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Illustrating cerebral function: the iconography of arrows

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For over a century the arrow has appeared in illustrations of cerebral function, yet the implications of using such symbols have not been previously considered. This review seeks to outline the nature, evolution, applications and limitations of this deceptively simple graphic device when it is used to picture functions of the brain.

The arrow is found to have been used in several different ways: as a means of endowing anatomical structures with functional properties; as a method of displaying neural function either in free-standing form or in a structural or spatial framework; as a device for correlating functional data with underlying brain topography; and as a technique for linking functions of the brain with the world outside and with various philosophical concepts.

For many of these uses the essential feature of the arrow is its directional characteristic. In contrast to the line, it is direction that enables the arrow to display information about time, which in turn can be exploited to depict functional rather than structural data.

However, the use of the arrow is fraught with difficulties. It is often unclear whether an arrow has been used to illustrate fact, hypothesis, impression or possibility, or merely to provide a decorative flourish. Furthermore, the powerful symbolic nature of the arrow can so easily confer a spurious validity on the conjectural.

Increasingly now there are insuperable difficulties when attempting to illustrate complex mechanisms of brain function. In the iconography of cerebral function, therefore, arrows with all their ambiguities may in certain circumstances become superseded by more non-representational symbols such as the abstract devices of the computational neuroscientist.

Keywords: arrows; cerebral function; iconography; illustration

1. INTRODUCTION

Arrows are very commonly seen in pictures illustrating brain function, but it was not always so. The arrow, which crept into neurological illustration almost unnoticed, has attracted little comment. This remarkable symbolic device, however, reveals much about the way we envisage brain function, and its use has had far-reaching implications for the way we depict brain function. Enabling one to visualize and expound the imperfectly understood, the arrow represents a unique but unexpectedly ambiguous graphic means for picturing the mechanisms by which the brain works.

What is an arrow? As a projectile with a history that dates back millennia its nature and its graphic representation present no problems. Beyond this literal sense, however, uncertainty occurs, for as a symbol an arrow means what we want it to mean and this depends on the context: 'The arrow points only in the application that a living being makes of it' (Wittgenstein 1958). This statement can be verified in everyday life; when displayed on a road sign an arrow that points vertically indicates a forward direction, whereas displayed by the side of an elevator the same vertical arrow indicates upwards. The meaning of an arrow is thus ambiguous if its context is unclear, which has obviously important implications in science.

The arrow probably first appeared as a metaphorical device in the compass rose of the Greeks around 150 BC, and was introduced into European cartography in the 12th century (Mijksenaar & Westendorp 1999). In scientific illustration, however, the arrow has had a surprisingly short history. Gombrich (1990) found this symbol to have been used no earlier than the 18th century, when it first appeared in diagrams in a treatise on hydraulics by the French engineer, Forest de Bélidor. In one of Forest de Bélidor's illustrations, arrows pictured in streams of water show in a straightforward manner the direction of flow. In another illustration, arrows indicate not only the direction of flow of water but also the direction of rotation of the waterwheel that would have been induced (Forest de Bélidor 1737). The arrow now perhaps suggests a functional consequence of the flow of water, a development relevant when applied to neurological illustration and an aspect discussed in § 2.

2. THE EMERGENCE OF THE ARROW IN ILLUSTRATIONS OF BRAIN FUNCTION

Arrows are not seen in the Renaissance drawings of the brain. For the Renaissance anatomists the ventricles, or cells, were the most striking parts of the brain, and the relationship between the ventricles was sometimes

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illustrated by means of simple lines (see Clarke & Dewhurst 1996). What the lines represent, however, is unclear and, crucially, it is not possible to discern from such lines either the direction or timing of processes that link the ventricles with each other.

The oldest diagrammatic representation of the neural pathways in the central nervous system is said to date from Descartes' *De homine* of 1662 (Jacobson 1993), but it was probably only in the 19th century, many years after the arrow had first been employed in illustrations relating to the physical sciences, that the use of arrows as graphic images emerged in neurology. The introduction of arrows into illustration of brain function appears to have evolved in different ways, which curiously took place almost simultaneously and over just a few decades.

(a) *Histological illustrations and arrows that suggest function*

Using arrows for illustration of brain function may well have been derived from arrows that had earlier been used to illustrate more abstract concepts on the neuron theory and reflex activity in the spinal cord, the arrows indicating supposed direction of interactions between the neural elements (see Jacobson 1993). Sometimes the function of the arrows was explicit; thus the microscopist, Arctic explorer and Nobel laureate Nansen, illustrating his histological studies on animals, commented 'The large arrows indicate the way the irritation of a sensitive nerve-tube has to pass to produce a reflex-movement . . . The small arrows indicate the way small parts of the irritation of the centripetal (sensitive) nerve-tube pass to arrive in other parts of the central nerve-system' (Nansen 1887). Nansen is here more specific than many other authors, deliberately stating the purpose of the arrows he used and that they relate, albeit imprecisely, to entirely inferred functions.

By the turn of the century, however, it was Ramón y Cajal who had most extensively and revealingly used arrows for illustrative purposes. His classical microscopical illustrations of the neural elements were extremely precise and detailed. When he tried to interpret what he saw, however, he resorted to the use of arrows (figure 1). For example, he states '. . . the impulses in the gray matter must go from the small pyramidals to the large pyramidals and from these to the polymorphic cells . . . the arrows indicate the direction of the impulses' (see DeFelipe & Jones 1988).

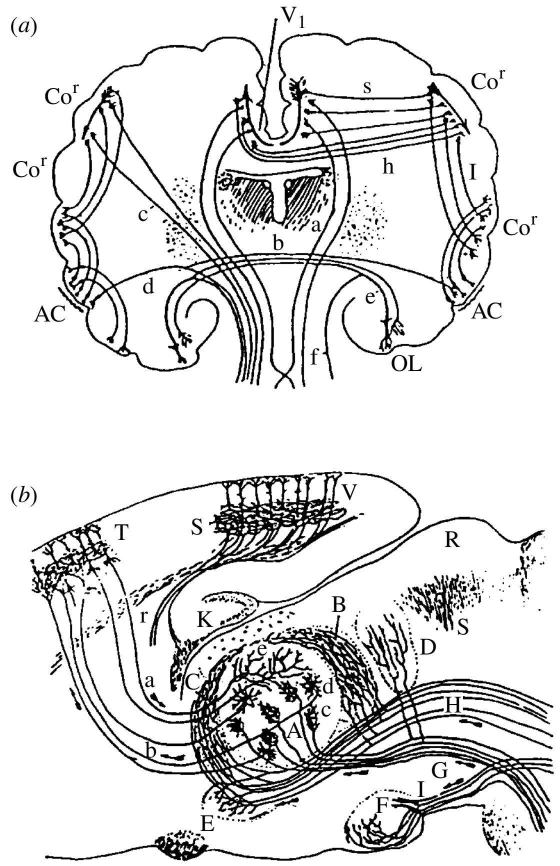

Figure 1. Examples of Ramón y Cajal's (1911) use of arrows showing (*a*) hypothetical links between the perceptive and primary and secondary memory centres related to the special senses, and (*b*) schematic afferent and efferent pathways of the sensorimotor area of the cerebrum (T), where the arrows refer to corticothalamic fibres (a) and thalamocortical or sensory fibres (b).

