the orientation of the masking grating throughout the experiment. The percentage of masking decreases as the angle of orientation of the target grating deviates on either side from the orientation of the masking grating. Figure 1 shows that dichopic masking clearly parallels monopic masking; both functions are systematically related to the angular separation between the gratings used for adaptation and for testing. The binocular control condition shows a slight hump in the region of the masking orientation, but this possible anchoring effect was not statistically significant.

The effect of the experimental conditions upon the extent of masking was measured by comparing the percentage of "blank" responses under condition (i) and under condition (ii) with the paired trials of the control condition (iii). The paired comparisons for each subject were found by Wilcoxon's test for paired replicates to be significant beyond the .01 level for both the dichopic and the monopic observations.

The significant masking found with dichopic viewing is evidence that interocular transfer of orientational effects does occur. This finding indicates that some higher-level neural adaptation of orientationally selective analyzers takes place in the human visual system and may be the result of contour-detecting mechanisms observed in lower animals that demand cortical integration in primate vision.

The relatively greater monopic than dichopic masking raises a question. But the finding that the masking effect in both conditions is a function of the angular separation between the test and the masking lines is of primary importance. At 10° to 20° away from the masking grating, the masking effect disappears or does not differ significantly from the control. This finding is consistent with a variety of studies (*6*) using different methods that show narrow orientationally tuned channels in the visual system of different species. The angular selectivity characteristic is much narrower than would be expected on a simple Cartesian coordinate system. This characteristic is in remarkable agreement with Hubel and Wiesel's description of the orientation sensitivity of cortical cells found by electrophysiological techniques.

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References and Notes

1. F. W. Campbell and J. J. Kulikowski, *J. Physiol.* **187**, 437 (1966); A. S. Gilinsky, *J. Opt. Soc. Amer.* **58**, 13 (1968); K. Houlihan and R. W. Sekuler, *J. Exp. Psychol.* **77**, 281 (1968).
2. D. H. Hubel and T. N. Wiesel, *J. Physiol.* **160**, 106 (1962); *J. Neurophysiol.* **28**, 229 (1965); *J. Physiol.* **195**, 215 (1968).
3. K. Dunlap, *Amer. J. Physiol.* **55**, 201 (1921).
4. J. Krauskopf and L. A. Riggs, *Amer. J. Psychol.* **72**, 248 (1959).
5. P. A. Kolers and B. S. Rosner, *ibid.* **73**, 2 (1960); P. H. Schiller and M. Wiener, *J. Exp. Psychol.* **66**, 386 (1963); C. McCollough, *Science* **149**, 1115 (1965); P. H. Schiller, *J. Exp. Psychol.* **69**, 193 (1965).
6. M. M. Taylor, *J. Opt. Soc. Amer.* **53**, 763 (1963); D. P. Andrews, *Vision Res.* **7**, 975 (1967); T. H. Mayo, A. S. Gilinsky, A. Jochnowitz, in *Proceedings of the 76th Annual Convention of the American Psychological Association, 1968* (American Psychological Assoc., Washington, D.C., 1968), p. 97.
7. This research was supported by NSF grant GB-6067.

26 February 1969

Homology and Analogy

The terms homology and analogy (*1, 2*) and their derivatives have had more than a century and a half of intensive, and often confusing, usage in biology (*3*). The term homology has become associated with two of the most important concepts in biology: first, structural correspondence (*1*) and second, common ancestry (*2*). On the other hand, the term analogy has been used to refer to the most diverse kinds of concepts from functional correspondences, especially the use of organs and parts, to structural noncorrespondences, which are the opposite of homology.

Owen's (*4*) definitions of the derivative terms may be considered classical:

> Homologue: The same organ in different animals under every variety of form and function.
> Analogue: A part or organ in one animal which has the same function as another part or organ in a different animal.

