Interestingly, their theory reduces to a specific type of gravity model when a homogeneous distribution of the populations (and thus opportunities) is assumed. This could explain why the gravity-theory analogy has been so persistent in mobility research, and also indicates that it is equivalent to an idealized scenario, one hardly ever encountered in real-life settings.

The radiation model may provide a route to further exploration. It could be useful for researchers interested in understanding processes mediated by human mobility, such as the introduction of animals and plants into a new habitat and the spread of human infectious diseases[2]. Until now, computational models in these areas relied on direct data implementation and gravity models to fill gaps in incomplete mobility data sets.

A pertinent question for future work is why some societies are more mobile than others. A comparative analysis between the United States and European countries would be a promising starting point for addressing this issue. ■

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CLIMATE CHANGE

A tale of two hemispheres

A reconstruction of temperature from proxy records shows that the rise in global mean temperature closely resembled, but slightly lagged, the rise in carbon dioxide concentration during the last period of deglaciation. **SEE ARTICLE P.49**

ERIC W. WOLFF

Between about 19,000 and 10,000 years ago, Earth emerged from the last glacial period. The whole globe warmed, ice sheets retreated from Northern Hemisphere continents and atmospheric composition changed significantly. Many theories try to explain what triggered and sustained this transformation (known as the glacial termination), but crucial evidence to validate them is lacking. On page 49 of this issue, Shakun *et al.*[1] use a global reconstruction of temperature to show that the transition from the glacial period to the current interglacial consisted of an antiphased temperature response of Earth's two hemispheres, superimposed on a globally coherent warming. Ocean-circulation changes, controlling the contrasting response in each hemisphere, seem to have been crucial to the glacial termination.

The centrepiece of Shakun and colleagues' study[1] is a reconstruction — using 80 marine, terrestrial and ice-core proxy records — of the latitudinal temperature pattern and global mean temperature throughout the termination. This is a major achievement: the difficulties of synchronizing the records and of ensuring that they are sufficiently representative of the whole planet, are considerable. Global mean temperature rose in two main steps, closely mirroring the rise in atmospheric carbon dioxide measured[2] in Antarctic ice cores (see Fig. 2 of the paper[1]). And in contrast to Antarctic temperature[2], global mean temperature lagged carbon dioxide rise by 460±340 years during the termination.

As anticipated from comparisons of Antarctic with Greenland temperatures[3], the Northern and Southern Hemispheres show different patterns of temperature change (see Fig. 4 of the paper[1]). The authors[1] quantify this difference by subtracting the mean temperature of the Southern Hemisphere from that of the Northern. This gives a W-shaped profile that is remarkably similar in timing and shape to a geochemical record[4] that is considered to be a proxy for the strength of the Atlantic meridional overturning circulation (AMOC). The AMOC is the branch of ocean circulation in the Atlantic that takes warm surface waters northwards, balanced by the flow of cold deep water southwards. The strength of this circulation has a considerable impact on the transfer of heat between the hemispheres.

Some studies have proposed[5,6] that changes in ocean heat transport are an essential part of glacial termination. Shakun *et al.*[1] combine their data with simulations based on an ocean–atmosphere general circulation model to present a plausible sequence of events from about 19,000 years ago onwards. They propose that a reduction in the AMOC (induced in the model by introducing fresh water into the North Atlantic) led to Southern Hemisphere warming, and a net cooling in the Northern Hemisphere. Carbon dioxide concentration began to rise soon afterwards, probably owing to degassing from the deep Southern Ocean; although quite well documented, the exact combination of mechanisms for this rise remains a subject of debate. Both hemispheres then warmed together, largely in response to the rise in carbon dioxide, but with further oscillations in the hemispheric contrast as the strength of the AMOC varied. The model reproduces well both the magnitude and the pattern of global and hemispheric change, with carbon dioxide and changing AMOC as crucial components.

The success of the model used by Shakun and colleagues in reproducing the data is encouraging. But one caveat is that the magnitude of fresh water injected into the Atlantic Ocean in the model was tuned to produce the inferred strength of the AMOC and the magnitude of interhemispheric climate response; the result does not imply that the ocean circulation in the model has the correct sensitivity to the volume of freshwater input[7].

Shakun and colleagues' work does provide a firm data-driven basis for a plausible chain of events for most of the last termination. But what drove the reduction in the AMOC 19,000 years ago? The authors[1] point out that there was a significant rise in temperature between 21,500 and 19,000 years ago in the northernmost latitude band (60–90° N). They propose that this may have resulted from a rise in summer insolation (incoming solar energy) at high northern latitudes, driven by well-known cycles in Earth's orbit around the Sun. They argue that this rise could have caused an initial ice-sheet melt that drove the subsequent reduction in the AMOC.

However, this proposal needs to be treated with caution. First, there are few temperature records in this latitude band: the warming is seen clearly only in Greenland ice cores. Second, there is at least one comparable rise in temperature in the Greenland records, between about 62,000 and 60,000 years ago, which did not result in a termination. Finally, although it is true that northern summer insolation increased from 21,500 to 19,000 years ago, its absolute magnitude remained lower than at any time between 65,000 and 30,000 years ago. It is not clear why an increase in insolation from a low value initiated termination whereas a continuous period of higher insolation did not.

