RESEARCH ARTICLES

PALEOCEANOGRAPHY

Onset of Mediterranean outflow into the North Atlantic

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Sediments cored along the southwestern Iberian margin during Integrated Ocean Drilling Program Expedition 339 provide constraints on Mediterranean Outflow Water (MOW) circulation patterns from the Pliocene epoch to the present day. After the Strait of Gibraltar opened (5.33 million years ago), a limited volume of MOW entered the Atlantic. Depositional hiatuses indicate erosion by bottom currents related to higher volumes of MOW circulating into the North Atlantic, beginning in the late Pliocene. The hiatuses coincide with regional tectonic events and changes in global thermohaline circulation (THC). This suggests that MOW influenced Atlantic Meridional Overturning Circulation (AMOC), THC, and climatic shifts by contributing a component of warm, saline water to northern latitudes while in turn being influenced by plate tectonics.

ectonic activity exerts primary control on sedimentation along continental margins and on seafloor morphology, whereby it also influences bottom current flow pathways. Sea level variation and climate also influence sedimentation along continental margins. Plate tectonic configuration plays an important role in climate (1), although uncertainty persists concerning the specific cause-effect relationships and their relative importance on a temporal scale. From the late Miocene to the Pleistocene, Earth experienced major plate tectonic, climatic, and oceanographic shifts that, along with orbital variation, contributed to present-day global climate dynamics (2). These events include the closure and reopening of gateways between the Atlantic and Mediterranean basins [~ 5.55 to 5.33 million years ago (Ma) (3)], the closure of the deep Central American Seaway (CAS) [4.5 to 3.0 Ma (4)] and the Indonesian Seaway [~4 Ma (2)], and the onset of Northern Hemisphere glacial (NHG) cycles in the late Pliocene (5). Neogene sedimentary sections also record Pliocene warming trends that culminate in the mid-Pliocene warm period [3.3 to 3.0 Ma (6)], the Panama seaway closure [~3.0 to 2.7 Ma (7)], and NHG intensification around 2.72 Ma [Marine Isotope Stage (MIS) G6 (5)]. During this period, increases in evaporation and precipitation facilitated ice sheet formation, higher albedo, and increased Atlantic Meridional Overturning Circulation (AMOC) (4, 8). The global transition to Quaternary glacial cycles at 2.7 Ma (5, 8), a predicted major glaciation at 2.15 Ma (9), and the recent mid-Pleistocene transition at ~0.9 to 0.7 Ma (10) also relate to the establishment and stabilization of present-day ocean circulation patterns.

Changes in the Mediterranean Outflow Water (MOW) co-occurred with some of these shifts in global ocean circulation and climate, but the exact timing of MOW evolution with respect to major climate events remains unclear. The Strait of Gibraltar strongly influences Mediterranean-Atlantic water mass exchange, contributing warm and highly saline MOW to the Atlantic Ocean. MOW currently enters the Strait of Gibraltar with a density of 29.12 kg/m³ (8); its density is 27.7 kg/m³ in the Gulf of Cadiz and off Brittany (11, 12) and 27.4 kg/m³ further afield along the Rockall Plateau of the northeastern Atlantic extension (12). MOW input thus enhances North Atlantic density and helps drive thermohaline convection. Estimates suggest that without MOW, the AMOC would decline by ~15% and North Atlantic sea surface temperatures would fall by up to 1°C (8). The Gulf of Cadiz and the western margin of Portugal record critical aspects of MOW development as well as the interaction between MOW and AMOC. Upon exiting the Strait of Gibraltar, MOW consists of relatively warm and highly saline water (Fig. 1) that settles into an intermediate bottom current within the mid-slope region, between 400 and 1400 m water depth, at an overflow rate of 0.67 ± 0.28 Sv (11). This region lies beneath Atlantic Water (AW) inflow but rafts above North Atlantic Deep Water (NADW).

This paper interprets the sequence of events that established an important MOW contribution

to North Atlantic thermohaline dynamics, and makes inferences concerning how these dynamics relate to Neogene and Quaternary climatic and tectonic events. Our study combines geophysical and drill core data acquired along the southwestern Iberian margin during Integrated Ocean Drilling Program (IODP) Expedition 339 aboard the research vessel JOIDES Resolution (Fig. 1).

The southwestern Iberian margin is located near the Azores-Gibraltar Fracture Zone, which is a section of the convergent plate boundary between Eurasia (Iberia subplate) and Africa (Nubia subplate). The plates currently converge at a rate of ~4 to 5 mm/year in a WNW-ESE direction. Counterclockwise rotation is accommodated by a series of thrusts and dextral strike-slip faults (13, 14) active since at least 1.8 Ma. Starting in the late Miocene, the southwestern Iberian margin evolved by oblique convergence between the Iberia and Nubia subplates (13) and westward rollback subduction of an oceanic lithosphere slab beneath the Gibraltar Arc, both of which facilitate development of the Cadiz Allochthonous Unit (CAU) (15) or accretionary

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*Corresponding author. E-mail: javier.hernandez-molina@rhul. ac.uk wedge (16). Distinct periods of crustal deformation, fault reactivation, and halokinesis related to plate motion have contributed to the tectonostratigraphic evolution of the area (13). Sediments within the Gulf of Cadiz record the opening of the Strait of Gibraltar, and event that initiated MOW intrusion into the North Atlantic. Subsequent intensification of MOW established along-slope depositional systems and generated an extensive contourite depositional system (CDS) (17) that provides a sedimentary record of the paleoceanographic events analyzed and interpreted here.

Seismic records and drill cores as tracers of MOW dynamics from the late Miocene to the present

Major regional discontinuities appear as highamplitude seismic reflections within late Miocene to present-day sediments around the Gulf of Cadiz (Fig. 2 and fig. S1). These discontinuities provide a record of MOW circulation relative to coeval tectonic and climatic events. Pliocene deposits appear in seismic profiles as sheeted drifts overlying a weakly reflecting Miocene unit that progrades downslope (Fig. 2 and fig. S1). The late Pliocene to lower Quaternary section provides a record of substantial synsedimentary deformation associated with two discontinuities that define a major truncation surfaces (fig. S2). Quaternary deposits are distinguished by highamplitude seismic reflections and show clear upslope progradation.