Now these definitions were in need of further elaboration and extended discussions are to be found in Owen's later works. He gave a report to the British Association for the Advancement of Science in 1846, which was published the following year in the *Report of the Meeting.* The title was "Report on the archetype and homologies of the vertebrate skeleton." This extensive address was reprinted in 1848 with some additional facts and illustrations (*5*). I do not wish to refer to all the types of homology that Owen discusses, namely, general, special, and serial, but only to the "special homology"; that is, the essential structural similarity of the corresponding parts of organisms, and the criteria that were useful in the recognition of these correspondences.

In Owen's words, "These relationships are mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of form, proportion, substance, function, and similarity of development." In regard to the latter criterion he stated, "There exists doubtless a close general resemblance in the mode of development of homologous parts: but this is subject to modification."

These quotations indicate that, for Owen, homology meant structural correspondence; and this meaning has been attached to this term longer than any other. On the other hand the term analogy always meant to Owen a similarity in "function" or use to the organism and *never* implied the opposite of homology. This is made absolutely clear in the following words: "but homologous parts may be, and often are, also analogous parts in a fuller sense, viz., as performing the same functions: thus the fin or pectoral limb of a Porpoise is homologous with that of a Fish, inasmuch as it is composed of the same or answerable parts: and they are the analogues of each other, inasmuch as they have the same relation of subserviency to swimming."

So much for the classical usages that were pre-Darwinian. But even after Darwin's *Origin of Species* was published, Owen continued with the same definition of homology. In the first volume of his *Comparative Anatomy and Physiology of Vertebrates* (*6*), he accepts "an ascent from the general or lower to the particular or higher condition of organism."

"The most intelligible idea of homologous parts in such series is that they are due to inheritance." But the occurrence of evolution did not, for Owen, warrant a redefinition of homology so as to include the requirement that homologous parts must be "due to common ancestry." Owen's caution was, to me, quite admirable, for, then as now, inferences in regard to the common ancestry of parts are based chiefly on the kinds and amounts of structural correspondence among them. In discussing homology, Woodger (*7*) commends such caution. "Nothing is more striking in this science [biology] than the contrast between the brilliant skill, ingenuity, and care bestowed upon observation and experiment, and the almost complete neglect of caution in regard to the definition and use of concepts in terms of which its results are expressed."

In brief, during "Darwin's Century" there has been a steady erosion of the classical definition of homology such as to tend to reduce the structural, and to exaggerate the genetic, implications of the term. Finally we have Bock's (*8*) statements:

> Contrary to common opinion, the twin concepts of homology and analogy have nothing to do with similarity of features; they are only associated with common origin versus non-common origin.

Bock further claims that "the use of analogy for the opposite of homology is close to the original idea of Owen." This is simply not true. Now if Bock's definition of homology is to replace Owen's, there is then left no respectable term to refer to the relation of essential structural correspondence—which still is "morphology's central conception" [J. Huxley in De Beer (*9*)]. My own proposals were, and still are, to use homology and analogy in Owen's senses and thus to distinguish clearly between structural correspondence and similarities in use. For the concept of common genetic origin, many terms are available and have been since the early post-Darwinian days. Lankester (*10*) suggested that organs or parts which could be traced to a single representative in a common ancestor should be referred to as "homogenetic." And from the same period we have Haeckels' terms homo- or monophyletic to convey the idea of the common ancestry of organisms. These terms make it possible to distinguish clearly in our discussions between levels of structural correspondence of importance to comparative anatomists and systematists, indeed to all biologists, and inferences in regard to the implied amounts of genetic relationship among the organism concerned.

The acceptance of this line of thinking and use of terms could have several important consequences. First, it could resolve the confusion resulting from using homology to mean both correspondence and ancestry, in that each concept is important in its own right and fully entitled to a term of distinction. Second, it could help to focus attention upon the amounts and kinds of structural correspondences that occur among existing and preexisting organisms and leave the drawing of conclusions in regard to phylogeny to those who prefer the backward look at presumed origins. And indeed it is time we had another look at the often referred to "homology" of the mammalian ear ossicles and parts of the mandibular and hyomandibular arches of sharks. This is referred to by Bock (*8*), and led him to say that "many homologous structures are not at all similar." My own suggestion would be that if indeed these parts are "not at all similar" they should not be called homologous!

