response to the change in plate motion that occurred after chron 3a (Fig. 4).

The Le Géographe and L'Astronome TFs survived the changes in plate motion and apparently only evolved into WFZs, probably because the initial offset was too large to allow the transition from FZ to GOSC. Instead, they may have followed one of the alternative models described in (15). On the other hand, the traces of two FZs (respectively named FZ A and Antipodes FZ) are interrupted at the boundary of the large V, south of the Udintsev FZ. At their intersection with the ridge axis, OSCs are present, respectively, near 60°11'S, 152°15'W and near 58°23'S, 148°40'W. The transitions from TFs to OSCs occurred between chrons 6c and 5d for FZ A, and between chrons 4a and 3a for Antipodes FZ, coincidentally with changes in plate motions.

The proximity of the Euler poles of rotation of the Pacific and the Antarctic plates and the fact that the spreading rate is close to the threshold value over most of the ridge length amplify the effects of the changes in plate motions. The increase in spreading rate and the clockwise change in the direction of the Pacific-Antarctic relative motion since 6 Ma have had three main consequences: (i) the axial morphology has changed from a rift valley to an axial high, (ii) rift propagation was triggered, and (iii) axial geometry has been rearranged, with the linkage of ridge segments and transitions from FZs to OSCs. Extrapolation of shipboard data interpretations suggests that this scheme has persisted over the last 30 to 35 My and explains most of the large V-shaped structure. This V, which initiated south of the Udintsev FZ shortly after chron 130 (33.5 Ma), results from a change in axial morphology that propagated southward. Its boundaries are the fossil traces of pseudofaults related to ancient PRs (such as on the Antarctic plate near 59°20'S, 132°W, near 61°S, 141°W, and near 61°30'S, 146°20'W), or the fossil traces left on the sea floor by numerous transitions from FZ to giant OSC.

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# Inner Core Rotation Rate from Small-Scale Heterogeneity and Time-Varying Travel Times

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The time it takes seismic waves to propagate from South Atlantic earthquakes through the inner core to station COL in Alaska has decreased systematically over the past 30 years. Travel times from three earthquakes in 1991 to an array of 37 seismometers in Alaska suggest that lateral gradients in seismic wavespeeds are steep in this part of the inner core. This combination of observations can be explained by postulating that the inner core is rotating 0.2° to 0.3° per year faster than the mantle.

Numerical modeling of fluid flow in Earth's outer core has produced realistic models for the geodynamo that generates Earth's magnetic field (1-4). Rotation of the inner core should be coupled by magnetic Lorentz forces to fluid flow near the base of the outer core which, in some calculations, is consistently faster than the rotation rate of the mantle (2, 3) and in others fluctuates between faster and slower (4). Systematic variations in the travel times of seismic waves through the inner core during the past 30 years have led some seismologists to conclude that the inner core is rotating faster than the mantle by 1° per year (5) to 3° per year (6). On the other hand, gravitational coupling between small aspherical variations in the topography of the inner core and in the density structure of the mantle are thought to prevent differential rotation between the inner core and

mantle unless the inner core can deform its large-scale shape on time scales of years. To reconcile these fast differential rotation rates with gravitational coupling seems to require that the viscosity of the inner core is less than  $3 \times 10^{16}$  Pa s (7, 8).

The primary evidence that the inner core is rotating at a different rate than the mantle comes from careful observations by Song and Richards (5) of differential traveltime residuals between the phases  $P'_{BC}$  and  $P'_{DF}$ . The  $P'_{DF}$  (or  $PKP_{DF}$ ) ray goes through the solid inner core, while the P'BC ray traverses nearly the same path throughout the mantle, but turns near the base of the fluid outer core. As a result, the difference in travel times for these two rays is sensitive to the structure of the inner core but is much less sensitive to structure in the crust and mantle. Song and Richards found that the differential time residuals observed at station COL in Alaska from earthquakes near the South Sandwich Islands increase systematically by about 0.3 s as a function of

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**Fig. 1.** (A) Observed  $P'_{BC} - P'_{DF}$  travel-time residuals and (B) percent residuals normalized by total travel time through the inner core for station COL in Fairbanks, Alaska, as a function of event date. Epicentral distance (in degrees) of each observation is shown by symbol type in the key. SEM is shown

as bars for four time bins separated by the years 1973, 1980, and 1987. Predictions from model 1 (Table 1 and Eqs. 1 through 3) are shown as solid lines. They are calculated at the mean epicentral distance of the data (150.7°).