The concept that lay behind these arrows deserves comment. Ramón y Cajal appears to have regarded structure as having been designed for its function; the use of arrows was invaluable for illustrating this teleological approach, being his 'way of illustrating the theory of dynamic polarization of the neuron . . . The arrows are intended to show that function of the system is determined by the form of the neurons, especially the features that make axons differ from dendrites. The entire system is depicted as if designed for a definite purpose, allowing nervous activity to flow in an orderly pattern . . .' (Jacobson 1993). Even more deliberately than Nansen, Ramón y Cajal used arrows to illustrate entirely conjectural mechanisms. His work had been pivotal in developing the concept of the individuality of nerve cells and laying to rest the notion of a diffuse network connecting the cells and made up of their processes. One senses that he was using macroscopic arrows to support the dynamic polarization theory envisaged at microscopic level, and that the arrows might have been employed to provide a functional interpretation to the histological observations he had made. The arrows can be viewed as breathing vitality into the inert microscopical structures, thereby inferring some form of structure–function relationship. But the directional properties of the nervous impulse were not then known, and the fanciful arrows contrast strikingly with the illustrations of what he had actually seen and had so painstakingly and accurately drawn. The polarization of neurons that was illustrated was a hypothesis that only later proved to be correct. The boldness of the then unqualified assertion about impulses and their direction is thus particularly striking, and presaged a century of uncomfortably similar applications of the arrow in illustration of brain function.

(b) *The developing use of arrows to illustrate mechanisms of brain function*

Whilst the histologists' arrows endowed neural structures with hypothetical functional properties, a different development in the use of arrows was occurring at the same time: neural functions were themselves being illustrated by means of arrows, sometimes in the form of an isolated or 'free-standing' diagram, sometimes in the setting of some structural or spatial framework.

During the 19th century, arrows were introduced to illustrate the increasingly studied functions of the nervous system and particularly the brain. For example, Marshall Hall used arrows to illustrate how the nervous system supposedly malfunctioned, and how 'disease of the cerebrum can only induce spasm or convulsion through the Spinal System' (Hall 1850). Here arrows were used to reveal how disease processes were mediated by reflex arcs involving the spinal cord and brain, although he indicated his illustrations were 'mere sketches, only intended to convey an Idea'.

Probably the first diagrammatic illustration using arrows in the context of a brain disease that would be recognized today appeared in a case report on aphasia. The paper by Baginsky, which was published in 1871 in the *Berliner klinische Wochenschrift*, showed a simple form of flow diagram of the processes involved in speech (figure 2*a*), and by the beginning of the 20th century at least 19 examples of different diagrams incorporating arrows that depicted supposed speech mechanisms had appeared (see Moutier 1908). These illustrations of brain function often comprised fanciful, decorative and sometimes highly complex schematic illustrations. The technique of using arrows in diagrammatic or 'free-standing' diagrams, such as those seen in Baginsky's drawing, the later drawings of Lichtheim, Wernicke, Broadbent (figure 2*b*) and numerous other early 'diagram makers', continues to be used in diagram making today (figure 2*c*).

The arrows seen in the diagrams illustrated in figure 2 are necessary devices for connecting the 'black boxes', which in turn represent centres in the brain where a particular cerebral function is thought to be located. Arrows are used to show supposed connectivity, which is almost always inferred, and it is of interest that the technique has endured unchanged for a century. McCarthy & Warrington (1990) discuss these diagrams, commenting that the diagrams were 'almost entirely based on clinical impressionistic accounts rather than on controlled observation and quantification of phenomena'. Whilst their observations were mainly in respect of the classical diagrams as seen in figure 2*a*,*b*, modern diagram making is thought to have benefited from this approach and to resemble 'flow diagram models of "information-processing" psychology', as perhaps is represented by figure 2*c*. Nevertheless, the use of arrows connecting 'black boxes' must presumably imply the presence of some physical connection. However, the basis for such connections and what information passes along them, at least in humans, relies more on inference than fact. Even in respect of spatial connections, 'details [of these pathways] are based on the results of blunt dissection which can only yield crude impressions of the general dispositions of fibres en masse. Accurate knowledge of association fibres can only be established by experimental methods not yet applied to most cortical regions' (Williams *et al*. 1989). How much more conjectural are the arrows illustrating functional connections, many of which remain uncertain, hypothetical or even fanciful.

