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Evolution of the visual cortex and the emergence of symmetry in the Acheulean techno-complex

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Abstract

Several recent studies have examined human evolution with reference either to the symmetry of Acheulean tools or brain structure but although these investigations have been informative they have not generally taken into account the psychology of perception in relation to recent insights into neural pathways of the visual brain. Similarly, the interest in symmetry has largely been restricted to understanding tool morphology that has ignored research on how this property might be processed by the brain that could help provide new insights into cognitive evolution. The purpose of this paper is therefore to bring these diverse approaches together in an effort to assimilate the various findings so that a fuller understanding of the cognitive profile of hominins during the early to Middle Pleistocene can be achieved. To cite this article: D. Hodgson, C. R. Palevol 8 (2009). © 2008 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

Résumé

Évolution du cortex visuel et émergence de la symétrie dans le techno-complexe Acheuléen. Plusieurs études récentes ont examiné l'évolution humaine en se référant, soit à la symétrie des outils acheuléens, soit à la structure du cerveau. Mais quoique les recherches aient été informatives, elles n'ont, en général, pas pris en compte la psychologie de la perception, en relation avec les récents aperçus sur les itinéraires des nerfs du cerveau visuel. En même temps, l'intérêt pour la symétrie a été largement restreint à la compréhension de la morphologie de l'objet, qui a ignoré la recherche d'explication de la manière dont cette propriété peut avoir été traitée par le cerveau, qui puisse aider à trouver de nouveaux aperçus sur l'évolution cognitive. C'est pourquoi, le propos de cet article est de cumuler ces diverses approches de manière à assimiler les nouvelles découvertes, afin qu'une compréhension plus complète du profil cognitif des Hominidés entre le Pléistocène inférieur à moyen puisse être atteinte. Pour citer cet article : D. Hodgson, C. R. Palevol 8 (2009).

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There has been much discussion as to the significance of the refined symmetries that typify Late Acheulean

hand-axes. Some investigators argue that this symmetry goes far beyond functional requirements and may be informative as to the cognitive outlook of those responsible for the end product [45]. It certainly appears to be the case that these tools show an increasing

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Fig. 1. The Elandsfontein handaxe –A typical example of a symmetrical Acheulean tool. This illustration and others are available from: http://antiquity.ac.uk./ProjGall/marshall.images/fig5.jpg. Fig. 1. Hâche à main d'Elandsfontein. Exemple typique d'un objet acheuléen symétrique. Cette illustration et d'autres sont disponibles sur : <http://antiquity.ac.uk./ProjGall/marshall.images/fig5.jpg>.

preference for symmetry (see for example Fig. 1.) absent in earlier Acheulean examples (predating 500,000 BP). One of the features of the symmetry of hand-axes is their uniformity across wide geographical locations and throughout a considerable period of time often made in great numbers in one location [35]. Conservatism of this order continues to perplex commentators who, for the most part, have tended to account for this homogeny in terms of functional demands or a consequence of the raw material utilised that affects knapping procedure [22,23]. However, as the symmetry of Late Acheulean tools seems to go somewhat beyond functional requirements [21], it is assumed something about cognitive and cultural determinants may be additionally involved [45]. Whether this is actually the case remains controversial but evidence seems to be accumulating supporting the relevance of cognitive factors to this issue. Here, I present data showing how the increasing preference for symmetry may have arisen from an "aesthetic" bias on the part of hominins that led to the making of the more complex profiles typical of Late Acheulean bifaces.

Kohn and Mithen [18] suggest that the prodigious symmetry of Acheulean hand-axes might be accounted for by sexual selection. Symmetry, however, has been found to be important in a number of contexts unrelated to mate preference [14,16]. Crucially, most biologically important objects, such as predator or prey, are symmetrical [7,8,44] and, in this respect, sensitivity to symmetry may have evolved because it is crucial for discriminating living organisms from inanimate objects [40]. In fact, symmetry seems to act as an early warning system that directs the visual system to further scrutinise an object until full recognition has occurred [26,41] Mirror symmetry is thought to have special status in human perception, precisely because it is such an important cue as to the presence of natural organisms [37]. This may be related to the fact that observers seem more sensitive to mirror symmetry than repetition symmetry [20]. The detection of symmetry, as Julesz [15] has established, is virtually automatic in that it is pre-attentive or preconscious. In this respect, studies [39] have demonstrated that humans are able to accurately discern symmetrical objects in less than a twentieth of a second and the eye is particularly rapid at discerning objects with vertical mirror symmetry, suggesting that the ability is hard-wired. And, once a line of vertical mirror symmetry has been detected, the eye will then only track parts of the object that have not yet been assimilated [19] to the extent that only the unassimilated side of the object are subsequently explored because the other facet is taken as given.

