invasions. Refuges from the invader often remain at some place in a native species' range. Whether native species can stably persist within these refuges is an open question. But in the short term, the number of invasions has far exceeded the number of resulting extinctions. This result has emphasized that most ecological systems are not 'saturated' with species.

Two puzzles

Nearly all problematic invasive species experience rapid population growth at some point in the invasion process. However, many of these invaders were seemingly present in the exotic range for a considerable period of time prior to exploding in numbers. A number of hypotheses have been proposed for this 'invasion lag', but the true explanation can be hard to pin down and likely varies by system. It may be that the invaders remain sparse until the climatic conditions appropriate for rapid expansion happen to occur. Alternatively, initially small invader populations may require time or multiple introductions to overcome 'Allee effects' or build-up the genetic diversity necessary for population expansion. Lastly, the lag may simply reflect that fact that exponential growth only becomes obvious once populations get relatively large.

A second invasions puzzle is why species that are apparently benign in their native range become so dominant in their exotic range. Classic thinking holds that in the introduced range, the invader escapes the specialist predators or pathogens that control its populations in its native range. Indeed, many exotic plants and animals have fewer specialist predators and pathogens in their exotic versus native range. However, the enemies release hypothesis also requires that consumers actually control the exotic species in its native range, and further, that generalist enemies in the exotic range do not compensate for the loss of specialist predators and pathogens. There is much weaker evidence for these more subtle, but equally important requirements of the hypothesis. Moreover, recent work suggests that generalist enemies often prefer exotic over native plants, counteracting benefits of specialist enemy release. In sum, the long-held hypothesis that

enemy release is responsible for the run-away success of exotic species is not nearly as well-supported as commonly believed. Developing alternative hypotheses to explain invader dominance in the exotic range may become a key priority.

Generality

The explosion of research into biological invasions over the last several decades has generated considerable understanding of the patterns and dynamics of individual invasions. The challenge, however, comes when moving from individual case studies to the development of general principles that apply across a broad range of invasions. Meta-analytical approaches over the last five years or so have yielded some of the most general conclusions in this research area, many of which form the basis of the principles outlined in this article.

Future insights on biological invasions will likely emerge from the current focus of the ecological community on the impacts of climate change. Worldwide, numerous studies are manipulating environmental factors such as temperature and precipitation to better understand how ecosystems will respond to forecasted changes in these variables. Many of these projects include exotic species and therefore present excellent opportunities to evaluate the role that climate plays in regulating invader establishment and impact. Through studies such as these, ecologists can begin to predict how biological invasions will alter the way ecological communities respond to a changing climate.

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Head turns bias the brain's internal random generator

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Numerical and spatial cognition rely on common functional circuits in the parietal lobes of the brain [1]. While previous work has established that the mere perception of numbers can bias a subject's attention in space [2], the method of random digit generation has only recently been introduced to a rapidly growing literature exploring asymmetries in number space [3]. Here we show that human subjects' attempts to generate numbers 'at random' are systematically influenced by lateral head turns, which are known to reallocate spatial attention in the outside world. Specifically, while facing left, subjects produced relatively small numbers, whereas while facing right they tended to produce larger numbers. These results support current concepts of parietal cortex as mediating the interplay between spatial attention and abstract thought [4].

Numerical magnitudes supposedly are represented on a 'number line' that extends from left (small numbers) to right in mental space. Several lines of evidence suggest that this analogue, oriented representation of numbers is mediated by those parietal lobe regions of the brain that also process left and right in outside space. First, patients who have suffered damage to the right parietal lobe, and who consequently fail to attend to the left side of space ('hemispatial neglect'), also exhibit neglect in number space. For instance, when they are asked to indicate the median number of orally presented number pairs — "which number is halfway between 9 and 17?" — they deviate towards too large, 'right-sided' numbers [5]. Second, work with healthy subjects showed that the universal left-sided attention bias in spatial exploration ('pseudoneglect' [6,7]) is also found

in number space — normal subjects typically bisect segments of the number line at too small a number [8]. In a recent study [9], the deviation in graphic line bisection predicted the performance in number line bisections, which implies equivalent functional asymmetries in physical and representational space. Moreover, results from a transcranial magnetic stimulation study [8] inducing a transient disruption of cortical functions indicate the parietal lobes as the loci of interactions between space and numbers.

