Neonatal postcrania from Mezmaiskaya, Russia, and Le Moustier, France, and the development of Neandertal body form

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Neandertal and modern human adults differ in skeletal features of the cranium and postcranium, and it is clear that many of the cranial differences—although not all of them—are already present at the time of birth. We know less, however, about the developmental origins of the postcranial differences. Here, we address this deficiency with morphometric analyses of the postcrania of the two most complete Neandertal neonates—Mezmaiskaya 1 (from Russia) and Le Moustier 2 (from France)—and a recent human sample. We find that neonatal Neandertals already appear to possess the wide body, long pubis, and robust long bones of adult Neandertals. Taken together, current evidence indicates that skeletal differences between Neandertals and modern humans are largely established by the time of birth.

body proportions | climatic adaptation | *Homo neanderthalensis* | infracranial | ontogeny

It is well established that Neandertal and modern human adults differ in skeletal features of the cranium and postcranium (1–7). Furthermore, it is clear from multiple morphometric studies of the cranium (8–13) that many of the differences in cranial form—although not all of them—are already present around the time of birth. However, there have been only a few morphometric analyses of postcranial form in Neandertals < 1 y of age (11, 14, 15), although we know more about Neandertal children ~2 y of age or older (16–20).

We would like to know if postcranial diversification followed a similar developmental path to cranial diversification. Additionally, knowing which Neandertal characteristics are present early in development has implications for determining whether postcranial differences between Neandertals and modern humans have evolutionary (e.g., genetic drift, natural selection) or lifetime behavioral (e.g., activity levels, gait patterns) causes (21). Newborn individuals are particularly important in this regard because their skeletons have been subject to only in utero mechanical loading, so it is not possible for their skeletons to have been influenced by locomotion or other habitual activities of adults or older subadults.

Here, we study the postcranial skeletons of the two most complete Neandertal neonates—Mezmaiskaya 1 (from Russia) and Le Moustier 2 (from France)—to quantify the extent to which Neandertal postcranial features are present around the time of birth. We base our analyses on 11 linear measurements (Table S1) of the Neandertals (Table S2) and a recent human sample of African Americans and European Americans (Tables S3 and S4).

Results

Adult European Americans and African Americans differ, on average, in body proportions, with European Americans having a wider trunk relative to limb length and relatively shorter distal limb segments (22, 23). These contrasts are much the same, although less extreme, as those between high- and low-latitude human groups (24, 25), and result from the geographic ancestries of European Americans and African Americans [Bergmann's (26) and Allen's (27) "rules"]. Similar proportional differences are already detectable in our fetal/infant sample (Fig. 1), which is consistent with other studies of subadult body proportions (28, 29). European Americans tend to have a wider and a longer ilium relative to femur length (Fig. 1 *A* and *B*), a shorter radius relative to humerus length (Fig. 1*C*), and a shorter tibia relative to femur length (Fig. 1*D*). Consistent with the "cold-adapted" body proportions of adult Neandertals (24, 30, 31), both Mezmaiskaya 1 and Le Moustier 2 have a very large ilium relative to femur length (Fig. 1 *A* and *B*), and Mezmaiskaya 1 has short distal-to-proximal limb lengths (Fig. 1 *C* and *D*; the results for tibia–femur proportions are less conclusive than for radius–humerus proportions because, although Mezmaiskaya 1 plots just below the European-American curve, the curves are minimally separated in this part of the graph). However, unexpectedly, Le Moustier 2 has a long radius relative to humerus length (Fig. 1*C*).

In our fetal/infant sample, African Americans and European Americans do not show a consistent difference across size (i.e., age) in how long the pubis is relative to the size of the ilium (Fig. 2), which is in line with the similarity between African- and European-American adults in ilium–pubis index (ratio of

Significance

One of the oldest questions in human evolutionary studies is: why do Neandertals look different from present-day and ancient modern humans? This question can be addressed at different levels, but a critical component of a complete answer is understanding the developmental basis of adult differences. We now know that many skull differences are present by the time of birth. We know less, however, about the developmental basis of differences in the rest of the body. By studying the two most complete Neandertal neonates, we were able to establish that, as for the skull, many differences in body form are present by the time of birth. Neandertals largely look like Neandertals, regardless of age.