It appears therefore that the visual brain is especially responsive to symmetry suggesting that this preference may derive from enduring evolutionary factors. The recognition of animal forms would have been particularly relevant to the survival of homo-so it may well be that this sensitivity is related to the need to rapidly discern symmetry for the purpose of survival [37]. Fundamentally, it has been established that the human brain contains neurones specifically sensitive to symmetry in an area known as the medial occipital gyrus (MOG). This reflects the fact that early areas, such as the primary visual cortex at a more basic level of processing, are also preferentially tuned to particular features such as vertical and horizontal lines in that humans have a raised sensitivity to such elements because these are preferentially represented in this part of the brain [6]. The reason for this is to be found in the fact that the natural visual array has implicit within it more horizontal and vertical lines

than any other orientation. The evolution of the visual brain seems thereby to have taken advantage of these affordances to the extent that it has become embedded in the underlying neurophysiology that has consequences for perceptual awareness.

One of the main ways by which visual information is thought to be processed involves the interpolation of the tuning curves of neurones. For example, the visual cortex may store a relatively few sample 2D views of a 3D object that are used for the purpose of recognition of actual objects [43]. The procedure will be enacted as one ascends the visual hierarchy including the lateral surface of MOG [41], or lateral occipital cortex or LOC [38] (more precisely the dorsolateral occipital or DLO [40]) where long-range integration of scene features begins to take place. At this level, there may be a limited number of symmetrical forms encoded that, through a process of interpolation, are capable of accessing the full array of symmetrical forms. The importance of this area for detecting symmetry is underlined by the fact that damage or lesions to LOC leads to difficulties in perceiving bilateral symmetry [40]. Moreover, there is evidence that adjacent and earlier areas of visual cortex, mainly V4, V3A and V7 are also involved in symmetry extraction [31] that may be linked to the parieto-occipital area in relation to the intraparietal sulcus for processing 3D shape from motion for the manipulation of tools [12,24,42]. Interestingly, Sasaki et al. [31], also found that the response to symmetry in the brains of macaques was much weaker than in humans indicating that the presenting stimulus had to be much more pronounced to produce a response in the former compared to the latter. These studies support the fact that the human visual system exploits symmetry as a means of facilitating the recognition of objects [43].

Such observations are corroborated by Stout et al., [33] in a preliminary PET brain scan investigation that found, as well as premotor cortex, the above cited areas of the brain were preferentially activated when a modern knapper made a symmetrical Acheulean hand-axe. Interestingly, the same areas were activated, but to a lesser degree, in a previous study involving the making of Oldowan tools [32]. The prefrontal cortex, however, was not activated to any great extent in either study that adds some credence to Wynn and Coolidge's [46] hypothesis that enhanced working-memory, which is often associated with the executive functions of the frontal cortex, did not become important in this context until some 50,000 BP. De Beaune [3], on the other hand, sees analogical thinking, which is not so dependent on working memory, relevant to the Oldowan technologies of early homo - a capacity which became more important during the

Acheulean that may be related to the above cited neural correlates. De Beaune [4] has also suggested exaptation is pertinent to this issue whereby one function, which may have been evolutionarily adaptive, is reassigned for another purpose not directly related to natural selection. In this sense, symmetry, as a crucial perceptual contingency for detecting form, was initially adaptive but was subsequently reassigned, or exapted, for the purpose of realising the symmetrical morphologies of stone tools. Importantly, this reassigned function would itself have led to further adaptive benefits in that this allowed easier access to greater amounts of meat-protein/fat rich resources etc. The ability of humans to exploit symmetry during the Acheulean period may be related to the fact that from 1.6 million years up to about 300,000 BP tools began to evince more complex symmetries just as the hominin brain was undergoing considerable expansion in the parietal area with a probable rearrangement and enhancement of neural tracts [2,11,13,30] that is required for the multivariate task demands required to produce Acheulean tools [9]. It seems that an interest in symmetry that went beyond purely functional demands from about 500,000 onwards may be an indication of an awareness of form for its own sake [36] that is evidence of an increasing cognitive sophistication of hominins during this period.

