Improbable areas in the visual brain

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Recent results from anatomical, physiological and imaging experiments cast doubt on the existence of some areas in the primate visual brain and call for a much overdue re-assessment of what is a conceptually highly unsatisfactory view of how the primate visual brain is organized, a view that has survived more or less unscathed for at least 15 years and has been embraced uncritically by a significant element in the human brain imaging community. That view can be summarized as follows: that there are areas in the visual brain that represent only one quadrant of the visual field, leaving the other quadrant of the hemifield unrepresented, or represented in another area, leading to what Jon Kaas has called ‘improbable areas’. It is not the improbability of such a view that is surprising; rather, it is its ready acceptance on the basis of questionable evidence.

The right half of the visual field is represented in the left brain hemisphere, and vice versa, the two separate representations being unified by a commissure that links the two cerebral hemispheres, the corpus callosum (Fig. 1). The discovery of many visual areas in the brain [1–4] with the promise of more to come, naturally raises the question of which criteria should be used in conferring the status of a visual area on a cortical zone. Two obvious ones are that an area should be activated by visual stimuli and should have an independent and more or less complete map of the contralateral visual field, to include both the upper and lower quadrants. This is so, even if a given quadrant, or part of the retina, claims a disproportionately large space in a cortical area, as happens even at the level of the primary visual cortex (V1). To this can be added other features, such as a distinct set of anatomical (including callosal) connections, identifiable and unique functional properties [1] and a distinctive architecture, although the search for the latter has not always been fruitful. In 1986, Van Essen’s group [5] proposed a radical departure from this list by purporting to show that one of the areas constituting the visual brain, area V3, does not have a complete representation of the visual field, as had been supposed from earlier anatomical studies [6,7]. Instead, they conceived of this area, which occupies a narrow strip anterior to area V2 (Figs 1 and 2) as consisting of two different areas – a dorsal one called V3 and a ventral one known as ‘VP’ – each representing one quadrant only of the contralateral hemifield. They proposed this even though the retinotopic map in ‘VP’ in both the human [8–10] and the monkey [3,11] is a mirror image of that in upper V3 (Fig. 1). The separation into two distinct areas was based on the supposition that lower V3, unlike its upper counterpart, not only lacks a direct anatomical input from V1, but also has a high proportion of colour-selective cells [5]. The implication was obvious: ‘VP’ is an area registering activity only in the upper contralateral quadrant, without the capacity to register the same activity (including, above all, colour) when it occurs in the lower contralateral quadrant – or leaving it to some other improbable area, one registering activity in lower quadrant alone, to do so. This, in turn, leads to the supposition that there could be other improbable areas in which only one quadrant of the visual field is represented (Fig. 3). This is odd: psychophysical experiments have shown that some attributes are more readily perceived when presented in one quadrant than in another [12,13], but none has ever shown that an attribute can be perceived only when presented in one quadrant alone.

In fact, the evidence against such improbable areas in the visual brain is mounting. The notion that there is an asymmetrical anatomical input from V1 to upper and lower V3 was questioned years ago, when it was shown that there is a direct input from V1 to lower V3 in Cebus. 

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Fig. 1. Representation of the visual field in visual cortex. (a) Representation of the right hemifield in the primary visual cortex, V1. The upper quadrant of the hemifield (red) is represented below the calcarine sulcus, whilst the lower quadrant (green) is represented above the calcarine sulcus. The corpus callosum is shown in blue. (b) The representation of the visual field in visual areas V1 to V3, shades of red and pink indicating representation of the upper quadrant and shades of green indicating representation of the lower quadrant. The dotted lines show the representation of the horizontal meridian of the visual field (horizontal dotted line in part a) in these visual areas. The solid lines between the areas show the representation of the vertical meridian.
monkeys [14] and when detailed recording experiments showed that there is a continuous representation of visual fields in V3 from lower to upper quadrants as one proceeds dorsoventrally [11]. Such findings, made in New World monkeys, have been substantially reinforced by a more recent study [15] showing that in the Old World macaque monkey, too, there is a direct input from V1 to V3. That study, with other supporting evidence [16], has led Lyon and Kaas to conclude that V3 is one continuous area, not two separate areas, and that it is characteristic of all primates. Thus, one of the main criteria for separating V3 into two areas, namely an asymmetry in anatomical input from V1, has lost its force.