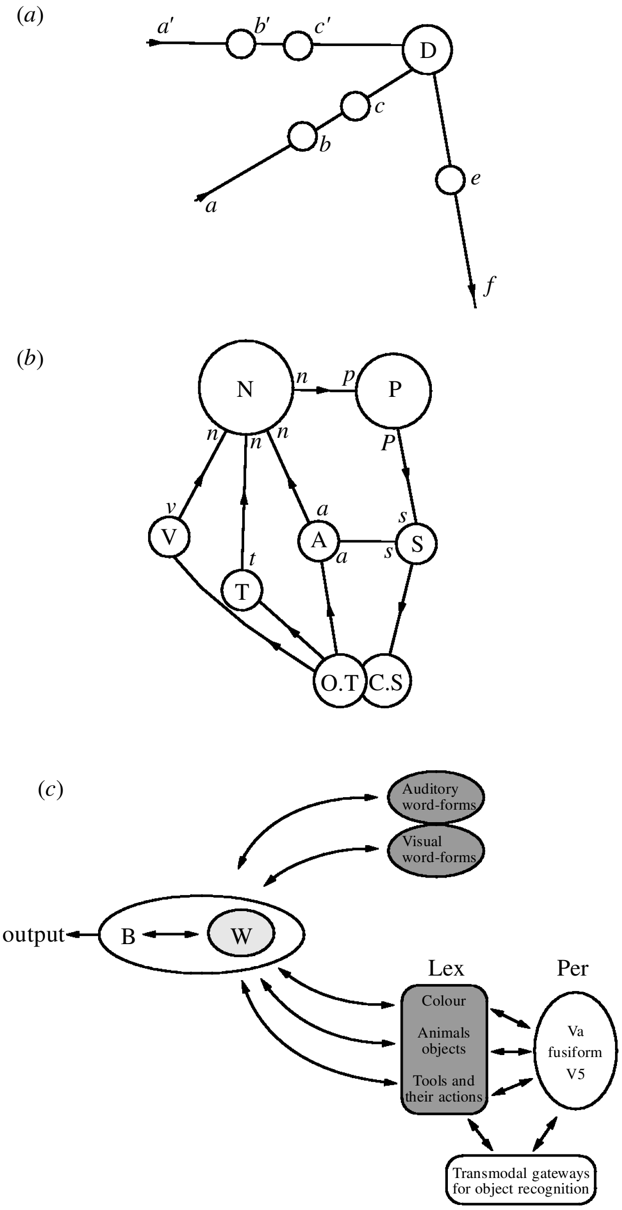

Figure 2. Arrows used to illustrate some mechanisms subserving speech. (*a*) The earliest arrowed diagram, by Baginsky (1871): links between auditory and visual inputs, the centre for construction of ideas (D), and motor outputs. (*b*) Broadbent's (1878) scheme, published in the first volume of *Brain*, linking input into the naming (N) and the propositioning (P) centres from visual (V), auditory (A) and tactile (T) centres. (*c*) Published in *Brain* a century later, Mesulam's (1998) contemporary schematic representation of some aspects of lexical retrieval and word comprehension involving Broca's and Wernicke's areas and prelexical, perceptual, auditory and visual word-form areas; 'Arrows represent reciprocal neural connections'. Reprinted with permission of the author and Oxford University Press.

(c) *Arrows correlating brain function with underlying brain structure*

Arrows could also be used to correlate brain functions with those structures in which the functions supposedly took place. The technique of superimposing arrows illustrating function upon images of brain structure was again especially used for depicting mechanisms of speech (see

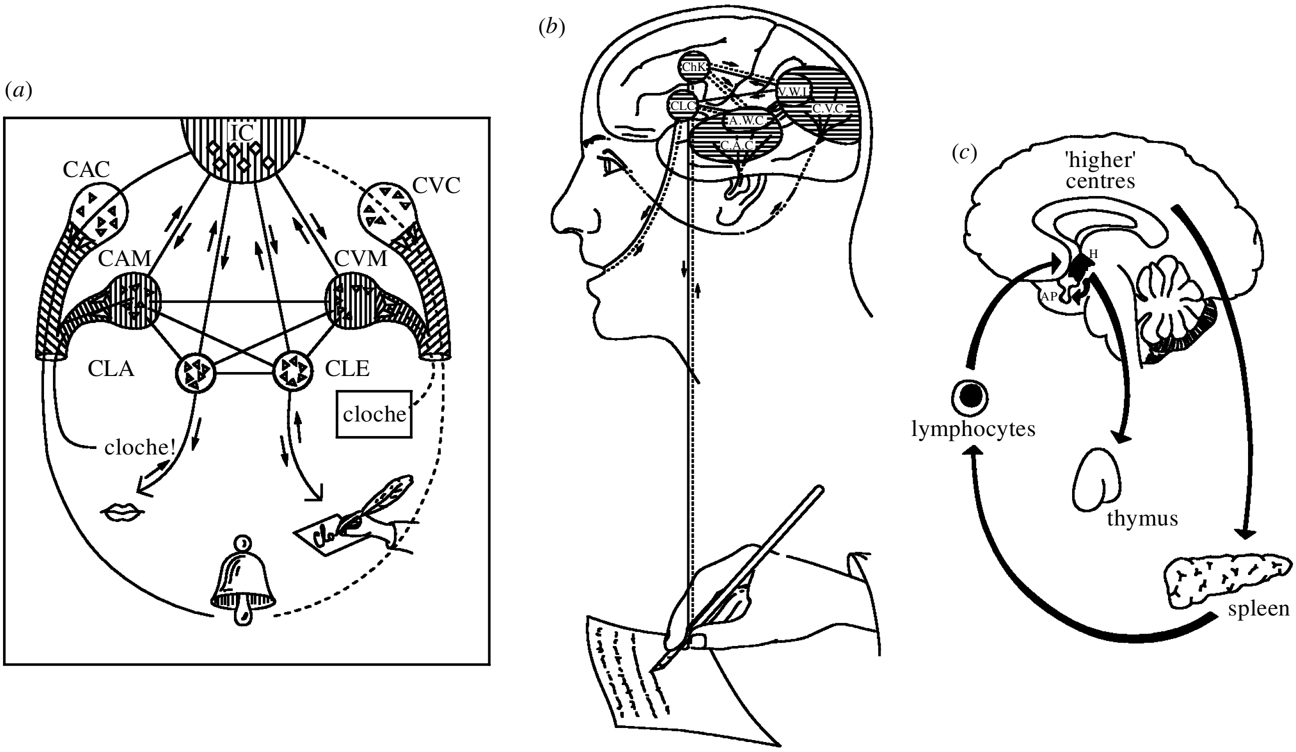

Figure 3. Arrows linking brain functions with the literal, outside world. (*a*) Charcot's concept of independent reading and writing centres incorporating everyday objects, as illustrated by Bernard (1885). (*b*) Bastian's (1898) illustration of two-way links between speech centres in the brain and the writing hand. (*c*) A contemporary illustration in which arrows show bidirectional communications between functions of the brain and the neuroendocrine and immune systems (AP, anterior pituitary; H, hypothalamus). Reprinted from Nisticò & De Sarro (1991), with permission from Elsevier Science.

Moutier 1908), but the same illustrative device could be used when illustrating other systems such as those subserving vision. Here too there was very little established basis for the authors' suppositions; the pathways were largely inferred and the arrows, symbols fancifully superimposed upon structures, had properties which were both vague and conjectural.

(d) *Arrows linking brain function with the world outside and the mind within*

Arrows have been used to link supposed cerebral mechanisms with the recognizable and familiar world; a famous example being Charcot's picture of the bell diagram that became well known when reproduced by Charcot's intern, Bernard (1885) (figure 3*a*). In this diagram, the two-way arrows connect auditory and visual centres for language with general and cortical centres and an 'ideation centre' (see Goetz *et al.* 1995); sound, speech and writing are represented visually and connected to cerebral mechanisms again by means of two-way arrows, but the anatomy of the 'ideation centre' to which the arrows pointed was never clarified, and understandably the arrows merely indicate hypothetical connections.