The importance of symmetry is underlined by the fact that infants as young as 4 months are capable of discriminating mirror symmetry from other kinds of more complex symmetry [1]. This hypothesis is supported by the fact that the perception of symmetry seems to be inborn and develops early, even among young children from isolated communities that have no previous training or exposure to illustrations of abstract symmetrical forms [5]. In fact, this study found that core geometric concepts are part of a basic human cognitive development shared by young children throughout the world and concluded that a sophisticated analysis of shape appears to be a common human heritage.

Reber et al. [28] have put forward the concept of perceptual fluency to describe the process whereby symmetry acts as an important cue helping to parse the visual array. Fluency signifies that objects with symmetry are processed with greater speed and efficiency. In other words, this contingency reflects ease of perception and success in recognition that is associated with positive affect because it is a signal that something has been successfully categorized [29]. The detection of symmetry may also be related to prototypes in that symmetry, in its broadest sense, is an indication that something remains the same despite change. In fact, symmetry is commonly referred to in mathematics in a corresponding way whereby a rule, or formula, is able to represent the unchanging nature of things despite complexity [34]. This analysis of symmetry has significance for understanding Acheulean tool making in that, in order to make a tool, one has to remain cognisant of the fact that, although an object may undergo transformation through rotation, at the same time there are crucial aspects of the form that remain unchanged. As is the case with symmetry, prototypical shapes are processed faster than distorted ones and involve fewer neural resources [25,27]. It has also been established that prototypicality leads to positive regard because of error free processing and means of realising successful recognition [47]. Symmetry, therefore, seems to be an important perceptual indicator arising out of evolutionary imperatives closely tied to how the visual brain functions. Such factors may well have been subserved by the increasing ability of Homo erectus to assimilate the "what" (involved with recognising objects) and "where/how" (involved with manipulating objects in 3D) brain pathways leading to better eve-hand coordination for the making of more efficient, evenly-shaped tools [10].

The foregoing suggests symmetry is fundamental to visual perception and appears to be driven by an automatic function involving a dedicated brain network residing in MOG and related structures. The evolution of this network as a hard-wired contingency meant the Homo erectus or Homo heidelbergensis was pre-evolved to make ever more symmetrical tools through a ratchetlike effect thereby explaining the uniformity in shape over such a long period. It may be this pre-adaptation that formed the basis on which more complex tools morphologies and types came to be based especially during the latter part of the Acheulean period and on which a more detached "aesthetic" response led to the nonfunctional features that appear to characterize such tools [17]. The "aesthetic" referred to here, it should be added, is closely associated with the concept of perceptual fluency already mentioned concerning an affective response to symmetry because such shapes are important to how the world is successfully perceived.

The object of this paper has been to bring attention to the significance of symmetry in processing perceptual information that was important to the survival of hominins. It is hypothesised that this contingency came to be exapted for the purpose of making symmetrically shaped tools and, because this was initially based on hard-wired contingencies to do with the MOG and related areas, this led to the uniformity in shape profile during the Lower to Middle Palaeolithic that culminated in Acheulean technologies. Subsequent more complex tools may have involved cultural factors that exploited an evolutionarily disposed cognitive domain that was initially premised on brain expansion and reorganisation that was taking place during the Oldowan to Acheulean period. Such changes to the brain, especially in the posterior parietal region and areas including the MOG and adjacent pathways seemed to have been part of a reciprocal disposed dynamic. Before 0.5 Ma., the form of Acheulean tools, as testified by the conservatism in shape, was thus probably more tightly coupled with brain evolution whereas, after this date, the appearance of a greater range of tool types suggests that a more complex interaction was taking place involving technical/cultural traditions.