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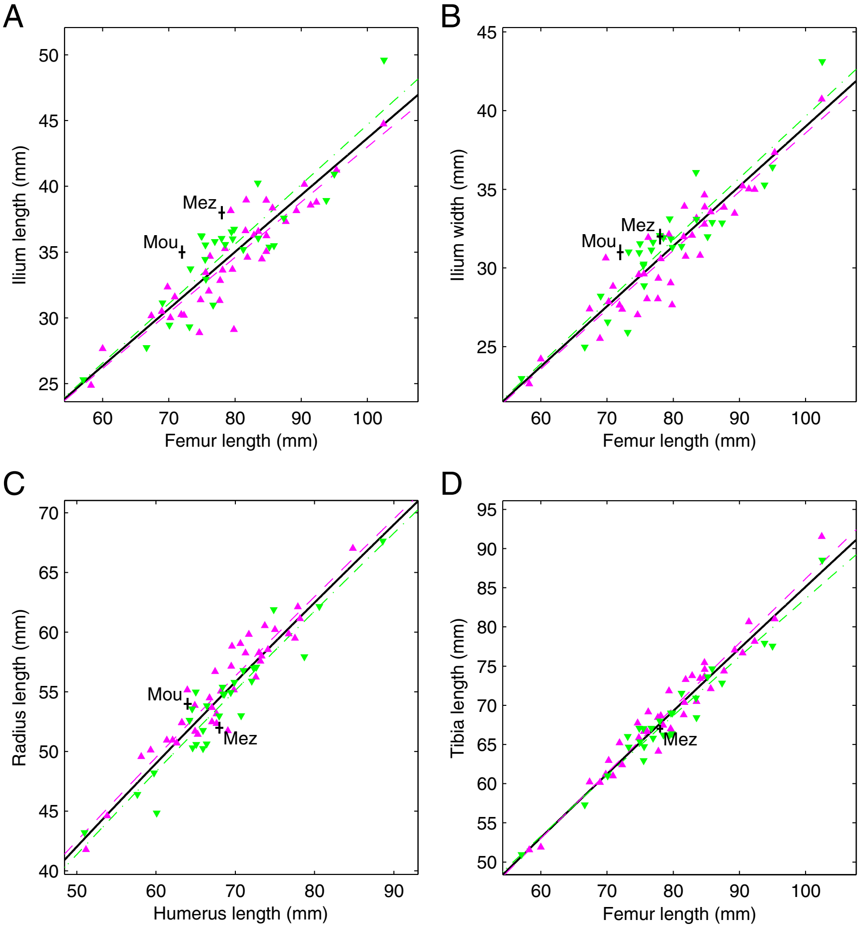

Fig. 1. Body proportions. (*A*) Ilium length vs. femur length; (*B*) ilium width vs. femur length; (*C*) radius length vs. humerus length; and (*D*) tibia length vs. femur length (Table S1 includes measurement descriptions). The purple triangles are recent African Americans, the green inverted triangles are recent European Americans, and the black plus signs are Neandertals (Mez, Mezmaiskaya 1; Mou, Le Moustier 2). The plus-sign horizontal and vertical dimensions are ±0.5 mm. The purple dashed curve is the relationship for the African Americans, the green dash-dot curve is the relationship for the European Americans, and the black solid curve is the relationship for all recent humans (Table S6 includes fit statistics).

distance between the anterior- and posterior-superior iliac spines to pubis length) (32). Adult Neandertals have a long pubis (33–35), and this characteristic is already present in Mezmaiskaya 1 (Fig. 2).

Adult European Americans and African Americans differ, on average, in the shapes of their long bones, with European Americans having thicker shafts and larger articulations relative to shaft length (23, 36). In dry-bone samples of young individuals, it is not possible to compare articulation size to shaft length, because the articulations are mostly or completely cartilaginous. However, it is possible to compare the diaphysis end (i.e., metaphysis) size, which should be related to articulation size, to diaphysis length. Our fetal/infant sample does not show a uniform contrast between European Americans and African Americans in end size to length (Fig. 3). For the humerus (Fig. 3*A*) and femur (Fig. 3*C*), African Americans tend to have larger ends relative to length; for the tibia (Fig. 3*D*), European Americans tend to have larger ends relative to length; and for the radius (Fig. 3*B*), there is no consistent difference across size (i.e., age) in end size relative to length. Adult Neandertals have thick shafts and large articulations relative to shaft length (36–38), and Mezmaiskaya 1 and Le Moustier 2 may anticipate this feature of adult Neandertals by having long bone diaphyses with very large ends relative to length (Fig. 3).

