PERSPECTIVE

Resolving the organization of the territory of the third visual area: A new proposal

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Abstract

In primates, the cortex adjoining the rostral border of V2 has been variously interpreted as belonging to a single visual area, V3, with dorsal V3 (V3d) representing the lower visual quadrant and ventral V3 (V3v) representing the upper visual quadrant, V3d and V3v constituting separate, incomplete visual areas, V3d and ventral posterior (VP), or V3d being divided into several visual areas, including a dorsomedial (DM) visual area, a medial visual area (M), and dorsal extension of VP (or VLP). In our view, the evidence from V1 connections strongly supports the contention that V3v and V3d are parts of a single visual area, V3, and that DM is a separate visual area along the rostral border of V3d. In addition, the retinotopy revealed by V1 connection patterns, microelectrode mapping, optical imaging mapping, and functional magnetic resonance imaging (fMRI) mapping indicates that much of the proposed territory of V3d corresponds to V3. Yet, other evidence from microelectrode mapping and anatomical connection patterns supports the possibility of an upper quadrant representation along the rostral border of the middle of dorsal V2 (V2d), interpreted as part of DM or DM plus DL, and along the midline end of V2d, interpreted as the visual area M. While the data supporting these different interpretations appear contradictory, they also seem, to some extent, valid. We suggest that V3d may have a gap in its middle, possibly representing part of the upper visual quadrant that is not part of DM. In addition, another visual area, M, is likely located at the DM tip of V3d. There is no evidence for a similar disruption of V3v. For the present, we favor continuing the traditional concept of V3 with the possible modification of a gap in V3d in at least some primates.

Keywords: Primates, Visual cortex, Area 17, Area V3, Vision

Introduction

The issue of how cortex along the rostral border of V2 in primates is organized has been difficult to resolve, and a number of different proposals are currently viable. One popular proposal, put forward by Zeki (1971) and supported by Gattass et al. (1988), is that a single visual area, V3, forms most of the rostral border of V2 and gets direct input from V1. This concept has been challenged in two ways. First, Allman and Kaas (1975) presented microelectrode mapping data that seemed to support the conclusion that part of the territory of dorsal V3 (V3d), thought to represent only the lower visual quadrant, represented part of the upper visual quadrant instead. Allman and Kaas (1975) proposed that this part of the V3 territory was part of a dorsomedial (DM) visual cortical area, that represented both the upper and lower visual quadrants, as a “proper” visual area should (Kaas, 1993a; Zeki, 2004; Kaas, 2005a). This evidence for the representation of the upper visual quadrant along the dorsal border of V2 has received considerable support from the results of subsequent microelectrode mapping experiments (e.g., Allman et al., 1979; Krubitzer & Kaas, 1993) and from studies of the connections of cortex along the border of dorsal V2 (V2d) (e.g., Beck & Kaas, 1998). From the beginning, this type of evidence was considered to be incompatible with the V3 concept, and it is not easy to dismiss.

The other argument against the V3 concept is based on the conclusion that V1 does not project to the ventral V3 (V3v) territory (e.g., Van Essen et al., 1986; Felleman & Van Essen, 1987, 1991; Felleman et al., 1997; Nakamura et al., 2004). Although the microelectrode mapping data (Gattass et al., 1988) revealed a retinotopic organization that is highly compatible with the proposed organization of V3v, direct projections from V1 to V3v are expected from the Zeki (1971) proposal. Instead, the V3v region was considered to be either a different visual area, the ventral posterior (VP) area (Newsome et al., 1986), with the improbable feature of representing...
only the upper visual quadrant, or part of a complete visual area with an unknown other half. Other data from related studies on neuron response properties were interpreted as further evidence that the V3d region and the V3v region are not parts of the same visual area (Burkhalter & Van Essen, 1986; Burkhalter et al., 1986; Felleman & Van Essen, 1987). Thus VP and V3d were considered to be different visual areas representing only one visual quadrant, the upper (VP), or the lower (V3d) visual quadrant. This argument against the V3 concept has now been dismissed, at least in our minds, by recent and compelling evidence that V1 projects in a similar magnitude and in the expected retinotopic pattern, to both V3d and to V3v (or VP) (Lyon & Kaas, 2001; 2002a,b,c). Uncertainties about the areal locations of recorded neurons in single unit studies, as well as procedural differences, allow a reconsideration of the proposed differences in the response properties of neuron populations in V3d and VP (V3v), but the evidence for part of an upper visual quadrant representation along the rostral border of V2d continues to be supported by more recent evidence.