References

- D.M. Beck, M.A. Pinsk, S. Kastner, Symmetry perception in humans and macaques, Trends Cog. Sci. 9 (2005) 405–406.
- [2] E. Bruner, Geometric morphometrics and paleoneurology: brain shape evolution in the genus Homo, J. Hum. Evol. 47 (2004) 279–303.
- [3] S. de Beaune, Technical invention in the Paleolithic: what if the explanation came from the cognitive and neuropsychological sciences? Paper presented at XV UISPP conference, Lisbon. sub C05-01, #73, 2006 (Sept.) Abstract available from: http://www.uispp.ipt.pt/UISPPprogfin/Livro2.pdf. (Visited on 12 September 2007).
- [4] S. de Beaune, L'homme et l'outil, CNRS Éditions, Paris, 2008.
- [5] S. Dehaene, V. Izard, P. Pica, E. Spelke, Core knowledge of geometry in an Amazonian Indigene Group, Science 311 (2006) 381–384.
- [6] V. Dragoi, C.M. Turcu, M. Sur, Stability of cortical responses and the statistics of natural scenes, Neuron 32 (2001) 1181–1192.
- [7] M. Enquist, A. Arak, Symmetry, beauty and evolution, Nature 372 (1994) 169–172.
- [8] M. Giurfa, B. Eichmann, R. Menzel, Symmetry perception in an insect, Nature 382 (1996) 458–546.
- [9] J.A.J. Gowlett, The elements of design form in Acheulean bifaces: modes, modalities, rules and language, in: N. Goran-Inbar, G. Sharon (Eds.), Axe Age: Acheulean Tool-making from Quarry to Discard, Equinox, London, 2007, pp. 203–221.
- [10] D. Hodgson, More on Acheulean Tools, Curr. Anthropol. 46 (2005) 647–650.
- [11] D. Hodgson, Understanding the Origins of Paleoart: The Neurovisual Resonance Theory and Brain Functioning. Paleoanthropology. (2006) 54-67. Available from: www. paleoanthro.org/journal/content/PA20060054.pdf. (Visited on 24 June 2007).
- [12] D. Hodgson. The reorganisation of primary visual cortex and extrastriate areas of the human brain in relation to evolution and behavioural indicators. Paper presented at Centre for Archaeology of Human Origins, Southampton University 2007, Palevol 5 (2006) 135-172 (26th April).
- [13] R. Holloway, Evolution of the human brain, in: A. Lock, C.R. Peters (Eds.), Handbook of Symbolic Evolution, Blackwell, Oxford, 1999, pp. 74–125.

- [14] D. Humphrey, Preferences in symmetries in drawings: Assymetries between ages and sexes, Empirical Studies of the Arts 15 (1997) 60.
- [15] B. Julesz, Figure and ground perception in briefly presented isodipole textures, in: M. Kubouy, J. Pomerantz (Eds.), Percpetual organization, Erlbaum, Hillsdale, NJ, 1981, pp. 27–54.
- [16] S. Kalik, L.A. Zebrowitz, J.H. Langlois, R.M. Johnson, Does human facial attractiveness honestly advertise health? Longitudinal data on an evolutionary question, Psychol. Sci. 9 (1998) 8–13.
- [17] O. Keller, Aux origines de la géométrie Le Paléolithique, Vuibert, Paris, 2004.
- [18] M. Kohn, S. Mithen, Handaxes: Products of sexual selection? Antiquity 73 (1999) 518–526.
- [19] P.J. Locher, C.F. Nodine, Symmetry catches the eye, in: J.K. O'Regan, A. Lévy-Schoen (Eds.), Eye movements: From Physiology to Cognition, Elsevier Science Publications, Holland, 1987, pp. 353–361.
- [20] E. Mach, The analysis of sensations, Open Court, Chicago, 1914/1959.
- [21] A.J. Machin, R.T. Hosfield, S.J. Mithen, Why are some handaxes symmetrical? Testing the influence of handaxe morphology on butchery effectiveness, J. Arch. Sc. 34 (2007) 883–893.
- [22] S.P. McPherron, Handaxes as a measure of the mental capabilities of early hominids, J. Arch. Sc. 27 (2000) 655–663.
- [23] A. Nowell, Coincidental factors of handaxe morphology, Behav. Brain Sci. 25 (2002) 413–414.
- [24] G.A. Orban, K. Claeys, K. Nelissen, R. Smans, S. Sunaert, J.T. Todd, Mapping the parietal cortex of human and non-human primates, Neuropsychologia 44 (2006) 2647–2667.
- [25] M.I. Posner, S.W. Keele, On the genesis of abstract ideas, 77, J. Exp. Psychol. (1968) 353–363.
- [26] V.S. Ramachandran, W. Hirstein, The science of art: A neurological theory of aesthetic experience, J. Consciousness Stud. 6 (1999) 15–51.
- [27] P.J. Reber, C.E.L. Stark, L.R. Squire, Cortical areas supporting category learning identified using functional MRI, P. Natl. Acad. Sci. USA 95 (1998) 747–750.
- [28] R. Reber, P. Winkielman, N. Schwarz, Effects of perceptual fluency on affective judgements, Psychol. Sci. 9 (1998) 45–48.
- [29] R. Reber, N. Schwarz, P. Winkielman, Processing fluency and aesthetic pleasure: Is beauty in the perceiver's processing experience? Personal Soc. Psychol. Rev. 8 (2004) 364–382.
- [30] P.E. Roland, Brain Activation, Wiley-Liss, New York, 1993.
- [31] Y. Sasaki, W. Vanduffel, T. Knutsen, C. Tyler, R. Tootell, Symmetry activates extrastriate visual cortex in human and nonhuman primates, P. Natl. Acad. Sci. USA 102 (2005) 3159–3163.
- [32] D. Stout, N. Toth, K. Schick, J. Stout, G. Hutchins, Stone tool-making and brain activation: Positron emission tomography (PET) studies, J. Arch. Sc. 27 (2000) 1215–1223.