In short, another ingredient is needed to explain the link between insolation and termination, and the triggers for the series of events described so well in Shakun and colleagues' paper[1]. The see-saw of temperature between north and south throughout the glacial period, most clearly observed in rapid Greenland warmings (Dansgaard–Oeschger events), is often taken as a sign that numerous changes in AMOC strength occurred. However, the AMOC weakening that started 19,000 years ago lasted for much longer than previous ones, allowing a much more substantial rise in southern temperature and in carbon dioxide concentration. Why was it so hard, at that time, to reinvigorate the AMOC and end this weakening? And what is the missing ingredient that turned the rise in northern insolation around 20,000 years ago into the starting gun for deglaciation, when higher insolation at earlier times failed to do so? It has been proposed[8] that terminations occur only when northern ice-sheet extent is particularly large. If this is indeed the extra ingredient, then the next step in unwinding the causal chain must be to understand what aspect of a large ice sheet controls the onset and persistence of changes in the AMOC that seem to have been key to the last deglaciation. ■

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NEUROSCIENCE

The symphony of choice

The brain's parietal cortex seems to orchestrate decision-making without single neurons performing 'solos'. Rather, decision-specific motifs emerge as highly organized sequences of short-lived neuronal activity. **See Article p.62**

EDUARDO DIAS-FERREIRA & RUI M. COSTA

Sometimes it may be necessary to turn down that Vivaldi concerto while driving, to catch up with the traffic news. But a warning of an upcoming traffic jam would be totally useless if the driver could not sort out the specific sequences of left and right turns along an alternative itinerary. Such transitions from perceptual decisions (choosing one option on the basis of sensory information) to movement planning rely on the brain's parietal cortex[1,2]. But what neuronal dynamics underlie such complex chains of events? On page 62 of this issue, Harvey and colleagues[3] report decision-specific sequences of neuronal activity in the parietal cortex of mice during a memory-guided navigation task. Remarkably, the animals' choices were not signalled by sustained activity of particular neurons during the decision-making period, as has been shown in other studies[1,2]. Rather, the choice was indicated by the activation of specific sequences of intermingled neuronal populations, with each neuron transiently active during a particular period of the task.

Harvey *et al.*[3] used a virtual T-shaped maze that mice, with their heads restrained, explored by running on a spherical treadmill. At the same time, the authors tracked the activity of individual neurons in a specific layer of the animals' parietal cortex by imaging cellular calcium levels — an indication of neuronal activity — using two-photon microscopy. In each trial, the mouse would actively navigate through a first part of the maze, where a visual cue would be presented. After that, there was a delay period in which it would continue straight ahead until it faced a crossroad where, depending on the initial cue, it had to take either a left or a right turn to reach a reward (Fig. 1a).

The authors recorded the activity of sufficient numbers of neurons simultaneously to notice that neurons with sustained activity during an entire task period (cue, delay or decision) were rare. Moreover, the choice made by the mouse — left or right turn — could be predicted at any point in the maze from a sparse pattern of the neuronal activity at the ensemble level. From a bird's-eye view, these activation patterns showed an ordered progression through specific neuronal populations, reflecting not merely the spatial and temporal progression of the mouse through the maze, but its future choice (Fig. 1b).

Compared with other studies[1,2], neurons with sustained activity were rare in these experiments[3]. This disparity probably stems from differences in task structure between the studies. In Harvey and colleagues' virtual maze[3], the mice were allowed to continue moving during the delay period, whereas in the other studies[1,2] they were required to stay immobile during that period, fixating on a point on a screen. Hence, one intriguing possibility would be that the sustained activity of certain neurons observed by other authors during the delay period represents a slowing down of ensemble dynamics during 'fixation'. It is interesting that — in the present study[3], as in previous reports[1,2] — the divergence of neuronal dynamics for different choices starts from the moment of cue presentation, before the delay period.

Could the neuronal dynamics reported by Harvey and colleagues[3] be related to visual information processing or motor performance, rather than to choice or action planning? This does not seem to be the case, as there was no correlation between the animals' running trajectories and the neuronal activity before choice. Furthermore, when the authors injected a drug to inactivate the parietal cortex, the animal's performance of the (memory-guided) task was impaired. But this was not the case for a visually guided version of the task, in which the visual cue was presented at the crossroad, rather than earlier in the maze. Moreover, during virtual linear-track tests (which required running and turning behaviours similar to those in the T-maze), and during open-loop experiments (in which images simulating runs through the maze were played to the mice), the parietal cortex was less engaged and less tuned to specific maze locations than during the memory-guided T-maze experiment. Therefore, the choice-specific sequential activation of neurons along the maze probably reflects the emergence of functional motifs for action planning.

Since Hubel and Wiesel's discovery[4] in the 1950s that neurons are arranged in functional columns in the brain's visual cortex, it has been tempting to think of cortical circuits as being organized in anatomically discrete functional domains. Harvey *et al.*[3] do find that the activities of the parietal-cortex neurons are slightly more closely correlated with those of nearer neurons than with those of more distant ones. However, choice-specific functional motifs are intermingled: there was no apparent local organization of neurons tuned for specific task periods or for specific choice preferences (Fig. 1b). It is not clear whether the type of spatial organization reported by the authors is an exception to Hubel and Wiesel's initial observations[4] or a more common mode of organization than previously thought, given the growing body of evidence for anatomically intermixed functional motifs[5,6], especially in mouse brain circuits.