Closure of the Strait of Gibraltar and the Betic-Rharb corridors during the Messinian Salinity Crisis (5.56 to 5.33 Ma) prevented Mediterranean-Atlantic water exchange (*3*). Exchange resembling present-day flows through these channels is thought to have begun with the opening of the Strait of Gibraltar and the related onset of the latest Miocene flooding at ~5.33 Ma (*3*). Widespread discontinuities evident in seismic records and pervasive hiatuses evident in Expedition 339 drill cores suggest four major phases of MOW evolution after the opening of the Strait of Gibraltar (Fig. 2, Fig. 3, and fig. S1).

The primary phase of downslope activity occurred during the early Pliocene (~5.2 to 4.5 Ma) as downslope mass transport deposits (slumps and debrites) and turbidites developed in response to widespread tectonic activity. These deposits overlie a regional discontinuity (Fig. 2 and fig. S1) above the late Miocene hemipelagic deposits (Fig. 4 and fig. S3). Drill core results suggest only a limited degree of contourite deposition beginning in the Pliocene. The opening of the Strait of Gibraltar caused slope instability (*3*), leading to gravitational-collapse breccia deposits (*18*).

The second phase began with the onset of limited MOW circulation between ~4.5 and 3.5 Ma. Persistent sequences of contourite facies from 4.5 to 4.2 Ma show clear evidence of initial MOW circulation into the Gulf of Cadiz and subsequent interaction between MOW and the North Atlantic.

The third phase is defined by enhanced MOW circulation from 3.2 to 2.1 Ma. Two major hiatuses, at 3.2 to 3.0 Ma and at 2.4 to 2.1 Ma, indicate erosion by bottom currents and enhanced interaction between MOW and the North Atlantic. Major and uninterrupted contourite deposition occurs



Fig. 1. Regional water masses, major tectonic features, and Gulf of Cadiz CDS site locations sampled during IODP Expedition 339.

only above the upper Pliocene hiatus at 3.2 to 3.0 Ma, where dolostones and debrite deposits occur (Figs. 2 and 4). Interbedded turbidites and contourites are also common in the upper Pliocene section. Dolostone deposits are closely linked to the aforementioned hiatus, wherein they may have precipitated as a result of shallow diagenetic processes (Fig. 2). That hiatus is the first major event evident within the sedimentary stacking pattern throughout the northern Gulf of Cadiz slope (19) and within the Strait of Gibraltar (18). Quaternary successions show a much more pronounced phase of contourite deposition and drift development. These deposits consist of sandy and muddy contourites with periodic turbidite intercalations. They also show a considerable phase of downslope sedimentation at ~2 Ma. A regional hiatus, which occurs within the Quaternary section at ~2.4 to 2.1 Ma, is also associated with dolostones and debrite deposits (Figs. 2 and 4). This hiatus appears as an important discontinuity within drift near the base of the Quaternary. It records a period of tectonic instability coeval with erosion by bottom currents and substantially higher volumes of MOW input into the North Atlantic relative to flow onset at 4.5 to 4.2 Ma.

The final phase, beginning with the establishment of present-day circulation at 2.1 Ma and continuing to this day, is evident from increased sedimentation rates and rapid contourite development. A younger major regional discontinuity with local erosion is clearly evident in the seismic records (Fig. 2 and fig. S1) and is attributed to the mid-Pleistocene transition (*17, 20*), with a tentative age of 0.9 Ma (17). A pronounced change in the drift sedimentary stacking pattern appears at this time horizon as enhanced upslope progradation and mounded morphology, indicating an intensification of MOW (17, 20). A specific hiatus or condensed section, however, is not found in all of the drill core material at the 0.9 to 0.7 Ma time horizon (Fig. 3). Ongoing analysis seeks to further constrain the exact age and duration of this discontinuity.

Hiatuses, mass transport deposits (debrites, slumps), and tectonic events occurring at the end of the Miocene (3), 3.2 to 3.0 Ma (19, 21), 2.4 to 2.0 Ma (13), or ~0.9 Ma (17) around the Gulf of Cadiz appear to coincide with major climatic shifts during this period. Tectonic activity has been a key factor controlling seafloor morphology,



which in turn influences MOW flow pathways and, by extension, deep-water sedimentation. The stratigraphic events thus reflect changes in the Iberia-Nubia subplate kinematics during the Pliocene and Quaternary, which established the present-day transpressional regime. Deformation of the CAU, which initially emplaced in the Algarve basin (fig. S2) in the late Miocene, occurred with reactivation of blind thrusts during the Pliocene and Quaternary. The CAU could therefore record tectonic episodes associated with plate reorganization. Shifts in the Africa-Eurasia plate trajectory after the Messinian Salinity Crisis contributed to the deepening of the gateway (13). The NW-SE to WNW-ESE shift in convergence direction (13, 22) coincides with tectonic events between 3.2 and 2.0 Ma. A hiatus previously described from IODP Expedition 339 core records reflects these events, as do other hiatuses identified near the Strait of Gibraltar (23), in the Alboran Sea (24), and in the eastern Atlantic between Gibraltar and the equator (25). The shift in plate convergence direction for the southwestern Iberian margin coincides with a decline in westward migration and thrusting activity for the accretionary wedge. Reactivated blind thrusts accommodated shortening and minor sedimentary accretion (*16*). At ~1.8 Ma, the oblique convergence between the Iberia and Nubia subplates reactivates WNW-ESE dextral strike-slip faults as well as shallower WNW-directed thrusts (*14*).

Global implications

The spatial distribution of these hiatuses can help to refine our understanding of MOW development and its overall effect on thermohaline circulation (THC) and deep-water sedimentation. The interpreted sequence of events is summarized in Fig. 5.

Lower Pliocene sedimentary deposits show no clear evidence of MOW input into the Atlantic prior to 4.5 Ma. This time constraint indicates a lag between the full opening of the Strait of Gibraltar (~5.33 Ma) and the establishment of





consistent MOW interaction with the North Atlantic (fig. S4). Similarities in the densities of Mediterranean seawater and Eastern North Atlantic Central Water in the beginning of the early Pliocene (8) may have contributed to this lag. By the early Pliocene, Antarctic Bottom Water (AABW) flowed northward and extended into the North Atlantic with greater intensity. This intensification coincided with a weaker AMOC, especially during glacial stages (25).