the earthquake dates during the past 30 years. Apparently, something has changed along the ray paths of either P'BC or P'DF during this time interval. The most likely cause for time-varying changes in structure within Earth is that the inner core is rotating with respect to the mantle and that the elastic structure of the inner core is not axi-symmetric. Indeed, the inner core appears to be strongly anisotropic with a symmetry axis that is close to, but not exactly parallel to, the spin axis (5, 6, 9, 10). Alternatively, the inner core may be laterally heterogeneous (11-13). Either type of structure would cause travel times from a source-region to a station to vary as a function of earthquake date if the inner core is rotating with respect to the mantle. Song and Richards (5) estimated the rotation rate of the inner core from the observations at COL and an inner core model that is homogeneous and anisotropic with a symmetry axis that is tilted with respect to the spin axis. Here, I analyze 51 P'<sub>BC</sub>-P'<sub>DF</sub> times recorded at 37 stations of the Alaska Seismic Network (ASN) and find that this part of the inner core exhibits steep lateral gradients in wavespeeds, such that small values of differential rotation rates explain the observations at COL.

I analyzed data from station COL in Fairbanks, Alaska, that were recorded between 1967 and 1996. This station was upgraded from short-period analog to shortperiod digital in January 1982, to broadband in February 1987, and then to a higherquality broadband station in March 1991. The instrument responses for these seismometers are known. I deconvolved the known instrument responses and reconvolved in a standard DWWSSN (Digital World-Wide Standardized Seismograph Network) short-period response so that the seismograms appear as if they all came from the same seismometer. This response is peaked at a period of 1 s. I also analyzed seismograms recorded at the ASN for three earthquakes on 15 June and 27 and 28 December 1991, a period spanning only 6 months. Instrument responses for these stations are not as well calibrated as COL. I deconvolved the response of an L4 seismometer and reconvolved with the standard DWWSSN response. The amplitude responses of the ASN seismometers are similar to one another in the pass band of the DWWSSN seismometer, so the errors associated with inexact knowledge of the responses are expected to cause differential travel-time errors less than 0.1 s. The  $P'_{DF}$ and P'BC phases were windowed by hand and cross-correlated to obtain accurate differential travel times with picking uncertainties of 0.1 s (14). Only unambiguous seismograms were analyzed, so it is unlikely that there are any cycle-skipping problems, which would produce errors on the order of 1 s. Travel-time residuals were calculated from the observed differential times, using earthquake locations from Engdahl and others (15), the radial earth model AK135 (16), and ellipticity corrections (17).

My observations at COL confirm those of Song and Richards (5) that the residuals increase at a rate of nearly 0.1 s per decade during the past 30 years (Fig. 1). The linear correlation coefficient between the 36 event dates and the observed residuals is 0.61. Given this observed correlation, the null hypothesis that there is no correlation between event date and travel-time residual can be rejected with 99.98% confidence (18). Souriau and others (19) propose that a correlation between body-wave magnitude and travel-time residuals provide an

Fig. 2. (A) Vertical cross section AB showing innercore ray turning depths and location along the section (no vertical exaggeration) and (B) map view of ray turning points. Rays are nearly parallel to one another and perpendicular to the section. They sample a volume 500 km horizontally, 50 km vertically, and 1400 km along the ray paths. Symbols represent P'BC-P'DF travel-time residuals normalized by the time through the inner core  $(\delta t_i^{obs}/\tau_i) \times 100\%$ . Observations vary from 1.8 to 2.8%, circles are less than 2.4% and plusses (+)and crosses (×) are great-



er than 2.4%. Observations at COL are white in (A) and crosses in (B). Other symbols are ASN stations. Contours indicate percent velocity anomaly averaged along paths perpendicular to cross section AB as given by the parameters in model 1 (Table 1).

alternative explanation for the COL data (5). On the other hand, the correlations between my normalized residuals and bodywave magnitude, epicentral distance, or back azimuth from the station are weak. The null hypothesis that they are not correlated can be rejected with only 33, 88, and 23% confidence, respectively.