Principal components (PCs) of residuals from the all-recent-human regressions provide a multivariate synthesis of the bivariate analyses (Fig. 4). PC1 encompasses 37% of the variance, and it mainly reflects differences in ilium size relative to femur length and long bone diaphysis end to length dimensions; PC2 encompasses 23% of the variance, and it mainly reflects differences in distal to proximal limb lengths; and PC3 encompasses 19% of the variance, and it mainly reflects differences in pubis length relative to ilium size, ilium length relative to femur length, and radius length relative to humerus length (Table S5). Mezmaiskaya 1 has a highly positive score on PC1 (Fig. 4*A*), which reflects its large ilium relative to femur length and long bone diaphyses with large ends relative to lengths. Differences between African Americans and European Americans along PC2 and PC3 appear to reflect differences in body proportions, and Mezmaiskaya 1 plots within but near the edge of the European-American convex hull (Fig. 4*B*).

Discussion

We found that many Neandertal postcranial characteristics are present around the time of birth. Neonatal Neandertals already appear to possess the wide body, long pubis, and robust long bones of adult Neandertals. In fact, the only exception we could find was a relatively short radius, which Mezmaiskaya 1 had, whereas Le Moustier 2 had a relatively long radius. This ambiguous result may not be so surprising, given that adult Neandertals show less shortening of the radius relative to the humerus than they do of the tibia relative to the femur (39), and that the

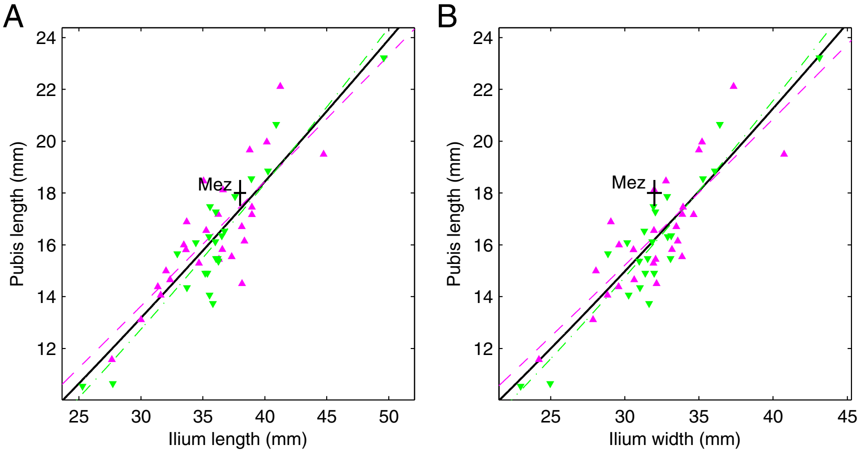

Fig. 2. Relative pubis length. (*A*) Pubis length vs. ilium length and (*B*) pubis length vs. ilium width (Table S1 includes measurement descriptions). The purple triangles are recent African Americans, the green inverted triangles are recent European Americans, and the black plus sign is the Mezmaiskaya 1 (Mez) Neandertal. The plus-sign horizontal and vertical dimensions are ±0.5 mm. The purple dashed curve is the relationship for the African Americans, the green dash-dot curve is the relationship for the European Americans, and the black solid curve is the relationship for all recent humans (Table S6 includes fit statistics).

Dederiyeh 1 subadult Neandertal has a relatively long radius (18). Unfortunately, the clavicles of Mezmaiskaya 1 and Le Moustier 2 are too fragmentary to reliably estimate the length, but the somewhat older Amud 7 Neandertal seems to already have a clavicle that is long relative to humerus length (14).

Consistent with our results, Golovanova et al. (40) concluded that Mezmaiskaya 1 had relatively short distal limb segments and relatively large ends of the radius and femur in comparison with a recent human infant of similar dental age; and Ponce de León et al. (11) found that Mezmaiskaya 1 had absolutely large distal ends of the humerus and femur, absolutely long ilium and pubis, and a relatively short tibia in comparison with the means of measurements collected by Fazekas and Kósa (41) on a recent Hungarian fetal skeletal sample.