At ~4.5 Ma, MOW began to circulate into the North Atlantic as an intermediate and deep-water circulation (6). Some authors have reported an additional MOW intensification stage at ~3.8 Ma (23) and 3.5 Ma (12), which coincides with more active circulation in the North Atlantic (12). This second stage demonstrates increasing MOW influence on the North Atlantic and a sedimentary signal shared by MOW- and THC-related phenomena. Notably, the CAS (fig. S4) shoaled by ~4.5 to 3.5 Ma and began to hinder intermediatelaver circulation. These events blocked NADW flow into the Pacific but enhanced NADW flow into the South Atlantic, initiating the modernday deep-water circulation pattern (6). The modernday pattern delivers warmer, saltier surface water to more northerly locations in the Arctic Ocean, enhancing evaporation, precipitation, and ice sheet formation. These factors established the initial conditions for the mid-Pliocene warm period (4, 8). Around this same time (~4.5 Ma), Labrador Sea Water (LSW) began to circulate as part of the North East Atlantic Deep Water (NEADW) layer (7). This led to increased AMOC circulation between 4.5 and 4.0 Ma, as well as increased drift sedimentation in the North Atlantic (2).

Two phases of MOW intensification occurred, one at 3.2 to 3.0 Ma and the other at 2.4 to 2.1 Ma. The timing of these events correlates with higheramplitude phases of temperature and insolation oscillations related to the 400,000-year, eccentricitymodulated cycle (*6*), suggesting a relationship between orbital changes and MOW production.

The first enhanced MOW period began after 3.2 Ma and coincides with widespread evidence of NEADW circulation. This event contributed to the formation of the present-day NADW (4) through southward deflection of the AABW-NADW contact (south of the Azores). NADW arrival at extreme southerly latitudes around Antarctica in turn cooled the Antarctic water and increased production of AABW, augmenting its flow into the southwest Atlantic (26). A coeval decrease in sedimentary accumulation rates in North Atlantic drift deposits accompanied these events (2). Model experiments indicate that NADW production increased around the time of the final CAS closure at 3 Ma (6). However, the increased strength of the AMOC also suggests additional saline and warm water transport to high latitudes in the North Atlantic. MOW could have supplied this additional saline water component of the AMOC. The present study shows that MOW intensification between 3.2 and 3.0 Ma contributed salt water at intermediate depths to northerly latitudes, thus enhancing AMOC and overall Northern Hemisphere deep-water formation and reducing pole-to-equator temperature gradients during the mid-Pliocene warm period. Prior to 3.4 Ma, the density of MOW slightly exceeded the present-day value of 27.8 kg/m³ (*12*). Density increased about 1 kg/m³, maximizing around 3.3 to 3.2 Ma and persisting at this level until ~3.0 Ma (*12*). The temporal boundary of this density event coincides with the age of the hiatus identified in the Gulf of Cadiz. MOW intensification therefore also contributed salt water at intermediate depths to northerly latitudes, thus enhancing THC, AMOC, and overall Northern Hemisphere deep-water formation.

The second enhanced MOW period (2.4 to 2.1 Ma) coincided with a sizable stratigraphic gap reported for the northeast Atlantic (24), suggesting synchronous reactivation of the THC and AMOC. This new event would suggest an additional increase in MOW density, which is surprisingly coeval with apparent major glaciation at 2.15 Ma (9).

Present-day MOW dynamics (fig. S4) commenced in the earliest Quaternary and coincided with a shift from long-term global cooling trends (27) marked by the final NHG intensification (4). The shift included a decline in atmospheric CO₂ levels, global cooling (27), and a fall in sea level (28). The 41,000-year obliquity cycle replaced the 23,000-year precessional cycle as the primary orbital mechanism influencing climate. This shift is also associated with a progressive increase in the amplitude of Earth's orbital obliquity (4).

While cooler deep waters formed with the subsequent increase in deep ocean stratification, deepwater circulation (and sedimentation), upwelling, and biogenic productivity at low latitudes followed a somewhat asymmetric temporal pattern (29). The present-day NADW configuration deflects the AABW-NADW contact southward during interglacial periods, whereas AABW deflected this contact back in a northward direction during glacial periods (2, 29). These dynamics were reinforced by the mid-Pleistocene revolution or transition (0.9 to 0.7 Ma), which established longer periods for glacial/interglacial cycles. This transition coincided with an increase in the 100,000year cycle amplitude and a major eustatic drop in sea level (8, 28), which might relate to the MOW intensification and the formation of the mid-Pleistocene discontinuity (17, 20). This increase in MOW coincides with intensification in the AMOC (2). After that transition and subsequent glacial stages, MOW density increased, as it did during the last glaciation when it exceeded (~31.29 kg/m³) the present-day values (30). Rates of MOW flow were also higher (30), as evident from the morphology of the slope (23).

The aforementioned tectonic events in the Gulf of Cadiz are coeval with other events recorded throughout the Northern Hemisphere (*31*). The temporal overlap of these events suggests that they relate to overall plate reorganization in the North Atlantic (*31*) or to widespread mantle activity [e.g., (*32*)]. More general hypotheses (*33*) affirm this relationship, further corroborating the role of plate tectonics in modulating climate over a wide range



Fig. 4. Lithologic summary of IODP Expedition 339 CDS sample sites, showing major hiatuses. Age model is based on biostratigraphic and magnetostratigraphic data (ky = 1000 years).

Fig. 5. Neogene and Quaternary evolution of the CDS within the Gulf of Cadiz and the western Portuguese margin. Regional evolution is compared with major events affecting the North Atlantic basin and shifts in global climate (2, 27, 28, 34).



of time scales (1). These should be reconsidered in climatic and sea level reconstruction because, for example, they could explain the discrepancy between the benthic δ^{18} O record and the Gibraltar relative sea level that assumes no tectonic changes in the geometry of the Gibraltar Gateway and adjacent areas (9).