Each of the 87 rays to COL and the ASN exhibit large positive  $P'_{BC} - P'_{DF}$  residuals, varying from 2.2 to 3.5 s. These early  $P'_{DF}$ times correspond to ray paths in the inner core that are close to being parallel to Earth's spin axis and have been attributed to inner core anisotropy [for example (9)]. Standard radial earth models such as AK135 (16) predict that each ray follows a nearly straight path through the inner core, bending by only about 1°. Each of the rays analyzed here are nearly parallel to one another. The median ray path direction through the inner core is 26.4°N, 179.6°E. The root-mean-square (rms) variation of ray path directions with respect to this direction is only 1°. Thus, their inner core sampling can be visualized by a map view of turning points and by the cross section AB through the inner core that is perpendicular to the rays (Fig. 2). These rays sampled a region of the inner core that varies by 24° in longitude (500 km horizon-tally) and 2° in epicentral distance (150° to 152.1°; 50 km variation in ray turning radius), whereas the path lengths within the inner core vary from 1300 to 1440 km. I parametrized each path by its epicentral distance  $\Delta_i$  and the azimuth  $\xi_i$  of the turning point relative to a reference source location (56°S, 27°W) at the mean position of the earthquakes. This angle parametrizes distance along the cross section ranging from 295° to 325° at points A and B, respectively (Fig. 2). I consider a model of the following form

$$\begin{split} \delta t_i^{\text{obs}} &= \delta t_i^{\text{BC}} - \delta t_i^{\text{DF}} = -\delta t_i^{\text{IC}} + \delta t_{\text{mantle}} \beta_i \\ &+ \delta t_{\text{COL}} \delta_i \quad \{i = 1 \dots N\} \end{split}$$

where N is the number of observations and  $\delta t_i^{obs}$  are the observed  $P'_{BC} - P'_{DF}$  differential travel-time residuals.  $\delta t_i^{obs}$  is interpreted in terms of contributions from the inner core ( $\delta t_i^{IC}$ , whose sign is negative because it depends on the  $P'_{DF}$  branch of the differential time) and two small corrections for the aspherical structure beneath Alaska:  $\delta t_{mantle}$  and  $\delta t_{COL}$ .  $\beta_i$  is 1 for stations within 120 km of COL and 0 otherwise, and  $\delta_i$  is 1 for station COL and 0 otherwise. The inner core contribution is parametrized by

$$-\delta t^{\rm IC} = \int_{\rm IC} \frac{\Delta v}{v_0} dt = \delta \nu(\xi, \Delta) \int_{\rm IC} dt$$
$$= \delta \nu(\xi, \Delta) \tau \qquad (2$$

where  $\Delta v$  is a three-dimensional perturbation of the anisotropic compressional wave speed to  $v_0$ , the reference model AK135. The integrals are over travel time (dt) along the inner core ray paths,  $\tau$  is the theoretical total travel time through the inner core, and  $\delta\nu(\xi,\Delta)$  is the dimensionless fractional velocity anomaly averaged along ray paths through the inner core. Because inner-core ray paths are nearly straight and parallel, the complex three-dimensional variations in anisotropic velocity structure of the inner core can be parametrized as variations with respect to  $\xi$  and  $\Delta$ , which describe ray position in cross section AB (Fig. 2). I expanded  $\delta \nu$  in a first-order Taylor Series with respect to distance and azimuth

$$\begin{split} \delta\nu(\xi,\Delta) &= \delta\nu_0 + \partial\nu/\partial\xi \ (\xi - \xi_0 \\ &- \alpha\gamma T_i) + \partial\nu/\partial\Delta \ (\Delta - \Delta_0) \end{split} \tag{3}$$

 $T_i$  is the earthquake origin time in years since a reference date of 1991.8,  $\xi_0$  and  $\Delta_0$ are reference values of 311° and 151°, and  $\gamma$ = 1.1 is a dimensionless factor relating the change in distance  $\xi$  along AB to change in longitude, which is directly related to innercore rotation (Fig. 2). There are four free parameters:  $\alpha$  (degrees per year) is the relative rotation rate of the inner core with respect to the mantle, and  $\delta \nu_0$ ,  $\partial \nu/\partial \xi$ , and  $\partial \nu/\partial \Delta$  describe the velocity anomalies of this small part of the inner core. The first parameter is dimensionless, and the other two have dimensions of 1 per degree.