We focused our analyses on a set of linear measurements, but, based on other studies, Neandertals < 1 y of age already seem to show other distinctive postcranial features, including bowed long bones (Kiik Koba 2, Mezmaiskaya 1, Le Moustier 2) (11, 42, 43); robust, rounded rib shafts (Kiik Koba 2) (42); an incipient dorsal axillary sulcus of the scapula (Kiik Koba 2) (44); a medially directed radial tuberosity (Mezmaiskaya 1) (40); subequal proximal and distal thumb diaphyses (Le Moustier 2) (43); an opponens pollicis flange on the first metacarpal (Kiik Koba 2) (37); and very thick long bones (Le Moustier 2) (15). However, other studies appear to indicate that at least some Neandertals developed elevated long-bone cross-sectional properties (14, 45) and a thin superior pubic ramus (16, 46) later in life.

Taken together, current evidence indicates that, with some exceptions [e.g., neurocranial globularity (12, 13), thin superior pubic ramus (16, 18, 46), and perhaps radius/humerus proportions (this study)], skeletal differences between Neandertals and modern humans are largely established by the time of birth. Features that are present on the skeletons of neonatal Neandertals could not have developed in response to mechanical loading associated with adult/older-subadult behaviors (e.g., hunting), so they must either have an evolutionary explanation or result from environmental influences on the fetus (e.g., maternal diet).

If we consider that evolutionary changes are a more likely explanation than fetal environment for skeletal differences between Neandertals and modern humans, climatic adaptation is the best-supported explanation for many aspects of Neandertal postcranial form because Neandertals have body proportions close to present-day humans with ancestry in cold climates (24, 30, 31), it appears that multiple generations are necessary for appreciable changes in body proportions (i.e., an evolutionary timescale is needed) (24, 25), a wide variety of taxa exhibit similar ecological relationships (47–49), and laboratory experiments on human subjects demonstrate that body proportions influence heat loss (50) [see also Churchill (51)]. Recent research, however, has cast some doubt on this explanation. Because the modern human expansion from Africa that gave rise to recent human groups had a substantial south-to-north component, differences among recent human groups in body proportions could have more to do with population history than climatic adaptation (52–54). Additionally, a wide body may have been the ancestral condition for *Homo* (7, 55–57), even though the earliest members of our genus presumably lived in warm climates. Consequently, although it remains likely that many postcranial differences between Neandertals and modern humans stem from contrasts in body proportions (21, 36, 38, 58), further research will be necessary to establish whether climate played an important role in shaping these differences in body proportions.

Finally, it is important to note that, even if climatic adaptation explains Neandertal body proportions, climatic adaptation alone cannot explain a long pubis relative to dimensions of the pelvic inlet (59, 60). The alternative explanations for a long pubis include a posteriorly positioned acetabulum related to differences in gait between Neandertals and modern humans (60), or a wide pelvis coupled with a transversely oval outlet of the birth canal (as opposed to the anteroposteriorly oval outlets typical of modern humans), because Neandertals had a different birth process than modern humans (59).

Materials and Methods

Mezmaiskaya 1 and Le Moustier 2 Neandertals. Mezmaiskaya Cave is located in the northwestern Caucasus ~50 km south of the city of Maikop (Russia). Mezmaiskaya 1 consists of 141 identifiable postcranial bones, a cranium and mandible, and 14 dental crowns of deciduous teeth. The skeleton was recovered in anatomical association from the lowermost 3–5 cm of level 3, the oldest Middle Paleolithic layer (Figs. S1 and S2). Detailed stratigraphic assessments clearly indicate that the Mezmaiskaya 1 skeleton and level 3 were deposited at the same time, both dating to very close to or greater than the effective measurement limit of radiocarbon (~50 ka) and likely to 70–60 ka based on electron spin resonance mean early and late uptake model determinations for level 3 (11, 40, 61, 62).