Conclusions

Our results show that the initial MOW circulation into the Atlantic after the opening of the Strait of Gibraltar was relatively weak. Meaningful interaction between MOW and the North Atlantic did not begin until the late Pliocene. The establishment of MOW added relatively salty water at intermediate depths and contributed to enhanced THC and AMOC. The addition of the warm, salty MOW component reduced pole-toequator temperature gradients during the mid-Pliocene warm period (3.2 to 3.0 Ma), during the early Quaternary (2.4 to 2.0 Ma), and at 0.9 to 0.7 Ma. These climatic events coincide with widespread depositional hiatuses, pronounced changes in the sedimentary stacking pattern, and establishment of the present-day seafloor morphology. Hiatuses and shifts in depositional processes are related to regional tectonic events and margin instability. Similar changes in deep-water sedimentation and tectonics have been described in association with other margins and basins around the same time in both the Northern and Southern hemispheres, demonstrating that the relationship between climatic shifts and plate tectonic events operates over a wide range of time scales. The relationship between climate and plate tectonic events is especially relevant for this geographic locality because of its role as the site of major events in hominid migration and evolution (34).

REFERENCES AND NOTES

- 1. W. W. Hay, Geol. Rundsch. 85, 409-437 (1996).
- P. C. Knutz, Palaeoceanographic significance of contourite drifts. In *Contourites: Developments in Sedimentology, vol. 60*, M. Rebesco, M. A. Camerlenghi, Eds. (Elsevier, Amsterdam, 2008), pp. 511–535.
- M. Roveri et al., Mar. Geol. 10.1016/j.margeo.2014.02.002 (2014).
- G. Bartoli et al., Earth Planet. Sci. Lett. 237, 33–44 (2005).
- 5. I. Bailey et al., Quat. Sci. Rev. 75, 181-194 (2013).
- M. A. Maslin, X. S. Li, M.-F. Loutre, A. Berger, *Quat. Sci. Rev.* 17, 411–426 (1998).
- K. H. Nisancioglu, M. E. Raymo, P. H. Stone, *Paleoceanography* 18, 1006 (2003).
- M. Rogerson, E. J. Rohling, G. R. Bigg, J. Ramirez, *Rev. Geophys.* 50, RG2003 (2012).
- 9. E. J. Rohling et al., Nature 508, 477-482 (2014).
- H. Elderfield *et al.*, *Science* **337**, 704–709 (2012).
 N. Serra, I. Ambar, D. Boutov, *Ocean Sci.* **6**, 191–209
- N. Serra, I. Ambar, D. Boutov, Ocean Sci. 6, 191–209 (2010).
- 12. N. Khélifi et al., Geology 37, 811-814 (2009).
- N. Zitellini et al., Earth Planet. Sci. Lett. 280, 13–50 (2009).
- 14. J. Duarte et al., Mar. Geol. 289, 135-149 (2011).
- 15. T. Medialdea et al., Mar. Geol. 209, 173-198 (2004).
- 16. M.-A. Gutscher et al., Geology 30, 1071–1074 (2002).
- E. Llave et al., in Economic and Paleoceanographic Importance of Contourites, A. Viana, M. Rebesco, Eds. (Geological Society of London Special Publication, 2007), vol. 276, pp. 49–79.
- M. Esteras et al., Rev. Soc. Geol. Esp. 13, 539–550 (2000).

- R. A. Brackenridge, F. J. Hernández-Molina, D. A. V. Stow, E. Llave, Mar. Pet. Geol. 46, 36–50 (2013).
- C. Roque et al., Mar. Geol. 303–306, 42–62 (2012).
 J. F. Flinch, P. R. Vail, in Mesozoic and Cenozoic Sequence
- Stratigraphy of European Basins, SEPM Special Publication Series no. 60, P. C. de Graciansky, J. Hardenbol, T. Jacquin, P. R. Vail, Eds. (Society for Sedimentary Geology, Tulsa, OK, 1998), pp. 199–208.
- P. Martínez-García, M. Comas, J. I. Soto, L. Lonergan, A. B. Watts, Basin Res. 25, 361–387 (2013).
- 23. F. J. Hernández-Molina *et al.*, *Geology* **42**, 227–230 (2014).
- K. Billups, A. C. Ravelo, J. C. Zachos, *Paleoceanography* 13, 84–95 (1998).
- R. Stein et al., in North Atlantic Paleoceanography,
 C. P. Summerhayes, N. J. Shackleton, Eds. (Geological Society, London, 1986), pp. 103–118.
- M. T. Ledbetter, D. F. Williams, B. B. Ellwood, *Nature* 272, 237–239 (1978).
- J. Zachos, M. Pagani, L. Sloan, E. Thomas, K. Billups, *Science* 292, 686–693 (2001).

- K. G. Miller, G. Mountain, J. Wright, J. Browning, *Oceanography* 24, 40–53 (2011).
- 29. G. S. Dwyer et al., Science 270, 1347-1351 (1995).
- M. Rogerson, G. R. Bigg, E. J. Rohling, J. Ramirez, *Clim. Dyn.* 39, 589–598 (2012).
- S. Cloetingh, F. M. Gradstein, H. Kooi, A. C. Grant, M. Kaminski, J. Geol. Soc. London 147, 495–506 (1990).
- 32. N. White, B. Lovell, Nature 387, 888-891 (1997).
- 33. P. E. Potter. P. Szatmari. Earth Sci. Rev. 96. 279–295
- (2009). 34. P. B. deMenocal, Science **331**, 540–542 (2011).
- 54. P. B. demenocal, Science **551**, 540-542 (20

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/344/6189/1244/suppl/DC1 Materials and Methods Figs. S1 to S4 Table S1 References (35–61) 24 January 2014; accepted 8 May 2014 10.1126/science.1251306

NEURONAL REPAIR

Asynchronous therapy restores motor control by rewiring of the rat corticospinal tract after stroke