This use of arrows, however, also proves to be an illustrative technique by means of which brain function is linked with objects in everyday life, and such arrows have been used in numerous ways; pictures of hands shown writing which are linked by arrows to the brain (Bastian 1898) (figure 3*b*), and visual pathways linked to distant objects, are just two examples. Developed in the Renaissance, this technique of integrating diagram and drawing can make diagrams easier to understand, make the reader more comfortable with unfamiliar ideas and concepts (figure 3*c*), and allow the illustration to be seen in the prevailing intellectual and social context of the time (Kemp 1993).

Arrows too have been used, or arguably sometimes abused, in an attempt to bridge the divisions between the neurology of brain function, psychology and the philosophy of ideas. For example, when discussing the nature of the ego, in 1895 Freud incorporated arrows in a prescient illustration of the concept of a neural network, the function of which could be altered by psychological processes (Freud 1966) (figure 4*a*). The arrows in this remarkable diagram show the direction of a form of current, and Freud comments that the current flow will depend upon facilitatory or inhibitory factors; 'if it [the current] were uninfluenced, it would pass to neurone *b*; but it is so much influenced by the side-cathexis *a*-α that it gives off only a quotient to *b* and may even perhaps not reach *b* at all. Therefore, if an ego exists, it must *inhibit* psychical primary processes'. Freud's comments represent an early example from psychology of weighting, or what might currently be termed plasticity, in a neural network. The arrows here appear to show unidirectional flow, but then, as today, the identity of what is flowing remains unclear and the arrows are incorporated in a scheme that illustrates a concept rather than factual information.

Arrows linking the brain with the known or unknown world outside represent yet another, and enigmatic, use of the symbol. Such illustrations are still used today, and Eccles' arrows drawn between different parts of the brain

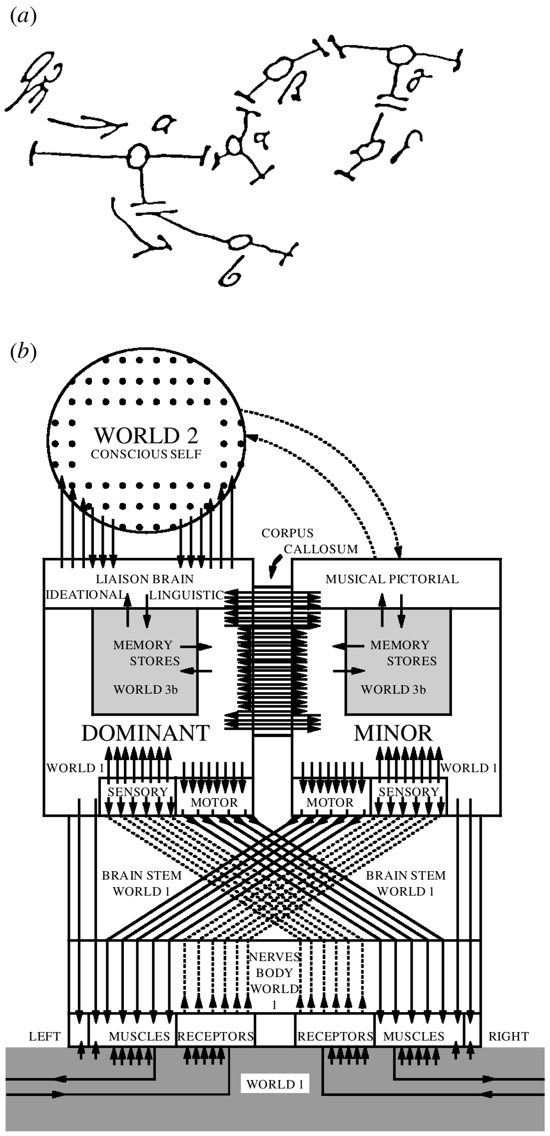

Figure 4. (*a*) Freud's illustration of the ego as a neural network, in which ill-defined neuronal flow or excitation is illustrated by arrows; the flow can be modified by inhibitory mechanisms represented by the Greek letters (Freud 1966). This remarkable diagram that he drew in 1895 represents a very early example of the concept of plasticity in the nervous system. Reprinted from Freud (1966), with permission of Sigmund Freud Copyrights, the Institute of Psycho-analysis and the Hogarth Press. (*b*) Arrows used by Eccles (1984) to illustrate communications to and from the brain and within the brain; the diagram also 'displays the modes of interaction between Worlds 1 and 2' and which include consciousness. Reprinted from Eccles (1984), with permission from Springer-Verlag.

and outer worlds (Eccles 1984) (figure 4*b*) have no currently known scientific basis and represent fantasy. These arrows recall the lines linking the brain with the spiritual world of the 17th century occultist philosopher Robert Fludd (see Clarke & Dewhurst 1996) and the earlier Renaissance illustrators, and it is for the reader to make what he or she can of them.

The arrows discussed in this section can be seen to reveal the longstanding ambiguity between the illustration of conceptual relationships and the supposed linkings of topographical entities. In their extreme form, such arrows even recall the cartoonist's lines of bubbles and speech marks that illustrate the bridge between what the subject thinks or says and the observer. The cartoonist, however, has the advantage that the fantastic nature of what are recognized to be artistic conventions is clearly understood, and here there is no ambiguity.

3. THE ENDURING NATURE OF THE ARROW

It is remarkable that the various uses of the arrow in neurological illustration that had developed up to the turn of the last century have continued so little changed up to the present time. Anatomists and histologists still use the arrow to suggest functional attributes to neural pathways. Physiologists and clinicians still use the arrow as a free-standing symbol reminiscent of the wiring diagram to represent often hypothetical brain functions, examples ranging from illustrations of cerebellar circuitry (Kawato & Gomi 1992) (figure 5*a*) to networks subserving dyslexia (Barry 1996) (figure 5*b*).

The arrows in figure 5*a*,*b* have a straightforward function. They show direction and are incorporated in circuit diagrams of various forms. The devices appended to the arrows, such as positive and negative signs (figure 5*a*) and interrupting crosses (figure 5*b*) are easy to interpret, and add further information to the direction of flow shown by the arrows themselves. Sometimes such arrows delineate more or less established information, such as the links between cerebellar structures (figure 5*a*). Sometimes, however, the precision of the graphic display belies the true uncertainty of what is represented by the arrows, and figure 5*b* recalls the diagram making referred to earlier (§2(b)), even if the crosses on the arrows represent an easily understood graphic device.