The rock shelters of Le Moustier are located in the Dordogne ~45 km southeast of Périgueux (France). The Le Moustier 2 skeleton comes from layer J through the top of layer H of the lower rock shelter, which contained

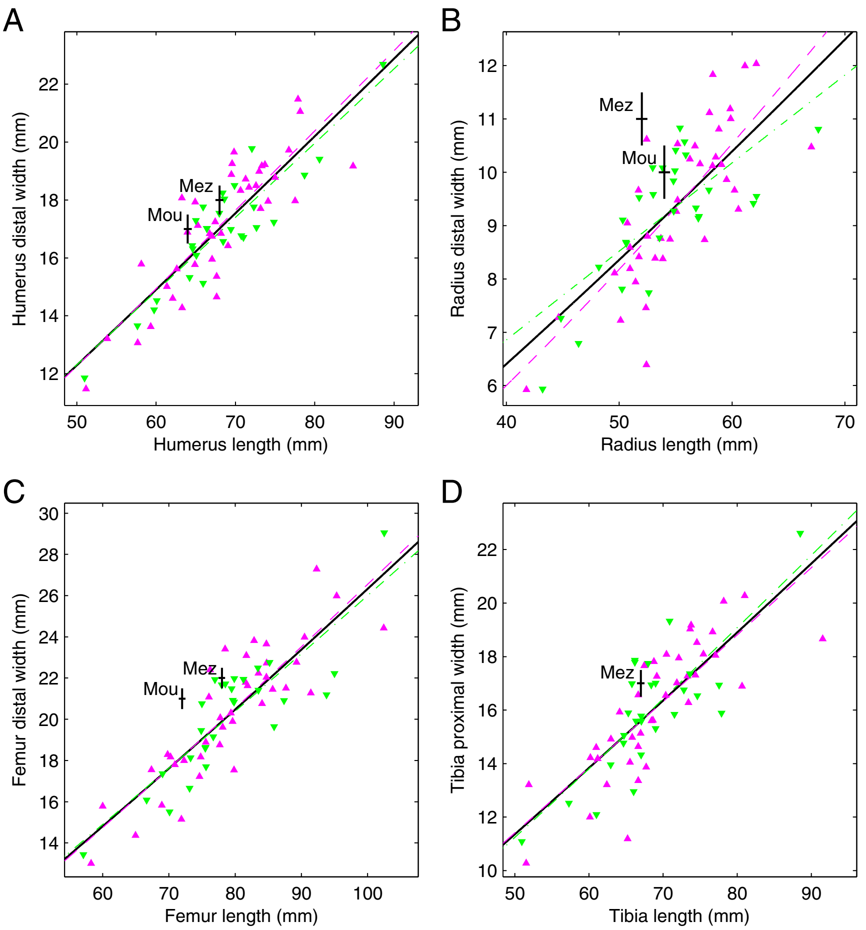

Fig. 3. Diaphysis end size to length. (*A*) Humerus, (*B*) radius, (*C*) femur, and (*D*) tibia (Table S1 includes measurement descriptions). The purple triangles are recent African Americans, the green inverted triangles are recent European Americans, and the black plus signs are Neandertals (Mez, Mezmaiskaya 1; Mou, Le Moustier 2). The plus-sign horizontal and vertical dimensions are ±0.5 mm. The purple dashed curve is the relationship for the African Americans, the green dash-dot curve is the relationship for the European Americans, and the black solid curve is the relationship for all recent humans (Table S6 includes fit statistics).

Typical Mousterian (layer J) and Discoid Mousterian (top of layer H) artifacts (Figs. S3 and S4). Based on thermoluminescence dating of level J, Le Moustier 2 dates to ~40 ka BP (43, 63–66).

These two fairly complete skeletons are the best preserved Neandertal neonates, and among the most complete Neandertals of any age (Figs. S2 and S4). We were able to collect the full measurement set on Mezmaiskaya 1 and