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The brain exhibits limited capacity for spontaneous restoration of lost motor functions after stroke. Rehabilitation is the prevailing clinical approach to augment functional recovery, but the scientific basis is poorly understood. Here, we show nearly full recovery of skilled forelimb functions in rats with large strokes when a growth-promoting immunotherapy against a neurite growth-inhibitory protein was applied to boost the sprouting of new fibers, before stabilizing the newly formed circuits by intensive training. In contrast, early high-intensity training during the growth phase destroyed the effect and led to aberrant fiber patterns. Pharmacogenetic experiments identified a subset of corticospinal fibers originating in the intact half of the forebrain, side-switching in the spinal cord to newly innervate the impaired limb and restore skilled motor function.

troke is a major cause of severe disability in the elderly population, and recovery after large strokes is limited (*I*, *2*). Current strategies to improve long-term outcome in humans include mostly rehabilitative training and, in experimental models, electrical stimulation and pharmacological interventions (*3*). However, all of these treatment options have had only limited success thus far (*4*, *5*). Here, we show that rehabilitative training, if preceded by a nerve growth-promoting antibody therapy, almost completely restored skilled

forelimb functions after cortical strokes in adult rats. Sequential application of the treatments was essential: When growth promotion by blockade of the neurite growth-inhibitory protein Nogo-A was simultaneously applied with intensive forced-use training of the forelimb during the first 2 weeks after the stroke, functional outcome was poorer compared with training, immunotherapy alone, or no treatment at all (6). Anatomically, Nogo-A neutralization promoted growth of corticospinal fibers from the intact forebrain motor cortex across the midline of the cervical spinal cord. In rats with simultaneous antibody treatment and training, fiber branching was abundant with anatomically aberrant terminations. In contrast, in animals trained for forelimb function subsequent to antibody treatment, axonal fibers originally terminating in the intact spinal hemicord crossed the midline and innervated the ventral motor regions of the spinal hemicord that had lost its input from the motor cortex. To prove the functional relevance of these newly grown, "side-switched" descending corticospinal tract (CST) fibers, we selectively and temporarily blocked these fibers by two different pharmacogenetic techniques, both of which suppressed the restored forelimb function. Our results demonstrate that a sequential strategy of first promoting fiber growth to enhance the low endogenous plastic potential of the brain and spinal cord, followed by rehabilitative training-induced selection and stabilization of functionally meaningful connections can lead to much higher levels of functional restoration after the formation of large brain lesions than currently obtained in conventional rehabilitation medicine.

Success of rehabilitation depends on timing

We compared four different therapy and rehabilitation schedules for promoting functional recovery of fine motor skills of forelimbs in a thrombotic stroke model in rats. Using the wellestablished technique of photothrombosis (6), we induced blood vessel blockade by multiple microthrombi, which destroyed >90% of the sensorymotor cortex of adult rats. Rats were then treated with intrathecal anti-Nogo-A or control antibody for 2 weeks (6, 7). In addition, we trained rats intensely in skilled forelimb reaching (100 reaches per day), either simultaneously with antibody application (parallel groups) or during the 2 weeks after antibody treatment (sequential groups) (Fig. 1A). To avoid a training effect of testing itself, we did not reassess the sequential groups (anti-Nogo-A/sequential and control sequential) during the first 2 weeks after lesion formation. When the growth-enhancing anti-Nogo-A treatment was followed by the rehabilitative training (anti-Nogo-A/sequential group), animals improved their performance from day 16 poststroke onwards, and their skilled reaching abilities almost completely recovered [reaching 86.3 \pm 2.0% of prestroke level; significantly better than all other groups; P < 0.001, two-way repeated measures analysis of variance (ANOVA) with post hoc Bonferroni] (Fig. 1, A and B). This group also performed best in two skilled forelimb use tasks tested at the end of the experiment

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Supplementary Materials for

Onset of Mediterranean outflow into the North Atlantic

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Materials and Methods Figs. S1 to S4 Caption for table S1 References

Other supplementary material for this manuscript includes:

Table S1 (Excel)

Materials and Methods

This study synthesized geophysical and drill core data from the southwestern Iberian margin to decode the ancient processes related to MOW evolution. Seismic interpretations refer to regional geophysical data compiled from studies conducted over previous decades (17, 19, 20, *35-37*). Stratigraphic correlation and specific age constraints were established during IODP Expedition 339 using (*38*, Table S1): I) lithostratigraphy, II) biostratigraphy, III) paleomagnetic data, IV) sediment core description, V) geochemical analysis and VI) borehole measurements. Biostratigraphic analysis marked the first and last occurrences of key marker species of calcareous nanofossils and planktonic foraminifera, along with one benthic foraminifer occurrence. The paleomagnetic age model derived from depth and timing of magnetic reversal events (*38*). Biostratigraphic and magnetostratigraphic ages showed very close correspondence. Age data were used for determining: the ages of key horizons (including several depositional hiatuses and stratigraphic boundaries) and the sedimentary accumulation rates (detail from IODP Expedition 339 can be accessed at http://iodp.tamu.edu/scienceops/expeditions/mediterranean_outflow.html).

- Table S1 (*Excel data tables*). Late Miocene, Pliocene and Quaternary chronostratigraphy for the sedimentary sections sampled during IODP Expedition 339 (cited references 39-47. Updated and revised from 38).
- Fig. S1. Seismic profile showing the major sedimentary stacking pattern, from the Pliocene sheeted drift to the Quaternary elongate and mounded drift, based on the correlation between Sites U1386 and U1387 and the multichannel seismic reflection line P74-45. The hiatuses and main type of contourite drifts are indicated (data courtesy of REPSOL). Profile location shown in Figure 1.
- Fig. S2. Seismic profile showing deformation of Pliocene deposits caused by olistostrome emplacement (the Cádiz Allochthonous Unit, CAU) within the Algarve basin, and by compressive tectonic events at ~2.1-2.4 Ma (data courtesy of TGS-NOPEC Geophysical Company, ASA). Profile locations shown in Figure 1.
- Fig. S3. Examples of the main sedimentary facies for Pliocene and Quaternary sections sampled during IODP Expedition 339.
- Fig S4. Diagram illustrating the circulation of the major water masses in the Central and North-Atlantic (adapted from 48-61). AABW- Antarctic Bottom Water; CC- Canary Current; DSOW- Denmark Strait Overflow Water; LDW- Lower Deep Water (or modified AABW); ISOW- Iceland Scotland Overflow Water; LSW- Labrador Sea Water; MOW-Mediterranean Outflow Water; NACW- North Atlantic Central Water; NADW- North Atlantic Deep Water; NBC- North Brazil Current; NEC- North Equatorial Current NECC-North Equatorial Counter Current; PSW- Polar Surface Water.