The arrow still continues to be used as a device for relating functions to structures, as in Magoun's use of arrows, which show projections of the cat's ascending reticular activating system superimposed upon the brainstem and cortex (Starzl *et al.* 1951) (figure 6*a*), and Penfield & Jasper's (1954) representation of afferents radiating to the frontal and cingulate cortices (figure 6*b*). This use of arrows is one of the various techniques by means of which function and structure are correlated. The arrows that display function need to be correlated in some way with where these functions take place. This correlative technique has subsequently been developed, and currently, for example, data from functional imaging studies may be correlated and visually displayed with anatomical data obtained from structural scanning. Before such techniques became available, however, functional data as indicated by arrows could be superimposed on an anatomical setting, providing useful information on structure–function relationships.

It is evident that the arrow has endured and remains a pervasive symbol in neuroscience, though the arrow is also used in almost every branch of science, ranging from the biochemist's metabolic pathways to diagrams of the evolutionary biologist. Yet the information that is represented by the arrow is often uncertain, fragmentary, and sometimes merely speculative, and there are several important and contentious issues that arise when this symbol is used and which are considered later (§7).

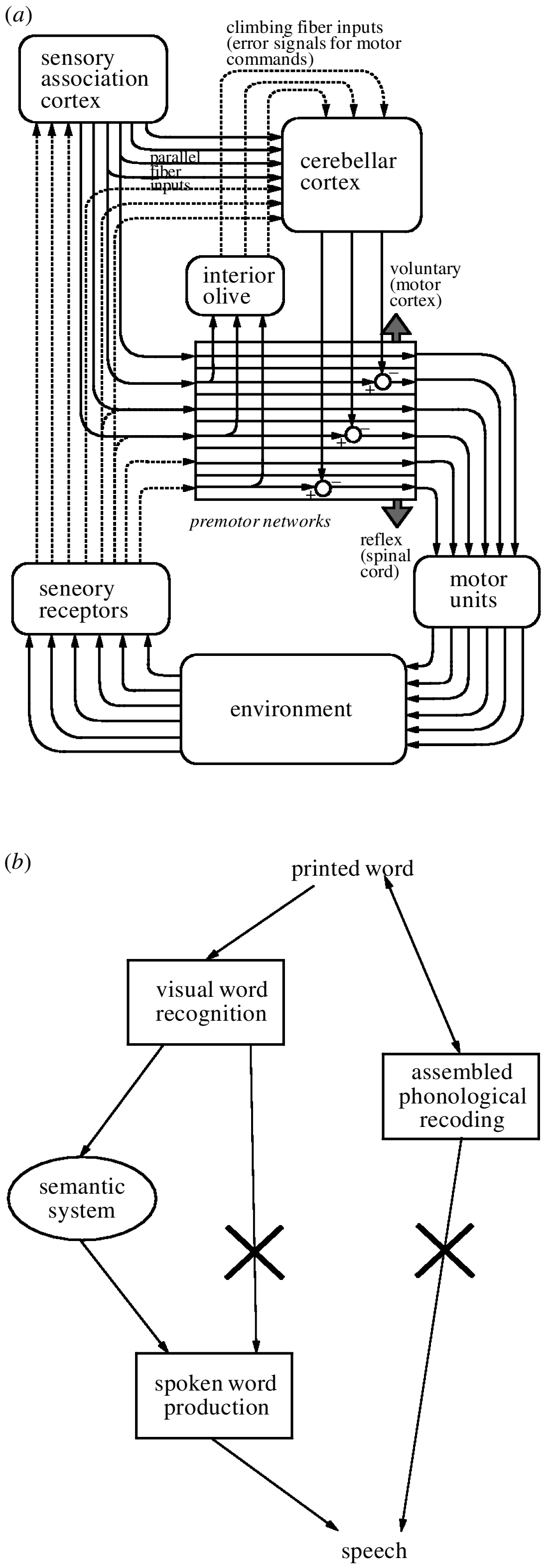

Figure 5. (*a*) '. . . how cerebellar motor learning processes might be incorporated in sensory-motor control'; a diagram which uses the form of the everyday circuit diagram. Reprinted from Kawato & Gomi (1992), with permission from Elsevier Science. (*b*) A simplified diagram of the processes involved in oral reading. Diseases can interrupt these processes, when schematically 'The crosses indicate the routes not available to deep dyslexic patients' (Barry 1996). Reprinted from Barry (1996), with permission from Psychology Press Limited, Hove, UK, and the author.

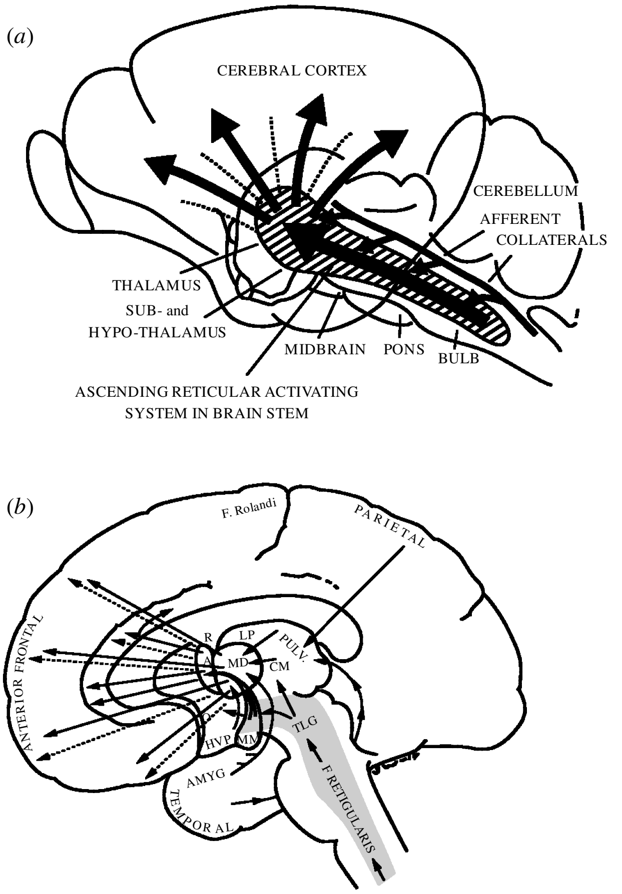

Figure 6. Arrows used to display function superimposed upon brain structure. (*a*) Projections of the cat's ascending reticular activating system superimposed upon the brainstem and cortex (Starzl *et al.* 1951). Reprinted from Starzl *et al.* (1951) with permission from the American Physiological Society. (*b*) Afferent projections radiating to the frontal and cingulate cortices (Penfield & Jasper 1954). Reprinted from Penfield & Jasper (1954), with permission from Churchill Livingstone.