In contrast to the small but consistent temporal variations of 0.2 to 0.3 s at COL,  $P'_{BC} - P'_{DF}$  times observed at the ASN stations from three South Sandwich Island events vary systematically by 1 s. This signal is most plausibly explained by smallscale heterogeneity within the inner core, most likely lateral variations in the degree or direction of crystal alignment (Figs. 2 and 3). Normalized residuals (Figs. 1B, 2, 3, and 4B), defined as differential times divided by the predicted total time through the inner core  $(\delta t_i^{obs}/\tau_i) \times 100\%$ , have been analyzed for two reasons. First, there is a significant increase in the observed residuals with increasing epicentral distance, which is reduced in the normalized residuals. Second, the dimensionless normalized times should equal the dimensionless model  $\delta \nu(\xi, \Delta) \times 100\%$ . Normalized residuals, superimposed on model 1 (Table 1), determined from ASN data only assuming  $\delta t_{mantle} = 0$  show a systematic decrease with increasing azimuth at a rate of  $-0.019 \pm 0.003\%$  per degree, which amounts to 0.5% over the 27° range of azimuths sampled (Figs. 2A and 3A). The uncertainty is optimistic because it assumes uncorrelated uncertainties in



**Fig. 3.** (A) Observed  $P'_{BC} - P'_{DF}$  residuals normalized by time through the inner core versus azimuth ( $\xi$  measured along cross section AB of Fig. 2). Solid line is model 1 evaluated at an epicentral distance of 150.7°. (B) Same as (A)

except times are corrected for  $\delta t_{mantle}$  (all circles) and  $\delta t_{COL}$  (open circles) before normalization, data are shifted in  $\xi$  to account for a rotation rate of 0.21° per year using the parameters in model 2 (Table 1), and solid line is model 2.

each observation of 0.15 s, which overestimates picking errors, but may underestimate unmodeled mantle heterogeneity that would produce correlated errors. The equivalent total radial variation is only 0.15%. This steep horizontal variation is of importance in determining the rate of rotation. The mean time through the inner core is 125 s, so the variation across the 24° of longitude sampled here (Fig. 2B) is 0.5% of 125 s = 0.6 s. A variation in the times at COL of 0.2 s per 30 years (Fig. 1) translates to (0.2 s per 30 years)/ (0.6 s per 24°) equals 0.3° per year. To quantify this rate, I used the three parameters of model 1 describing the velocity heterogeneity of the inner core, still assuming  $\delta t_{mantle} = 0$ , and combined Eqs. 1 through 3 to invert the COL data only for  $\alpha$  and  $\delta t_{\rm COL}.$  The best-fitting rotation rate is 0.31° per year, and  $\delta t_{COL} = 0.33$  s (Fig. 1, A and B).

In principle, the parameter  $\delta t_{COL}$  would not be needed, but the COL data are about 0.3 s above the line describing the model from the ASN data (Fig. 3A). To track down the source of this discrepancy, I picked the  $P'_{BC}$  times for the ASN data (Fig. 4A). Note that the stations within 1° of COL (Fig. 4A; inside dashed circle) consistently exhibit negative residuals, suggesting a fast anomaly along paths to these stations. If the slab descending beneath Alaska turns to a near vertical dip beneath the deepest seismicity ( $\sim 100$  km in this region) then rays to stations near COL would come up through the slab (Fig. 4A). For stations within about 1° of COL, the  $\mathbb{P'}_{BC}$  times are consistently early by about 1 s, but  $P'_{BC} - P'_{DF}$  are anomalously large by 0.3 s, so the  $P'_{DF}$  would be early by 1.3 s. If the descending slab is causing  $P'_{BC}$  to be early, it is causing  $P'_{DF}$  to be even earlier, consistent with a steeply dipping slab. Indeed, stations near COL (Fig. 3A; filled circles) also exhibit anomalously large  $P'_{BC} - P'_{DF}$  observations. Because the absolute  $P'_{BC}$  and the differential-time anomalies appear to correlate with the station locations, they probably have a common cause that is related to aspherical mantle structure on the receiver side of the paths, possibly, but not necessarily related to the subducting slab.