The ready acceptance of such a subdivision in the macaque, and its uncritical translation into the human brain (in which the two corresponding areas have also been called V3 and ‘VP’) is surprising, because all human imaging experiments have shown that upper and lower parts of V3 are activated in the same way [17]. This speaks against its separation into two areas. More significantly, no human imaging study has ever shown that human ‘VP’ is specifically or more vigorously activated with colour, even when the question has been directly addressed [18]. The second criterion for separating V3 into two independent areas (namely, an emphasis on colour in ‘VP’) is, thus, also weakened. The consensus of the evidence seems to be that there is no justification for separating V3 into two areas, on either anatomical or functional criteria. V3 is, instead, one whole area, in which both upper and lower fields are represented — as was originally proposed.

The ‘improbable’ becomes implicitly acceptable

A consequence of the unquestioning acceptance of the separation of V3 into two areas has been the implicit acceptance that there might be other such improbable cortical areas in which only one quarter of the visual field is represented. The advent of the phase-encoding method [19] for mapping visual fields in human cerebral cortex revealed, in some hands, an area ‘V4v’ [20,21] located posterior to the colour centre. Blue lines around V4 show the position of ‘V8’ according to Hadjikani et al. [24]. Purple circles caudal to V4 show the position of area ‘V4v’ of Sereno et al. [7] and Hadjikani et al. [24], which has yet to be shown to be a separate area [18]. Inset shows the visual field itself.

![Fig. 2. Areas of the visual brain. Areas V3 (dark blue), V3A (violet), V4 (red) and V5 (pink), and those of face and object recognition (blue), receive their input largely from V1 (yellow) and V2 (green).](http://tins.trends.com)

![Fig. 3. Two theories of how a hemifield is represented in the brain. The coloured quadrants on the screen (a) are represented in an arbitrary region in the contralateral side of the brain (b). (i) The conventional theory, which shows an orderly, continuous and more or less complete map of the contralateral hemifield. (ii) Van Essen’s theory that such areas could be subdivided into two independent areas on the basis of asymmetry in anatomical input and differences in function.](http://tins.trends.com)

![Fig. 4. A ventral view of the human brain showing the representation of the upper visual field (red) and the lower visual field (green) in V4 and V4α, the latter a newly discovered area within the human colour centre. Blue lines around V4 show the position of ‘V8’ according to Hadjikani et al. [24]. Purple circles caudal to V4 show the position of area ‘V4v’ of Sereno et al. [7] and Hadjikani et al. [24], which has yet to be shown to be a separate area [18]. Inset shows the visual field itself.](http://tins.trends.com)
are topographically mapped within human area V4 as originally defined [25], reveals eloquently the confusion that is traceable in large measure to the blind acceptance of the concept of visual areas with only a quarter-field representation of the visual field. Hadjikhani et al. showed, as we had before them [22], that there is a complete representation of the contralateral hemifield within the ventrally located colour centre, area V4. But because of their belief in the existence of an area 'V4v' that is distinct from our V4 and which represents only the upper contralateral hemifield, they imagined that they had discovered 'a new retinotopic area that we call V8'. This 'previously undifferentiated cortical area' was consistently located just beyond the most anterior retinotopic area defined previously, area V4v (my emphasis on the v). An examination of their results shows, however, that their 'new' retinotopic area has the same coordinates as our V4 and is, thus, nothing more than the re-discovery of a previously defined visual area (Fig. 4). Heywood and Cowey [25] accepted this claim of a new area uncritically. They wrote that a 'newlydefined [sic] color area' had been found and that it is this area, 'V8', rather than ‘the favorite candidate, V4’, that, when lesioned, produces cortical colour blindness. This led them unquestioningly to the view that ‘the human color center is distinct from area V4' (note how, in this uncritical acceptance, the small v has been dropped from the equation). This is despite the fact that the ‘newlydefined color area’ has the same brain coordinates as V4 (Fig. 4).