4. ABSENCE OF ARROWS

Arrows in the illustration of brain function may become less common or outmoded in the future, an aspect discussed below (§8). In a variety of circumstances, however, arrows have already been notably absent. To some extent the line doubtless substituted for the arrow in the centuries before the arrow had been devised as a symbol in science, and the line has always continued *pari passu* as a complementary graphic device. Even in the 19th century, however, arrows did not always appear when they might have been expected. For instance Exner (1894), in the earliest illustration of a neural network, does not use arrows on his diagram. He would perhaps have been aware of this symbol and even Ampère's speculative electrical network incorporating arrows which had appeared some 70 years earlier (Roche 1993). Again, Gowers (1888) used lines to link the different brain regions subserving speech, and seems to have avoided the arrows that had been used by others and that were to become popular in the years to come.

What accounts for the absence of arrows? Dissatisfaction with the hypothetical basis for such superimposed arrows might provide one explanation, another being when the author aims to be precise and eschews extraneous and conjectural graphic commentary. Yet another explanation is that when direction is so obvious that the simple line suffices, an arrow appears superfluous. An example is the line representing the visual pathways between retina and occipital cortex, when the direction of neural function is so obvious that arrows indicating direction are not needed; it is salutary to recall, however, that what is obvious today was not always so—for the Pythagoreans, vision emanated outwards from the eye (see Gregory 1981).

5. ARROWS FOR EDUCATION

Just as arrows are used in everyday educational texts of every sort, so arrows frequently appear on diagrams of the brain when ideas of brain function are being expounded. A striking example of the way in which the arrow can be employed for this purpose is Geschwind's studies on the cortical disconnexion syndromes. Geschwind's classical papers in *Brain* occupied over 100 pages of text in which no illustrations appeared (Geschwind 1965). Just two years later, however, and in the reverse sequence to the usual historical evolution from pictograph to word (Gombrich 1982), Geschwind used arrowed diagrams illustrating pathways subserving apraxia when writing for the general scientific reader (Geschwind 1967) (figure 7*a*) and again when later writing for the layman (Geschwind 1972); indeed the technique continues to be developed (Zilles 1990) (figure 7*b*). Such arrows have the specific purpose of explanation. They are figurative, and evidently are not used in a literal sense; indeed Geschwind annotates his diagram (figure 7*a*) with the comment 'the callosal pathway marked a probably does not exist'. The arrows therefore can be viewed as graphic aids to the understanding of concepts, rather than illustration of pathways that, as discussed above (§2(b)), have rarely if ever been fully established.

Both for the scientist and for the interested layman the arrow is an invaluable and familiar symbolic graphic device that can aid the reader in understanding numerous neurological concepts, as can be seen in countless examples that range from 19th century neurological texts such as Bernard's book on aphasia referred to earlier, to 20th century science books for 'ordinary busy people' (Wells *et al.* 1931). Perhaps such frequent use of the arrow is explicable because, at first sight, the ubiquitous symbol needs neither clarification nor explanation, but as will be discussed below (§7) the arrow itself often requires considerable interpretation.

6. THE NATURE AND EXTRAORDINARY SIGNIFICANCE OF THE ARROW

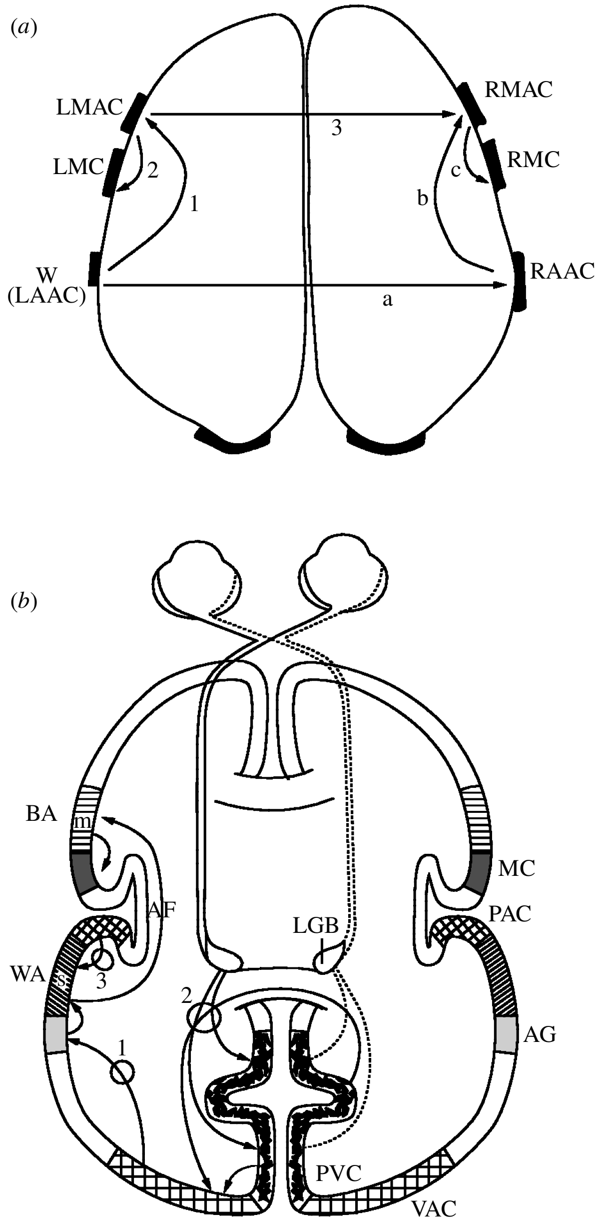

Figure 7. Arrows representing flow diagrams of specific neural function correlated with localized brain structure. (*a*) Geschwind's (1967) illustration showing connections between left and right motor association areas, although 'the callosal pathway marked a probably does not exist'. The numbers refer to apraxia and aphasic conditions that might occur when the connections illustrated by the arrows are interrupted. Reprinted with permission from Duquesne University Press. (*b*) A contemporary elaboration of these connections, with numbers referring to clinical deficits expected with lesions at the relevant site (Zilles 1990). Reprinted from Zilles (1990), with permission from Academic Press.

The arrow is one of the most frugal graphic symbols devised by man. It presumably developed from the line, which could also be adapted by various other means including labelling the ends of the line with letters and the current use of colour gradients (Young 1992). All these techniques endowed lines, including those used in neurological illustration of brain function, with directional properties. Sometimes conversion of line to arrow has even been explicit; thus when discussing cortical and thalamic projections, Crick & Koch (1998) use digraphs (directed graphs) with 'each line having an arrow on it to show its direction'. Such techniques have enabled the line, with its capacity otherwise restricted to straightforward mapping functions, to be developed into a linear symbol endowed with directional properties—that is the arrow. The arrow can then be developed further in order to provide additional functional information, using methods such as colour coding, interrupted lines and different thicknesses of arrow.