A second model is constructed assuming that whatever is affecting COL is also affecting the surrounding stations. I inverted the ASN data only for  $\delta t_{mantle}$  and the three parameters describing  $\delta v$  to construct model 2 (Table 1). The correction most consistent with the ASN data is  $\delta t_{mantle} = 0.20$  s, and the estimated horizontal gradient in inner-core velocity anomalies increases by 50% over model 1. I then inverted the COL data only for  $\alpha$  and  $\delta t_{COL}$  and obtained values of 0.21° per year and 0.16 s. The rotation rate in model 2 is smaller than that of model 1, because the estimated horizontal velocity gradients are steeper (Fig. 3B).

How confident are we that the inner core is rotating slightly faster than the mantle? First, this result depends on the observation that differential times at COL increase systematically with event date. This appears to be a robust inference based on my results and those of Song and Richards (5). Secondly, the ASN data showed a much larger signal of 0.6 s (model 1) to 0.9 s (model 2) of system-



**Fig. 4.** Map views of Alaska showing station locations (circles and pluses), contours of the subducting slab at depths of 50, 100, and 150 km (heavy lines), a dashed circle 1° from COL, and a dotted line showing points that are equidistant from the source region. (**A**)  $P'_{BC}$  residuals averaged at each station. Residuals were determined by cross-correlating the  $P'_{BC}$  phases at each station and removing the mean residual for each event. Circles are negative, plusses are positive, and largest circles represent residuals of about 1 s. End points of bars represent location of points where the  $P'_{BC}$  and  $P'_{DF}$  rays intersect 660-km depth. Thick bars correspond to stations near COL. (**B**) Normalized  $P'_{BC} - P'_{DF}$  residuals averaged at each station. All residuals are strongly positive. Circles are less than 2.4%, plusses are greater than 2.4%, and total range is 1.8 to 2.8%.

atic variation with respect to horizontal sampling location of the inner core. The variation of the 87 travel-time residuals with respect to ray path direction is such that rays more nearly parallel to the spin axis [or closest to the "fast axis" estimated in previous studies (5, 9, 10, 20)] correspond to systematically smaller residuals, whereas all these studies predict the opposite variation. Correcting for this effect would increase the horizontal gradients slightly, and decrease the estimated rotation rates. The primary source of uncertainty is separating the effects of inner core heterogeneity from mantle heterogeneity in the ASN data. The standard deviation of 158 highest quality, globally distributed, hand-picked  $P'_{BC} - P'_{DF}$  times (21) in the same epicentral distance range analyzed here is 0.24 s after correction for a three-parameter model of large-scale inner core heterogeneity. This places an upper bound on average contributions from source mislocations and the mantle (including the D" region). Furthermore, given the complexity of inner core structure inferred here, much of the 0.24 s signal from the globally distributed data is probably due to the inner core. Thus, the systematic 0.6 to 0.9 s variation in times across the ASN is more likely caused by the inner core than by the mantle.

Given that the travel-times change systematically by 0.6 to 0.9 s across the ASN, but only 0.2 to 0.3 s as a function of time for station COL, 0.3° per year is an upper bound on the rotation rate for the inner core relative to the mantle. If the inner core is rotating faster, a larger signal at COL should be observed. On the other hand, a lower bound is less certain. This is because the inner core may contain lateral velocity gradients over small scales that are locally much steeper than the mean gradient over the 500-km region I sample. Each observed travel time is sensitive to

**Table 1.** First three parameters, and their 65% confidence intervals, describe the perturbation of velocities in the inner core from a spherical model (Eq. 3).  $\delta v_0$  is dimensionless, and the other two parameters have units of 1 per degree.  $\alpha$  is the inner-core rotation rate with respect to the mantle (in degrees/year).  $\delta t_{mantle}$  and  $\delta t_{COL}$  (in seconds) are corrections for aspherical structure under Alaska (Eq. 1).