Evolutionary biologists seem to be in great danger of confusing the derivation of an organ or part with the nature of the derived part. In embryology, a host of differentiated organs or parts are not homologous with the parts from which they arise. In vertebrates, pouches from the primitive gut may give rise to parts of the notachord, lungs, and liver. But these parts are never considered to be homologous with the archenteron—nor are they homologous with each other. In evolution, on the other hand, it is the presumed ancestral derivation which is held to be decisive in defining the relationship of homology. Simpson (*11*) states

> There is now extremely little disagreement in usage: "homology" is practically always understood to be *defined* by common ancestry and 'homogeny' has become an unused synonym of "homology." When usage is as nearly unambiguous as this is, there is no sensible argument with it, and the fact that Owen or others before him did not thus define "homology" has only historical interest with no real bearing at all on present definitions.

I have a greater respect for our heritage of words and meanings than Simpson shows in the above quotation. It is a striking fact that "phylogenists" have such high regard for the presumed ancestry of structures and little regard for the known ancestry of the meanings of the terms they use. It is still "common opinion" (Bock, *8*) that homologous parts have structural correspondence, but it is also unfortunately true that the term homology has come to imply common origin to many and the letters of Winter, Walsh, and Neurath (*1*) on the side of structural correspondence, and Margoliash (*2*) on the side of common ancestry along with structural correspondence in proteins show that the debate is still with us.

One need not be so much concerned here with the validity of the evidences for common ancestry, whether on the gross anatomical or the molecular level. But what biologists mean when they use the terms which Owen introduced is of concern.

There are two great concepts or relations involved in these discussions: (i) structural correspondences of many kinds and amounts, and (ii) genetic relationships from low to high degree. Each of these relationships is worthy of study in its own right, and therefore we need appropriate and distinctive and *respectable* terms for each. For structural correspondences of high degree, we have the term homology in its ancestral and still common meaning. For the relationship of common ancestry, we have Lankester's term homogeny which carries a built-in sign of its proper meaning. For the common ancestry of individual organisms, we have Haeckels' terms homophyly or monophyly. Whatever the arguments may be in regard to the nature and validity of the evidence used to justify the use of each of these terms, their essential meanings would be clear. This is a consummation much to be desired. The fact that there has been a century of confusion in meanings should not cause us to give up in despair. The great concepts involved will last as long as biology does and present and future workers will benefit for a long time to come from the use of the terms as their history should dictate.

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References and Notes

1. W. P. Winter, K. A. Walsh, H. Neurath, *Science* **162**, 1433 (1968).
2. E. Margoliash, *ibid.* **163**, 127 (1969).
3. A. Boyden, *Quart. Rev. Biology* **10**, 448 (1935); *ibid.* **18**, 228 (1943); *Amer. Mid. Natur.* **37**, 648 (1947).
4. R. Owen, *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals* (Longman, Brown, Green and Longmans, London, 1843).
5. ———, *On the Archetype and Homologies of the Vertebrate Skeleton* (Van Voorst, London, 1848).
6. ———, *Comparative Anatomy and Physiology of Vertebrates* (Longmans, Green, London, 1866).
7. J. H. Woodger, *Biological Principles. A Critical Study* (Routledge and Kegan Paul, London, 1929).
8. W. J. Bock, *Amer. Nat.* **97**, 265 (1963).
9. G. R. De Beer, *Vertebrate Zoology* (Macmillan, New York, 1928).
10. E. R. Lankester, *Ann. Mag. Natur. Hist.* **6**, 35 (1870).
11. G. G. Simpson, *Proc. Amer. Phil. Soc.* **103**, 286 (1959).

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