When specifically considering illustration of the functions of the brain, the meaning and implication of arrows become clearer when viewed in the wider scientific context. In its earliest use in hydrology the arrow simply represented direction of flow, and this was probably what the arrow represented when it was first introduced into neurological illustration in the 19th century. The arrow, however, can also be used to show speed and force of water currents; there is now information not only about direction but also about the motion of the water—its functional properties. Similarly the arrow in electrical circuit diagrams can delineate not only direction but also magnitude of current; in studies of sound and music the arrow head indicates changes in loudness; and in chemistry the arrow often denotes the process taking place during a chemical reaction. Paralleling the development of the arrow in neurological illustration is the similarly 19th century development in the use of arrows in cartography and historical atlases; evolving historic events, intensity as well as direction of transportation of materials, and force of influence and invasion are some examples in which arrows can reveal dynamic, 'functional' information (see Black 1997). All these disparate examples indicate that the humble arrow can reveal far more complex information than just direction.

What of arrows drawn on the brain? Arrows are different from the lines that were used by the Renaissance draughtsmen of the past or by some diagram makers even today, for arrows by virtue of their shape show direction. Implicit in direction is a coming from and a going to, and this necessarily takes time. Thus the arrow, by providing directional information, concisely conveys information about time—that 'single-direction flow of events' (Gregory 1981). Time is a property that is inherent in function rather than structure, as exemplified in the neurological context by the time that is needed for a nerve impulse to propagate, or for substances within a nerve to flow. The arrow, which represents such temporal processes, therefore proves to be a graphic symbol that can most succinctly indicate function.

7. PROBLEMS WITH ARROWS

As with all symbols interpretation can be fraught with difficulties, for what do the different images of arrows truly convey? Representation of established processes, impressions, suppositions or possibilities? Arrows are commonly used with neither explanation nor indication of their contextual meaning. Often it appears that it is by virtue of our familiarity with the symbol and by our suspending critical evaluation that the arrow proves to be anything other than a visual embellishment, sometimes trivial and sometimes devoid of meaning. Yet our ways of thinking are highly influenced by what we see, and perhaps in general we too readily accept information that is conveyed by illustration. For example, serious doubts about the value of the block diagrams which appear particularly in the psychological literature were expressed by Weiskrantz (1968), who commented that these diagrams were 'just a labeling device but possess even less utility than most labels, because they have not even the virtue of providing us with the opportunity to learn what the labeled entity looks like . . .'. Indeed, 'the subtlety of ways in which diagrams have been pressed into service to represent concepts . . . carries implicit dangers; the convention becomes reality' (Roche 1993). On occasions the arrow seemingly buttresses information when this is particularly tenuous; even the simple drawings of the diagram makers of a century ago would have been as difficult to validate then as are today's arrowed diagrams, as for example those of cerebellar circuitry or of mechanisms delineating deep dyslexia referred to earlier (§3), though we view the diagrams with scarcely a thought.

A process, i.e. a function, must take place in a structural context, and this has led to the use of arrows superimposed upon structures—however slight the evidence for that correlation may be. Arguably the most contentious issue when arrows are used to illustrate brain function, however, is the assumption that there are more or less directionally ordered processes that take place consistently and in identifiable structures in the brain. The notion of simple structure–function relationships, which originated in its contemporary form from 19th century phrenology, is becoming increasingly questioned, and is tending to be replaced by concepts of functional and effective connectivity (Friston 1994) and widespread distributed networks. Again, conclusions about mechanisms of brain function reached from traditional stimulation or lesion studies are being consigned to history in the face of molecular pharmacological data indicating far more complex and widespread mechanisms than had previously been envisaged (Izquierdo & Medina 1998). It is not surprising, therefore, that arrows superimposed on structure appear increasingly difficult to justify.

The problem in using symbolic arrows in the face of uncertain mechanisms is exemplified by the example of arrows drawn coursing through the brain and delineating mechanisms subserving speech. Positron emission tomography (PET) studies reveal the considerable variation in patterns of cerebral activation seen in normals and in those recovering their speech after stroke (Frackowiak 1997); wisely avoiding the pitfall of simplicity, the scan images are not illustrated with arrows, for where and how could arrows be shown? Interrupted arrows would have to be, and indeed have been (figure 5*b*), drawn in order to illustrate the consequence of a stroke or other lesion, but how would the arrows be redrawn if speech returned? Arrows may be helpful in providing a simplistic, schematic outline of normal structural and functional correlations, but the clarity provided by the arrows is tenuous, and the imaginative and mostly speculative bases for these arrows generally renders them of limited use.

Whilst Ramón y Cajal knew what the neural elements looked like, he could only surmise how they might function—yet some of his drawings were adorned with arrows to suggest mechanisms that were not demonstrable. Even today, swathes of arrows are still pictured across the hemispheres or within the depths of the brain, superimposing sometimes uncertain information upon tracts and other structures for many of which, at least in humans, only rudimentary detail is available. For example, currently neural 'projections' are often represented by arrows which serve to correlate anatomical

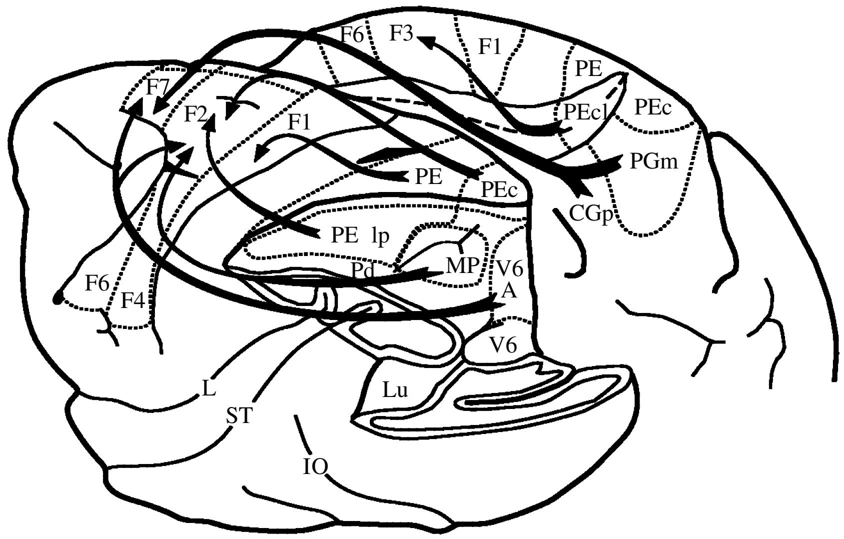

Figure 8. An example of the uncertain concept of 'projection'. Arrows showing parietal projections from areas located in the superior parietal lobule; the interpretation of the arrows and their relation to cerebral function are unclear. Reprinted from Rizzolatti *et al.* (1998), with permission from Elsevier Science.

