution. Insects detected during USDA import inspections were sent to the Entomology Department of the NMNH, where they were catalogued, retrievably stored, and curated for future research. The true value and full utility of this unparalleled collection have decidedly emerged now with the analysis reported by Suarez *et al.* [4].

Accumulating a comparable collection de novo would not only be prohibitively expensive, but would far exceed the time constraints for a typical research grant. In addition, unacceptable opportunity costs are incurred by decade-long delays of obtaining critical information on invasive species that are emerging as pests and biodiversity exterminators right now. Taking advantage of

existing collection infrastructure, those costs were saved because of the foresight by USDA researchers and NMNH curators 80 years ago. One wonders about the full potential of museum collections as repositories of internationally useful databases if museums received even a fraction of the support for their long-term research efforts as short-term efforts in physics or in space exploration.

Failure to adequately fund museums and biodiversity surveys will come at a massive cost in terms of lost future opportunity, one that will be paid by future generations. The study of long-term ecological processes, such as those affected by the accelerating global traffic of invasive species, will require far greater resources than currently made available; decisions based on expectations of instantaneous research results will be short-sighted. Like investments into schools and education, investment into museum collections, global biodiversity surveys and taxonomic training is investment benefiting future generations, with incalculable economic and health benefits [7].

The Future of Ant Invasion Ecology

Ants, which are present in large numbers in many ecosystems, drive numerous ecological processes [8]. Consequently, introduced ant species, especially a few high-impact ant invaders such as the fire ant, cause fundamental changes in their new habitat, to the detriment of native organisms. For example, by competitively excluding native seed-dispersing ants, invasive Argentine ants have caused major shifts in plant compositions in the South African shrublands [9]. Likewise, by eliminating the native ants, which serve as food for horned lizards, Argentine ants have likely led to declines in lizard populations in California [10].

To date, most research on exotic invaders has largely focused on plants, arguably the most conspicuous invaders with the most obvious effects on the environment. Ants and plants

share many life history traits, which make insights from one group potentially applicable to the other. For example, while invading plants have a tendency to reproduce clonally, so do invasive ants, whose colonies often bud, some species producing queens from 'asexual' fragments containing just workers and brood [11]. At the same time, the social structure and behavior of an ant colony is more easily dissected than the processes operating inside a plant, which may make ants a better model system to study organismal prerequisites enabling a successful invasion. Indeed, while the propensity for vegetative reproduction remains the only well-established ecological characteristic that unites invasive plants [12], successful ant invaders exhibit a suite of characteristics listed above [5,6,13]. With the aid of data compiled by Suarez *et al.* [4], future behavioral, ecological, and systematic research can directly test the relevance of these characteristics to the ants success as invaders, potentially answering questions relevant not just to ant invasions, but to biological invasions as a whole.

References

1. Lofgren, C.S. (1986). History of imported fire ants in the United States. In *Fire ants and leaf cutting ants: Biology and management*, C.S. Lofgren and R.K. Vander Meer, eds. (Boulder, CO: Westview Press), pp. 36–47.
2. Vinson, S.B. (1997). Invasion of the red

imported fire ant (Hymenoptera: Formicidae): Spread, biology, and impact. *Am. Entomol.* 43, 23–39.

3. Summerlin, J.W., Hung, A.C.F., and Vinson, S.B. (1977). Residues in nontarget ants, species simplification and recovery of populations following aerial applications of mirex. *Environ. Entomol.* 6, 193–197.
4. Suarez, A.V., Holway, D.A., and Ward, P.S. (2005). The role of opportunity in the unintentional introduction of nonnative ants. *Proc. Natl. Acad. Sci. USA* 102, 17032–17035.
5. Holway, D.A., Lach, L., Suarez, A.V., and Tsutsui, N.D. (2002). The causes and consequences of ant invasions. *Ann. Rev. Ecol. Syst.* 33, 181–233.
6. McGlynn, T.P. (1999). Non-native ants are smaller than related native ants. *Am. Nat.* 154, 690–699.
7. Suarez, A.V., and Tsutsui, N.D. (2004). The value of museum collections for research and society. *Bioscience* 54, 66–74.
8. Hölldobler, B., and Wilson, E.O. (1990). *The Ants* (Cambridge, MA: Harvard University Press).
9. Christian, C.E. (2001). Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature* 413, 635–639.
10. Suarez, A.V., and Case, T.J. (2002). Bottom-up effects on persistence of a specialist predator: Ant invasions and horned lizards. *Ecol. Appl.* 12, 291–298.
11. Peacock, A.D., Sudd, J.H., and Baxter, A.T. (1955). Studies in Pharaoh's ant, *Monomorium pharaonis* (L.). 12. Dissemination. *Entomol. Mon. Mag.* 91, 130–133.
12. Kolar, C.S., and Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16, 199–204.
13. McGlynn, T.P. (1999). The worldwide transfer of ants: geographical distribution and ecological invasions. *J. Biogeogr.* 26, 535–548.
14. Morrison, L.W., Porter, S.D., Daniels, E., and Korzhukin, M.D. (2004). Potential global range expansion of the invasive fire ant, *Solenopsis invicta*. *Biol. Invasions* 6, 183–191.

Integrative Biology, University of Texas at Austin, Austin, Texas 78712, USA.

DOI: 10.1016/j.cub.2006.02.001

Autism Spectrum Disorder: Seeing Is Not Understanding

Impairments in social and emotional skills are a defining feature of autism spectrum disorder. Recent research shows that structural and functional abnormalities within the neural system that matches observation and execution of actions — the mirror neuron system — may explain the social aspects of the pathophysiology of autism spectrum disorder.

Shirley Fecteau^{1,2},
Jean-François Lepage¹ and
Hugo Théoret¹

The discovery of 'mirror' neurons in the ventral premotor cortex of macaque monkeys — neurons which respond to both

observation and performance of a particular action — and the growing evidence that neurons with similar properties are present in the human brain have led many to suggest a fundamental role for the mirror neuron system in social cognition. Specifically, the mirror