- [33] N. Stout, N. Toth, K. Schick, Comparing the neural foundations of Oldowan and Acheulean Toolmaking: A pilot study using positron emission tomography (PET), in: N. Toth, K. Schick (Eds.), The Oldowan: Case Studies in the Earliest Stone Age, Stone Age Institute, Gosport, 2006, pp. 321–331.
- [34] I. Stuart, Why Beauty is Truth: The History of Symmetry, Basic Books, New York, 2007.
- [35] J.-M. Le Tensorer, L'Homo erectus au Proche-Orient, in: H. de Lumley (Ed.), Catalogue de l'exposition Homo erectus à la conquête du monde, Musée de l'Homme, Éditions du Muséum national d'histoire naturelle, Paris, 1999, pp. 13–15.
- [36] J.-M. Le Tensorer, Les cultures acheuléennes et la question de l'émergence de la pensée symbolique chez *Homo erectus* à partir des données relatives à la forme symétrique et harmonique des bifaces, C. R. Palevol 5 (2006) 135–172.
- [37] C.W. Tyler, Empirical aspects of symmetry perception, Spatial Vis. 9 (1995) 1–7.
- [38] C.W. Tyler, Human symmetry detection exhibits reverse eccentricity scaling, Vis. Neurosci. 16 (1999) 919–922.
- [39] C.W. Tyler, The Human expression of symmetry: Art and neuroscience, (2002) Available from: www.ski.org/cwt/CWTyler/ Art%20Investigations/Symmetry/Symmetry.html. (Visited on 8 April 2007).
- [40] C.W. Tyler, H.A. Baseler, L.L. Kontsevich, L.T. Likova, A.R. Wade, B.A. Wandell, Predominantly extra-retinotopic cortical response to pattern symmetry, NeuroImage 24 (2005) 306–314.
- [41] C. W. Tyler, H. A. Baseler, B. A. Wandell, Cortical regions responding to long-range symmetry patterns (1998), Available from: http://www.ski.org/CWTyler_lab/ CWTyler/PrePublications/SFN1998/SymmNatureNeuro.html. (Visited on 21 March 2006).
- [42] W. Vanduffel, D. Fize, H. Peuskens, K. Denys, S. Sunaert, J.T. Todd, G.A. Orban, Extracting 3D from motion: Differences in human and monkey intraparietal cortex, Science 298 (2002) 413–415.
- [43] T. Vetter, T. Poggio, H.H. Bültoff, The importance of symmetry and virtual views in three-dimensional object recognition, Curr. Biol. 4 (1994) 18–23.
- [44] J. Wagemans, Characteristics and models of human symmetry detection, Trends Cogn. Sci. 1 (1997) 346–352.
- [45] T. Wynn, Archaeology and cognitive evolution, Behav. Brain Sci. 25 (2002) 389–438.
- [46] T. Wynn, F. Coolidge, Did a small but significant enhancement in working memory capacity power the evolution of modern thinking? in: P. Mellars, K. Boyle, O. Bar-Yosuf, C. Stringer (Eds.), Rethinking the human revolution, McDonald Institute Monographs, Cambridge, 2007, pp. 79–90.
- [47] P. Winkielman, J. Halberstadt, T. Fazendeiro, S. Catty, Prototypes are attractive because they are easy on the mind, Psychol. Sci. 17 (2006) 799–806.