Parameter	Model 1	Model 2
$ \begin{array}{c} \delta \nu_0 \\ \partial \nu / \partial \xi \\ \partial \nu / \partial \Delta \\ \alpha \\ \delta \alpha t_{mantle} \\ \delta t_{COL} \end{array} $	0.0239* -0.00019† 0.00070‡ 0.31 0 0.33	0.0236* -0.00027† -0.00016‡ 0.21 0.20 0.16

The 65% confidence intervals are: \*, 0.0002; †, 0.00003; and ‡, 0.00035.

structure within a volume along the ray path whose Fresnel width (22) for 1-Hz  $P'_{DF}$  rays in the inner core is about 150 km. Lateral variations at much smaller scales will be smeared by the physical propagation of the waves. My observations exhibit considerable coherence on length scales up to 100 km, but variability at longer scales (Fig. 2A). The steepest lateral gradient that is admissible by the ASN data at 100-km length scales is 0.1% per degree (Fig. 3A; azimuths 310° to 317°). The rotation rate inferred from the COL observations and this gradient is 0.05° per year.

My preferred estimate is that the inner core currently rotates 0.2 to 0.3° per year faster than the mantle, but rates as low as 0.05° per year cannot be ruled out by the available data. The preferred values are 3 to 15 times smaller than, but in the same direction as, previous estimates (5, 6). This lower rotation rate raises Buffett's (8) estimate of the upper limit for inner core viscosity from  $3 \times 10^{16}$  to  $10^{17}$  Pa·s. The low inferred differential rotation rate is as much as 10 times slower than predicted from some dynamo calculations (3) and can be used to constrain parameters for future dynamo models.

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and from third to fourth is -0.01 s.

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## Regulation of Distinct Stages of Skeletal Muscle Differentiation by Mitogen-Activated Protein Kinases

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The signal transduction pathway or pathways linking extracellular signals to myogenesis are poorly defined. Upon mitogen withdrawal from C2C12 myoblasts, the mitogenactivated protein kinase (MAPK) p42Erk2 is inactivated concomitant with up-regulation of muscle-specific genes. Overexpression of MAPK phosphatase-1 (MKP-1) inhibited p42Erk2 activity and was sufficient to relieve the inhibitory effects of mitogens on muscle-specific gene expression. Later during myogenesis, endogenous expression of MKP-1 decreased. MKP-1 overexpression during differentiation prevented myotube formation despite appropriate expression of myosin heavy chain. This indicates that muscle-specific gene expression is necessary but not sufficient to commit differentiated myocytes to myotubes and suggests a function for the MAPKs during the early and late stages of skeletal muscle differentiation.

 $C_{2C12}$  myoblasts' proliferate in response to mitogens and upon mitogen withdrawal differentiate into multinucleated myotubes (1). Although much progress has been made in defining the mechanisms governing myogenesis at the transcriptional level (1, 2), the signal transduction pathways involved in myogenesis are poorly defined. Differentiation of C2C12 myoblasts is inhibited by serum, growth factors (3), oncogenic tyrosine kinases (4), and oncogenic forms of the small guanine nucleotide-binding protein Ras (5). These observations implicate the Ras pathway in relaying to the nucleus extracellular signals that repress myogenesis. One of the effector pathways of Ras leads to activation of MAPKs, which have been implicated directly in regulating proliferation and differentiation by phosphorylation of transcription factors in a variety of cellular systems (6, 7). However, the function of the MAPKs during skeletal muscle differentiation has not been elucidated.

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We induced C2C12 myoblasts to differentiate by transfer from growth medium (GM) to differentiation medium (DM) (8). Within 24 hours in DM, p42Erk2 activity (9) was reduced by 50%, whereas the activity of the related MAPK, c-Jun NH2-terminal kinase (JNK), remained unaffected (Fig. 1A). Concomitantly, expression of the skeletal musclespecific basic helix-loop-helix transcription factors MyoD and myogenin and the cell cycle inhibitor p21 (10) were increased, marking the onset of myogenesis and cell cycle withdrawal (Fig. 1B). By day 3, multinucleated myotubes had formed (11), correlating with expression of the terminal differentiation marker myosin heavy chain (MHC) (Fig. 1B). Between days 2 and 3 of differentiation, p42Erk2 activity remained low, whereas JNK activity increased by 1.8-fold (Fig. 1A). The amount of p42Erk2 and JNK proteins remained constant throughout differentiation (11).

These results suggest that inactivation of p42Erk2 might be required for C2C12 myoblasts to initiate myogenesis. If so, ectopic expression of a dual-specificity protein phosphatase with substrate specificity toward the MAPKs should facilitate myogenesis in the presence of mitogens. We sought to overex-

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