Figure - S1



Figure - S2



C

Figure - S3

with silty mud

eq

& sandy silt

Sand, siltv



Figure - S4

References

- 1. W. W. Hay, Tectonics and climate. *Geol. Rundsch.* **85**, 409–437 (1996). <u>doi:10.1007/BF02369000</u>
- P. C. Knutz, Palaeoceanographic significance of contourite drifts. In *Contourites:* Developments in Sedimentology, vol. 60, M. Rebesco, M. A. Camerlenghi, Eds. (Elsevier, Amsterdam, 2008), pp. 511–535.
- M. Roveri, R. Flecker, W. Krijgsman, J. Lofi, S. Lugli, V. Manzi, F. J. Sierro, A. Bertini, A. Camerlenghi, G. De Lange, R. Govers, F. J. Hilgen, C. Hübscher, P. T. Meijer, M. Stoica, The Messinian salinity crisis: Past and future of a great challenge for marine sciences. *Mar. Geol.* 10.1016/j.margeo.2014.02.002 (2014). doi:10.1016/j.margeo.2014.02.002
- G. Bartoli, M. Sarnthein, M. Weinelt, H. Erlenkeuser, D. Garbe-Schönberg, D. W. Lea, Final closure of Panama and the onset of northern hemisphere glaciation. *Earth Planet. Sci. Lett.* 237, 33–44 (2005). doi:10.1016/j.epsl.2005.06.020
- 5. I. Bailey, G. M. Hole, G. L. Foster, P. A. Wilson, C. D. Storey, C. N. Trueman, M. E. Raymo, An alternative suggestion for the Pliocene onset of major northern hemisphere glaciation based on the geochemical provenance of North Atlantic Ocean ice-rafted debris. *Quat. Sci. Rev.* 75, 181–194 (2013). doi:10.1016/j.quascirev.2013.06.004
- M. A. Maslin, X. S. Li, M.-F. Loutre, A. Berger, The contribution of orbital forcing to the progressive intensification of Northern Hemisphere glaciation. *Quat. Sci. Rev.* 17, 411– 426 (1998). doi:10.1016/S0277-3791(97)00047-4
- 7. K. H. Nisancioglu, M. E. Raymo, P. H. Stone, Reorganization of Miocene deep water circulation in response to the shoaling of the Central American Seaway. *Paleoceanography* 18, 1006 (2003). <u>doi:10.1029/2002PA000767</u>
- M. Rogerson, E. J. Rohling, G. R. Bigg, J. Ramirez, Paleoceanography of the Atlantic-Mediterranean exchange: Overview and first quantitative assessment of climatic forcing. *Rev. Geophys.* 50, RG2003 (2012). <u>doi:10.1029/2011RG000376</u>

- 9. E. J. Rohling, G. L. Foster, K. M. Grant, G. Marino, A. P. Roberts, M. E. Tamisiea, F. Williams, Sea-level and deep-sea-temperature variability over the past 5.3 million years. *Nature* 508, 477–482 (2014). doi:10.1038/nature13230 Medline
- H. Elderfield, P. Ferretti, M. Greaves, S. Crowhurst, I. N. McCave, D. Hodell, A. M. Piotrowski, Evolution of ocean temperature and ice volume through the mid-Pleistocene climate transition. *Science* 337, 704–709 (2012). <u>doi:10.1126/science.1221294</u> <u>Medline</u>
- N. Serra, I. Ambar, D. Boutov, Surface expression of Mediterranean Water dipoles and their contribution to the shelf/slope-open ocean exchange. *Ocean Sci.* 6, 191–209 (2010). doi:10.5194/os-6-191-2010
- N. Khélifi, M. Sarnthein, N. Andersen, T. Blanz, M. Frank, D. Garbe-Schonberg, B. A. Haley, R. Stumpf, M. Weinelt, A major and long-term Pliocene intensification of the Mediterranean outflow, 3.5-3.3 Ma ago. *Geology* 37, 811–814 (2009). doi:10.1130/G30058A.1
- 13. N. Zitellini, E. Gràcia, L. Matias, P. Terrinha, M. A. Abreu, G. DeAlteriis, J. P. Henriet, J. J. Dañobeitia, D. G. Masson, T. Mulder, The quest for the Africa-Eurasia plate boundary west of the Strait of Gibraltar. *Earth Planet. Sci. Lett.* 280, 13–50 (2009). doi:10.1016/j.epsl.2008.12.005
- 14. J. Duarte, F. M. Rosas, P. Terrinha, M.-A. Gutscher, J. Malavieille, S. Silva, L. Matias, Thrust-wrench interference tectonics in the Gulf of Cádiz (Africa-Iberia plate boundary in the North-East Atlantic): Insights from analog models. *Mar. Geol.* 289, 135–149 (2011). doi:10.1016/j.margeo.2011.09.014
- 15. T. Medialdea, R. Vegas, L. Somoza, J. T. Vázquez, A. Maldonado, V. Díaz-del-Río, A. Maestro, D. Córdoba, M. C. Fernández-Puga, Structure and evolution of the "Olistostrome" complex of the Gibraltar Arc in the Gulf of Cádiz (eastern Central Atlantic): Evidence from two long seismic cross-sections. *Mar. Geol.* 209, 173–198 (2004). doi:10.1016/j.margeo.2004.05.029
- 16. M.-A. Gutscher, J. Malod, J.-P. Rehault, I. Contrucci, F. Klingelhoefer, L. Mendes-Victor, W. Spakman, Evidence for active subduction beneath Gibraltar. *Geology* 30, 1071–1074 (2002). doi:10.1130/0091-7613(2002)030<1071:EFASBG>2.0.CO;2