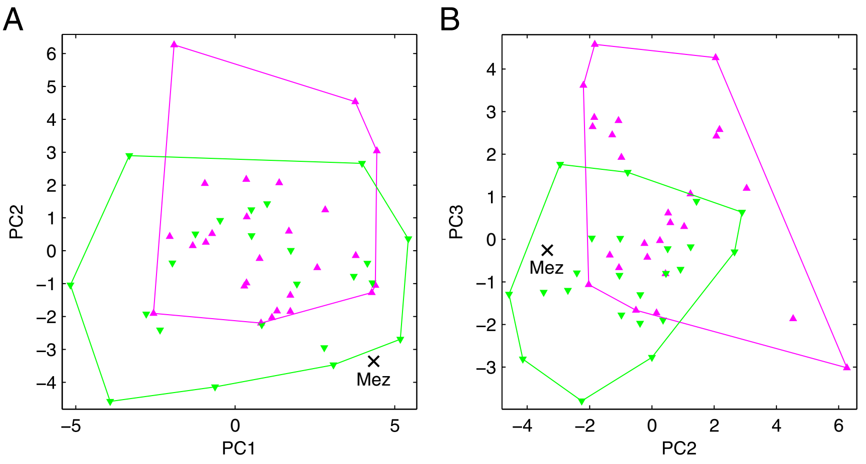

Fig. 4. PCs of residuals. (*A*) PC2 vs. PC1 and (*B*) PC3 vs. PC2. The purple triangles are recent African Americans, the green inverted triangles are recent European Americans, and the black "X" is the Mezmaiskaya 1 (Mez) Neandertal. The purple and green convex hulls indicate the extent of the African Americans and European Americans, respectively (Table S5 includes the eigenvectors).

all of the measurements except pubis length and tibia length on Le Moustier 2 (Table S2). The *SI Text* includes more details about the context and preservation of the Mezmaiskaya 1 and Le Moustier 2 Neandertals.

Recent Human Sample. The recent human sample is from the fetal skeletal collection housed at the National Museum of Natural History (Smithsonian). Various medical practitioners collected the fetuses, mostly from the Baltimore, MD, and Washington, DC, areas, at the end of the 19th and early 20th centuries and donated them to the museum between 1903 and 1917 (67, 68). Based on the documentation associated with the collection, we divided the sample into two groups: African Americans and European Americans, with approximately equal numbers of female and male specimens in each group (Table S3). Age at death is not precisely documented for much of the sample, but, based on femur length (measurement defined in Table S1; minimum, 57 mm; maximum, 102 mm; mean, 79 mm), the individuals ranged from ∼8 mo in utero to ∼4 mo after birth, with the mean approximately birth (41, 69).

Data Collection. We collected 11 linear measurements of the humerus, radius, ilium, pubis, femur, and tibia (Table S1) on the left and right sides, preservation permitting, on each of the individuals. We analyzed the mean measurement when both sides could be measured. For Mezmaiskaya 1 and Le Moustier 2 (Table S2), we rounded each measurement to the nearest millimeter and indicated ±0.5 mm on all of the graphs so as not to convey an undue sense of precision when visually comparing these specimens to recent humans.

T.D.W. collected the measurements of the recent humans directly with calipers. Mezmaiskaya 1 was scanned with a Skyscan 1172 micro-CT system (resolution ∼35μm for all dimensions), and Le Moustier 2 was scanned with a BIR ACTIS 225/300 industrial CT scanner (resolution of 20–30 μm for all dimensions). H.C., J.-J.H, B.M., and T.D.W. collected the measurements of Mezmaiskaya 1 and Le Moustier 2 directly with calipers and from CT scans with the Avizo (FEI) and Tivmi software packages.

Statistical Analyses. We fit nonlinear regressions of the form $y = ax^b$ (power laws) to the data in the bivariate graphs, where a and b are constants, and y and x are the response and predictor variables, respectively. For each graph, we fit three separate curves: for the African Americans, European Americans, and all of the recent humans (i.e., all individuals except Mezmaiskaya 1 and Le Moustier 2). As with ratios, these curves allow relative dimensions to be compared, but they have the advantage of allowing the ratio to vary with size (i.e., age). (An exponent [b] equal to one indicates that the ratio between the two variables remains constant.) Because relative dimensions are being compared, our analyses are independent of age estimates, which is advantageous given evidence that Neandertals may have matured faster than modern humans (70). Individuals with missing data for one (or both) of the variables were excluded from the particular bivariate analysis. Table S6 provides fit statistics for the bivariate analyses.

To provide a multivariate synthesis of the bivariate analyses, we performed PC analysis (PCA) of the residuals of the individuals from the all-recent-human regressions (i.e., the residuals from a particular bivariate analysis correspond to a variable in the PCA). We performed the PCA on the covariance matrix, and individuals with any missing data were excluded from this analysis. We performed all statistical analyses in Matlab (Mathworks).

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