We employed a demanding number generation task, the repeated naming of digits in a sequence as random as possible, to further investigate the spatial properties of numerical representations. While, in the past, randomization tasks have been widely employed to monitor a subject's working memory and frontal executive functions [10], we recently suggested that the known preference, in such tasks, for small over large numbers could have a spatial component [3]. With their eyes closed, subjects had to generate random numbers in the interval between 1 and 30, once with their head kept straight (baseline) and once while turning their head (see Figure 1A and the figure legend for details). Half of the subjects were required to visualize the 30 numbers on an imaginary ruler. The dependent variable was the number of 'small', supposedly 'left-sided' numbers (1 to 15) produced in each experimental run.

The results as described in Figure 1B clearly show the bias for small numbers and the influence of head turns. They allow for two principal conclusions. First, in the straight-ahead condition subjects produced more small numbers than expected by chance. In accordance with recent findings [3], the brain's internal random generator generally appears to be biased towards the production of smaller numbers. Previous speculations about linguistic, developmental or social-psychological causes of this bias are here complemented by the proposal that asymmetric parietal lobe contributions may be involved. Although it remains to be established whether in right-to-left reading cultures, a *large*-number bias may be evident, this would not in itself contradict the model of
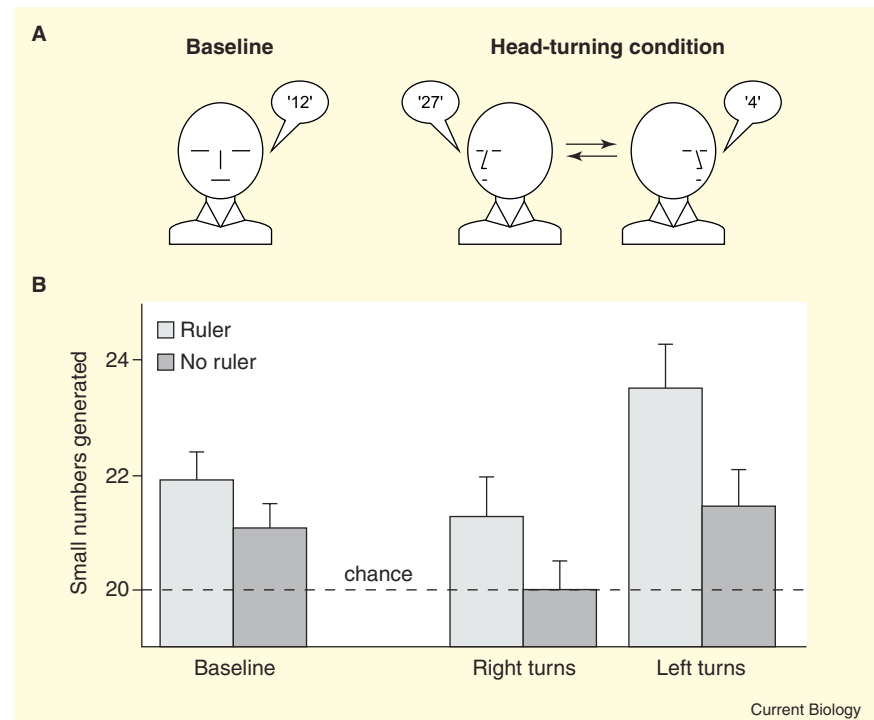

Figure 1. The number generation task.
(A) Forty healthy, right-handed subjects named, with their eyes closed, numbers between 1 and 30 in a sequence as random as possible. Each subject performed two runs, a baseline and a head-turning condition (counterbalanced order). Responses were paced by a metronome (0.5 Hz). In the baseline condition, 40 responses were generated while keeping the head straight. In the head-turning condition, subjects had to perform rhythmic head turns (~80° lateral extension). At each turning point of the sinusoidal movement, a random number had to be emitted spontaneously. Eighty responses — 40 to either direction — were collected. We also included an instructional manipulation. Half of the subjects were told that the imagination of a ruler with 30 units might facilitate performance ('ruler' group); no such information was given to the other 20 subjects ('no ruler' group). (B) Number of 'small' (<16; left on number line segment 1–30) numbers produced under baseline and left and right turning conditions (means and standard error). Overall, subjects produced more small numbers than expected by chance (20.0; dotted line) under the baseline (t = 4.3, p < 0.001) and left turning condition (t = 4.8, p < 0.001), but not after right turns (t = 1.4, n.s.). Numerically, there was an increase in small numbers for left turns compared to baseline, but a decrease for right turns. ANOVA with direction of head turning (baseline, left, right) and instruction group as factor revealed a main effect of head turning (F = 4.4, p < 0.02). Subjects generated significantly more small numbers after left turns than after right turns (t = 2.7, p < 0.011). The main effect of instruction group was significant as well (F = 8.4, p <0.01). Subjects who imagined a ruler evidenced a more pronounced preference for small numbers than subjects who conceived of the numbers in a more abstract sense.

pseudoneglect as a consequence of a cerebral hemispheric imbalance in favor of right parietal attentional functions [11]. The fact that, in our experiment, visual imagery instructions proved a potent means of exaggerating small-number preferences, further emphasizes the presumed 'spatiality' of number space.