- 17. E. Llave *et al.*, in *Economic and Paleoceanographic Importance of Contourites*, A. Viana,
 M. Rebesco, Eds. (Geological Society of London Special Publication, 2007), vol. 276,
 pp. 49–79.
- M. Esteras *et al.*, Evolución morfológica y estratigráfica plio-cuaternaria del Umbral de Camarinal (Estrecho de Gibraltar) basada en sondeos marinos. *Rev. Soc. Geol. Esp.* 13, 539–550 (2000).
- R. A. Brackenridge, F. J. Hernández-Molina, D. A. V. Stow, E. Llave, A Pliocene mixed contourite-turbidite system offshore the Algarve Margin, Gulf of Cádiz: Seismic response, margin evolution and reservoir implications. *Mar. Pet. Geol.* 46, 36–50 (2013). doi:10.1016/j.marpetgeo.2013.05.015
- 20. C. Roque, H. Duarte, P. Terrinha, V. Valadares, J. Noiva, M. Cachão, J. Ferreira, P. Legoinha, N. Zitellini, Pliocene and Quaternary depositional model of the Algarve margin contourite drifts (Gulf of Cádiz, SW Iberia): Seismic architecture, tectonic control and paleoceanographic insights. *Mar. Geol.* **303–306**, 42–62 (2012). doi:10.1016/j.margeo.2011.11.001
- J. F. Flinch, P. R. Vail, in *Mesozoic and Cenozoic Sequence Stratigraphy of European Basins, SEPM Special Publication Series no. 60*, P. C. de Graciansky, J. Hardenbol, T. Jacquin, P. R. Vail, Eds. (Society for Sedimentary Geology, Tulsa, OK, 1998), pp. 199– 208.
- 22. P. Martínez-García, M. Comas, J. I. Soto, L. Lonergan, A. B. Watts, Strike-slip tectonics and basin inversion in the Western Mediterranean: The Post-Messinian evolution of the Alboran Sea. *Basin Res.* 25, 361–387 (2013). <u>doi:10.1111/bre.12005</u>
- 23. F. J. Hernández-Molina, E. Llave, B. Preu, G. Ercilla, A. Fontan, M. Bruno, N. Serra, J. J. Gomiz, R. E. Brackenridge, F. J. Sierro, D. A. V. Stow, M. Garcia, C. Juan, N. Sandoval, A. Arnaiz, Contourite processes associated with the Mediterranean Outflow Water after its exit from the Strait of Gibraltar: Global and conceptual implications. *Geology* 42, 227–230 (2014). doi:10.1130/G35083.1
- R. Stein *et al.*, in *North Atlantic Paleoceanography*, C. P. Summerhayes, N. J. Shackleton, Eds. (Geological Society, London, 1986), pp. 103–118.

- K. Billups, A. C. Ravelo, J. C. Zachos, Early Pliocene deep water circulation in the western equatorial Atlantic: Implications for high-latitude climate change. *Paleoceanography* 13, 84–95 (1998). doi:10.1029/97PA02995
- 26. M. T. Ledbetter, D. O. U. G. L. A. S. F. Williams, B. R. O. O. K. S. B. Ellwood, Late Pliocene climate and south-west Atlantic abyssal circulation. *Nature* 272, 237–239 (1978). <u>doi:10.1038/272237a0</u>
- 27. J. Zachos, M. Pagani, L. Sloan, E. Thomas, K. Billups, Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292, 686–693 (2001). <u>doi:10.1126/science.1059412</u> <u>Medline</u>
- 28. K. G. Miller, G. Mountain, J. Wright, J. Browning, A 180-million-year record of sea level and ice volume variations from continental margin and deep-sea isotopic records. *Oceanography* 24, 40–53 (2011). <u>doi:10.5670/oceanog.2011.26</u>
- 29. G. S. Dwyer, T. M. Cronin, P. A. Baker, M. E. Raymo, J. S. Buzas, T. Corrège, North Atlantic Deepwater temperature change during late Pliocene and Late Quaternary climatic cycles. *Science* 270, 1347–1351 (1995). doi:10.1126/science.270.5240.1347
- 30. M. Rogerson, G. R. Bigg, E. J. Rohling, J. Ramirez, Vertical density gradient in the eastern North Atlantic during the last 30,000 years. *Clim. Dyn.* **39**, 589–598 (2012). doi:10.1007/s00382-011-1148-4
- 31. S. Cloetingh, F. M. Gradstein, H. Kooi, A. C. Grant, M. Kaminski, Plate reorganization: A cause of rapid late Neogene subsidence and sedimentation around the North Atlantic? J. *Geol. Soc. London* 147, 495–506 (1990). doi:10.1144/gsjgs.147.3.0495
- 32. N. White, B. Lovell, Measuring the pulse of a plume with the sedimentary record. *Nature* 387, 888–891 (1997). doi:10.1038/43151
- 33. P. E. Potter, P. Szatmari, Global Miocene tectonics and the modern world. *Earth Sci. Rev.* 96, 279–295 (2009). doi:10.1016/j.earscirev.2009.07.003
- 34. P. B. deMenocal, Climate and human evolution. *Science* 331, 540–542 (2011).
 doi:10.1126/science.1190683 Medline