Does 'V4v' exist?

In fact, V4 and the ‘newlydefined color area’ not only share the same coordinates, but also are both located anterior to ‘V4v’. Tootell and Hadjikhani have since admitted [27] that their 'new' cortical area is, in fact, nothing more than the previously defined colour centre but they have pleaded that it should be called ‘V8’, because the fourth visual map is constituted by their improbable area ‘V4v’. But does such an area exist? We have not been able to find any evidence for a separate area ‘V4v’. Nor, seemingly, have others [28]. The question has been directly addressed by Wade et al. in the most detailed topographic studies of the human visual brain to date [17]. They could not find a quarter-field representation corresponding to area ‘V4v’. Instead, they found that V4 constitutes the fourth visual map, abuts V3 and corresponds to the colour centre of the human brain (Fig. 5). Thus, the argument for calling the area ‘V8’ is etiolated. Given the evidence against brain areas with only quarter-field representations, it is up to the proponents of ‘V4v’ to demonstrate its existence convincingly or to withdraw it.

Precedence is finally used explicitly – the case of ‘KO’

The acceptance of the improbable ‘V4v’ was made possible by the implicit acceptance of the improbable ‘VP’. But the defunct and improbable ‘VP’ has also been used explicitly as a precedent for yet another improbable area, ‘KO’ (kinetic occipital area), claimed to be ‘specialized for the processing of kinetic contours’ [29]. Attempts are currently being made to equate human ‘KO’ with the dorsal part of area V4 in the macaque, ‘V4d’. The improbability of such an equation is reinforced by the improbability of the function imputed to ‘KO’ from the evidence currently available.

‘V4d’ is the part of area V4 in the macaque that represents lower visual fields but it has never been considered to be a separate area. The equation of this part of macaque V4 alone with human ‘KO’ implies that ‘KO’ represents the lower contralateral visual fields only. Recent evidence shows that ‘KO’ is engaged in extracting shapes from all sources and not from kinetic contours alone [30]; it is, therefore, not specialized for kinetic contours and, to avoid misleading functional names, is thus better referred to as area V3B [31]. It would be strange if such an area were to represent one quadrant alone, for this would imply that it extracts contours in only one quadrant – an improbability. In fact, Smith et al. [31] have concluded that V3B (‘KO’) represents only the lower contralateral visual field, but their figures could equally well be interpreted to mean that V3B contains a complete
and independent representation of the entire contralateral hemifield, with the lower quadrant claiming more cortical space. Moreover, other retinotopic studies of human visual cortex show that there is a complete representation of the contralateral hemifield in V3b (‘KO’) [18].

The equation of human V3b with only a part of monkey V4 (dorsal V4 or V4d) would mean that human V3b and monkey V4d are improbable areas – even though the evidence suggests that both human V3b and macaque V4 have a complete map of the contralateral hemifield – ‘V4d’ being nothing more than the dorsal part of V4 in the macaque. In trying to understand why such claims have been so uncritically accepted, it becomes obvious that precedent, and especially that of ‘VP’, has played a big role. Tootell and Hadjikhani have written that ‘Although such ‘separated’ quarter-field representations are conceptually unsatisfying, they are not unprecedented: the quarter-field representations in macaque ‘V3’ and ‘VP’ have long been considered separate areas by some investigators, based on empirical differences between V3 and VP’ [27]. But there are also many who do not accept such improbable areas, and the weight of evidence is on their side.

It is a wonder that so fragile a concept as that of visual areas in which only a quarter of the visual field is represented should have been so uncritically accepted for so many years, and that so much should have been built on such a flimsy view, even when much evidence speaks against it. This view was largely erected on the basis of empirical differences between V3 and VP [27]. But there are also many who do not accept such improbable areas, and the weight of evidence is on their side.

References