The second important conclusion derives from the observation that head turning can modulate healthy subjects' lateral biases along the mental number line. From work with patients with right parietal lesions and hemineglect it is known that forced left-turns of eyes and head may move their spotlight of attention towards the left side of both the outside world [12] and of mental images [13]. In healthy subjects, physical turning towards the left side has early been recognized as an indicator of contralateral hemispheric activation [14]. This right-hemisphere activation appears to stimulate left-sided attention not only in perception and action, but also in mental navigations through memory and number space.

Intuitively, random number generation seems to involve abstract cognitive processes devoid of any direct connection to body or space. It may

surprise that a low-level sensorimotor manipulation systematically influences the behavior in a task only implicitly evoking the notion of number magnitude. However, sensory and motor processes, which have originally evolved for basic interactions with the environment, are reportedly exploited during abstract cognition [15]. Intriguingly, as head turning can influence one's spontaneous spatial exploration, it also appears to affect predictably the apparent spontaneity of 'random' numerical choices.

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Experiments with robots explain synchronized courtship in fiddler crabs

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Male fiddler crabs (*Uca mjoebergi*) produce highly synchronized courtship waves. Is this a cooperative behaviour because females preferentially approach groups that wave synchronously? Or is it a competitive behaviour because of female choice for males that wave first, with the resultant selection on males generating synchrony as an epiphenomenon [1]? To find an answer we used robotic male crabs to measure female mating preferences. We show that females do not prefer males waving in synchrony, but they strongly prefer males that wave first ('leaders'). Synchrony therefore appears to be a by-product of competitive interactions between males.

Synchronized male sexual advertisement is a spectacular phenomenon occurring in several taxa. It almost always involves acoustic or bioluminescent signals [1]. There are two main explanations for its occurrence. First, synchronization is cooperative if females prefer synchronous groups so that all male participants potentially benefit. This could explain synchronized bioluminescence for long-range attraction by fireflies. Second, when two acoustic signals are produced in rapid succession, receivers often respond more strongly to leaders than followers ('precedence effect') [2,3]. Game theory modelling shows that selection on signal timing to increase the likelihood of leadership generates synchrony as an epiphenomenon. This mechanism can successfully explain synchronous acoustic choruses [4,5]. The precedence effect has, however, only been demonstrated for acoustic signals and the proximate mechanisms implicated (for example, call masking) are not necessarily applicable to other sensory modalities [2,3].

To date, we lack direct evidence that a standard visual signal based on reflected light that is produced synchronously by courting males has arisen either because of a female preference for synchronous groups or through a precedence effect. In fiddler crabs, however, where neighbouring males wave their claws in tight synchrony to attract females, there is a positive correlation between leadership and attractiveness [6]. This suggests that the precedence effect promotes synchrony, but experimental evidence for this is lacking [7]. We therefore built four robotic fiddler crabs that resemble courting males (see Supplemental data available on-line with this issue) to investigate synchrony in *U. mjoebergi* in Darwin, Australia. Mate-searching females approach a cluster of males and enter one male's burrow. If suitable, they stay and mate [8]. For 24 females we measured wave synchrony between the visited male and his nearest neighbour as $\alpha = [(t_n - t_v)/T_v] \times 360°$ ($t_n - t_v$ = time between wave onset by the neighbour and visited male; T_v is the interval between successive waves by the visited male) [4]. Synchrony is perfect if $\alpha = 0°$ or $360°$ and there is perfect alternation if $\alpha = 180°$. In *U. mjoebergi* there is tight synchrony ($\alpha = 5.2° \pm 6.8°$ s.e.; Rayleigh's test, $Z = 17.1$, $P < 0.0001$) (Figure 1A; see also Supplemental Movie S1).

Mate choice trials were conducted in the field. In each experiment one pair of robotic crabs was set up 40 cm from a second pair (robots 5 cm apart within pairs). All robots had identical wave rates. We then captured a burrowless female and placed her under a cup equidistant between the pairs. After acclimation, we released her and noted which robot she approached. Females exhibited behaviour characteristic of mate choice during their approach, such as typical jerky movements (Supplemental Movie S2). We only scored a trial if the female saw all four robots wave at least twice before choosing. *P*-values are from binomial tests (n = 40 females/experiment).

We first offered females a choice between a synchronous pair ($\alpha = 0°$)