- 35. E. Llave, F. J. Hernández-Molina, L. Somoza, V. Díaz-del-Río, D. A. V. Stow, A. Maestro, J. M. Alveirinho Dias, Seismic stacking pattern of the Faro-Albufeira contourite system (Gulf of Cádiz): A Quaternary record of paleoceanographic and tectonic influences. *Mar. Geophys. Res.* 22, 487–508 (2001). doi:10.1023/A:1016355801344
- 36. F. J. Hernández-Molina, E. Llave, D. A. V. Stow, M. García, L. Somoza, J. T. Vázquez, F. J. Lobo, A. Maestro, V. Díaz del Río, R. León, T. Medialdea, J. Gardner, The contourite depositional system of the Gulf of Cádiz: A sedimentary model related to the bottom current activity of the Mediterranean Outflow Water and its interaction with the continental margin. *Deep Sea Res. II* 53, 1420–1463 (2006). doi:10.1016/j.dsr2.2006.04.016
- 37. E. Llave, H. Matias, F. J. Hernández-Molina, G. Ercilla, D. A. V. Stow, T. Medialdea, Pliocene-Quaternary contourites along the northern Gulf of Cádiz margin: Sedimentary stacking pattern and regional distribution. *Geo-Mar. Lett.* **31**, 377–390 (2011). <u>doi:10.1007/s00367-011-0241-3</u>
- 38. D. A. V. Stow et al., Proc. IODP 339 (2013).
- 39. J. A. Flores, E. Colmenero-Hidalgo, A. E. Mejía-Molina, K.-H. Baumann, J. Henderiks, K. Larsson, C. N. Prabhu, F. J. Sierro, T. Rodrigues, Distribution of large Emiliania huxleyi in the central and northeast Atlantic as a tracer of surface ocean dynamics during the last 25,000 years. *Mar. Micropaleontol.* **76**, 53–66 (2010). doi:10.1016/j.marmicro.2010.05.001
- 40. B. W. Hayward, Late Pliocene to middle Pleistocene extinctions of deep-sea benthic foraminifera ("Stilostomella extinction") in the southwest Pacific. *J. Foraminiferal Res.* 32, 274–307 (2002). doi:10.2113/32.3.274
- 41. F. J. Hilgen, Extension of the astronomically calibrated (polarity) time scale to the Miocene/Pliocene boundary. *Earth Planet. Sci. Lett.* 107, 349–368 (1991).
 doi:10.1016/0012-821X(91)90082-S
- 42. S. Kawagata, B. W. Hayward, H. R. Grenfell, A. Sabaa, Mid-Pleistocene extinction of deep-sea foraminifera in the North Atlantic Gateway (ODP Sites 980 and 982). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 221, 267–291 (2005). doi:10.1016/j.palaeo.2005.03.001

- 43. L. Lourens *et al.*, The Neogene period. In *A Geologic Time Scale 2004*, F. M. Gradstein, J. G. Ogg, A. Smith, Eds. (Cambridge Univ. Press, Cambridge, 2004), pp. 409–440.
- 44. P. Maiorano, M. Marino, Calcareous nannofossil bioevents and environmental control on temporal and spatial patterns at the early–middle Pleistocene. *Mar. Micropaleontol.* 53, 405–422 (2004). doi:10.1016/j.marmicro.2004.08.003
- 45. I. Raffi *et al.*, A review of calcareous nannofossil astrobiochronology encompassing the past 25 million years. *Quat. Sci. Rev.* **25**, 3113–3137 (2004).
- 46. P. P. E. Weaver, B. M. Clement, Magnetobiostratigraphy of planktonic foraminiferal datums: Deep Sea Drilling Project Leg 94, North Atlantic. *Init. Repts. DSDP 94* (1987), pp. 815–829.
- 47. W. J. Zachariasse, J. D. A. Zijderveld, C. G. Langereis, F. J. Hilgen, P. J. J. M. Verhallen, 1989. Early late Pliocene biochronology and surface water temperature variations in the Mediterranean. *Mar. Micropaleontol.* 14, 339–355 (1989). doi:10.1016/0377-8398(89)90018-2
- 48. W. Krauss, E. Fahrbach, A. Aitsam, J. Elken, P. Koske, The North Atlantic Current and its associated eddy field southeast of Flemish Cap. *Deep Sea Res.* 34, 1163–1185 (1987). doi:10.1016/0198-0149(87)90070-7
- 49. J.-C. Faugères, M. L. Mézerais, D. A. V. Stow, Contourite drift types and their distribution in the North and South Atlantic Ocean basins. *Sediment. Geol.* 82, 189–203 (1993).
 <u>doi:10.1016/0037-0738(93)90121-K</u>
- 50. M. C. Iorga, M. S. Lozier, Signatures of the Mediterranean outflow from a North Atlantic climatology 1. Salinity and density fields. J. Geophys. Res. 104, 25985–26009 (1999). <u>doi:10.1029/1999JC900115</u>
- R. S. Pickart, T. K. McKee, D. J. Torres, S. A. Harrington, Mean structure and interannual variability of the slopewater System south of Newfoundland. *J. Phys. Oceanogr.* 29, 2541–2558 (1999). doi:10.1175/1520-0485(1999)029<2541:MSAIVO>2.0.CO;2
- 52. E. B. Colbourne, K. D. Foote, Variability of stratification and circulation on the Flemish Cap during the decades of the 1950s-1990s. J. Northw. Atla. Fish. Sci. 26, 103–122 (2000). doi:10.2960/J.v26.a5

- 53. K. Lavander *et al.*, Mid-depth recirculation observed in the Labrador and Irminger seas by direct velocity measurements. *Nature* **407**, 66–68 (2000).
- 54. M. Rhein, Drifters reveal deep circulation. *Nature* **407**, 30–31 (2000). <u>doi:10.1038/35024186</u> <u>Medline</u>
- 55. I. Yashayaev, 12 year hydrographic survey of the Newfoundland Basin: Seasonal cycle and interannual variability of water masses. *ICES CM 2000* (2000).
- 56. I. Yashayaev, A. Clarke, Evolution of North Atlantic water masses inferred from Labrador Sea salinity series. *Oceanography* 21, 30–45 (2008). <u>doi:10.5670/oceanog.2008.65</u>
- 57. J. Gil *et al.*, Geostrophic circulation and heat flux across the Flemish Cap, 1988-2000. J. Northw. Atl. Fish. Sci. 34, 61–81 (2008).
- 58. M. E. Raymo *et al.*, Stability of North Atlantic Water masses in face of pronounced climate variability during the Pleistocene. *Paleoceanography* **19**, PA2008 (2004). <u>doi:10.1029/2003PA000921</u>
- 59. J. Mackie, thesis, Dalhousie University (2005).
- 60. M. Stein, Oceanography of the Flemish Cap and adjacent waters. J. Northw. Atl. Fish. Sci.
 37, 135–146 (2007). doi:10.2960/J.v37.m652
- 61. F. F. Pérez, H. Mercier, M. Vázquez-Rodríguez, P. Lherminier, A. Velo, P. C. Pardo, G. Rosón, A. F. Ríos, Atlantic Ocean CO₂ uptake reduced by weakening of the meridional overturning circulation. *Nat. Geosci.* 6, 146–152 (2013). <u>doi:10.1038/ngeo1680</u>