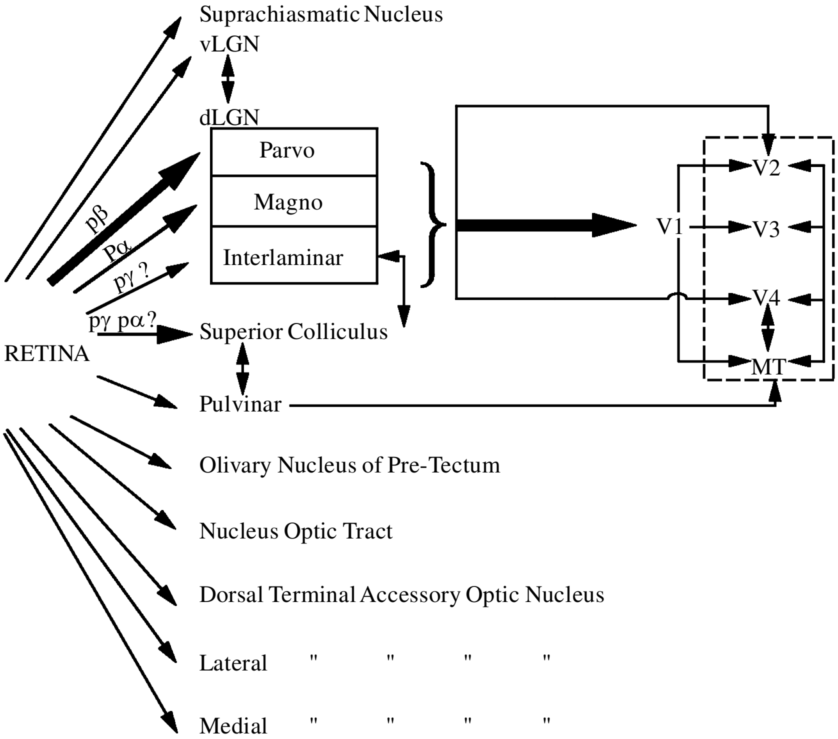

Figure 9. Arrows which simplify: a diagram showing the 'known pathways from the eye into the brain, together with the initial cortical projections. The thicker arrows indicate the heaviest and most studied projections'. Reprinted from Cowey & Stoerig (1991), with permission from Elsevier Science.

data revealed by neural tracing techniques with functional data obtained from single-neuron recording and intracortical microstimulation (e.g. Rizzolatti *et al.* 1998) (figure 8). The impressive arrows are of course stylized but they are also enormously elaborated from the relatively sparse data available. Arrows superimposed on the brain, in reality, may be little more than indicators of conceptual processes or supposed structure–function relationships, often based on physiological data largely or solely obtained from animal studies.

Many arrows drawn on pictures of the brain can best be viewed perhaps as graphic counterparts of 'association' as in the context of 'association areas', a pertinent analogy since the term 'association' has both an anatomical and a psychophysical meaning, as in the 'association of ideas' (Nathan 1969). That association fibres connecting parts of the cerebral cortex formed the basis for the psychological association of ideas and words is an old concept, but one which is uncomfortably reminiscent of many contemporary images of structure upon which are placed arrows related to function. One of the major problems that permeate the use of arrows in illustration of neurological function is that, except when double-headed or twin arrows pointing in both directions are used, only unidirectional and linear information is conveyed. It seems highly improbable that cerebral processes always or perhaps ever take place in this fashion, and bidirectional, omnidirectional and diffuse neural function could not possibly be illustrated by means of arrows.

Use of the arrow also involves another simplification; inevitably arrows (and lines) often reveal only selected pathways and functions. There has been understandable simplification but at the cost of accuracy and completeness. For instance, illustrations of the visual pathways rarely include either lines or arrows indicating alternative subcortical pathways. I suggest this is partly because these alternative pathways are less well understood and therefore less easy to illustrate, and partly because in many instances a diagram would become too complex and incomprehensible if all known pathways with their arrows were displayed. Such alternative visual pathways have been illustrated in other ways, as in the necessarily simplified and diagrammatic form using free-standing arrows (Cowey & Stoerig 1991) (figure 9). Here there is surely no ambiguity about what the authors intended when using arrows: a simple, schematic shorthand for some of the pathways and projections subserving vision.

8. ARROWS IN THE FUTURE?

We may have learnt to ignore or accept the problems inherent in arrows and other symbols that illustrate both known and speculative brain functions, but a new issue is now emerging. With these functions proving to be ever more complex, the ability to illustrate them by conventional graphic means often appears to have been overwhelmed. Arrows cannot usefully illustrate parallel processing, or three-dimensional functions, or countless simultaneous processes taking place over different timescales; as seen in figure 8, arrows also struggle to display functions superimposed upon structures. Not surprisingly, whilst arrows are sometimes used to show, for example, vector information in magnetoencephalographic studies, arrows very rarely appear on contemporary illustrations of positron emission tomography or functional magnetic resonance imaging data. This absence of arrows appears inevitable, because the temporal relationships and even the topographical connections between the coloured areas displayed on functional imaging scans are currently unknown.

The arrow will surely always remain useful as an explanatory device and teaching aid, but will the arrow as a means of representing brain function disappear from the specialist scientific literature? I suggest that when data become so complex as to defy display by means of graphic devices such as the arrow, then other visual techniques and resort to more non-representational and mathematical symbols become necessary. Such symbols are seen, for example, throughout the literature dealing with neural networks. Images that deal with brain function will inevitably become increasingly abstract and will be depicted, as in many areas of contemporary science, not by arrows but by the mathematical symbols that are the language of the physicist and computational neuroscientist.

9. CONCLUSION

The arrow, a symbol occupying 'the zone between the visual image and the written sign' (Gombrich 1982), is arguably the most remarkable diagrammatic symbol ever devised. In neurological illustration of brain functions, the use and interpretation of this elegant symbol prove to be unexpectedly complex and often contentious. Entering the scientific world in the middle of the 18th century, this intriguing graphic device reached the domain of the neuroscientist in the 19th century, became enormously popular in the 20th century, and may well decline in its usefulness in the 21st century, yielding to some extent in the scientific literature to the abstract symbols of mathematics.

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