Here, we consider the evidence for V3 and the various proposals for cortical organization in the V3 territory in more detail and suggest instead that V3d is not continuous but has a gap or hole in which part of the upper visual quadrant is represented (Fig. 1). Such a gap could account for much of the conflicting microelectrode mapping and connectional data. The gap may be an intrusion of part of some visual area other than DM, and the gap may or may not be present in all primate taxa. There is, yet, no comparable evidence for a gap in V3v. We propose that the collective evidence is most compatible with the concept of a complete V3 with dorsal and ventral halves, as originally proposed by Zeki (1969, 1971) andGattass et al. (1988) on connectional and mapping evidence, with the likelihood of a gap in V3d of at least some and perhaps all primates. DM remains as a complete visual area just rostral to V3d. We review evidence in support of this proposal, while recognizing that additional evidence may be gathered that would further support this or alternative proposals.

Evidence for V3

The concept of a third visual area, V3, in primates reflects a long history. Brodmann (1909) portrayed three visual areas in the occipital cortex of primates, a primary area 17, and two bordering and nearly surrounding band-like areas, area 18 and area 19. Other investigators were proposing two or three visual areas about the same time (see Kaas, 1997 for review). For example, von Economo (1929) divided occipital cortex of humans into occipital areas OC (area 17), OB, and OA, and later, Konorski (1967) labeled the early visual areas VI, VII, and VIII. Three architectonic visual areas, 17, 18, and 19, had also been proposed for cats (Otsuka & Hassler, 1962), and Hubel and Wiesel (1965) provided microelectrode mapping evidence for areas 17, 18, and 19 of cats, corresponding to retinotopic representations, VI, VII, and VIII (or more commonly today, V1, V2, and V3). Others provided further supporting evidence for these three visual areas in cats from more extensive microelectrode mapping (e.g., Tusa et al., 1979) and patterns of cortical connections (e.g., Wilson, 1968). Myers (1965) was one of the first to use patterns of cortical connections in macaque monkeys to subdivde occipital cortex, but his complex summary diagram had little subsequent influence. Soon, thereafter, on the basis of area 17 (V1) connections, Cragg (1969) identified two extrastriate targets as VII and VIII, while Zeki (1969) presented his similar results in terms of areas 18 and 19. The areas 18 and 19 of Zeki did not correspond very well with the architectonic fields 18 and 19 of Brodmann (1909), and the terms V1, V2, and V3 were subsequently used (Zeki, 1971). For the most part, the connections of V1 in subsequent studies in monkeys were interpreted as being with V2 and V3, or areas 18 and 19 (e.g., Rockland & Pandya, 1979; Perkel et al., 1986; however, see Spatz & Tigges, 1972).

Such early anatomical evidence for V3 was, however, incomplete, allowing for other interpretations of visual cortex organization. As the part of V1 (area 17) that is available on the dorsal surface of occipital cortex for study represents central and paracentral vision of the lower visual quadrant, the connections of V1 that were revealed in studies were mostly to the dorsal half of V3 that also represents the lower visual quadrant, and not the territory of V3v that represents the upper visual quadrant (see Lyon & Connolly, 2012). This lack of evidence on ventral V1 connections led to the conclusion that the territory of V3v does not receive projections from V1, while the territory of V3d does receive V1 projections. For this reason, together with proposed differences in cortical architectonics (Van Essen et al., 1986; Rottschey et al., 2007), single neuron response properties (Burkhalter & Van Essen, 1986; Burkhalter et al., 1986) and functional magnetic resonance imaging responsiveness (Tootell et al., 2004) in V3d and V3v regions, the territory of V3v was reidentified as the VP area. The term VP emerged from unpublished microelectrode mapping studies of Allman and Kaas,
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which revealed a retinotopy consistent with V3v. The term, VP was subsequently used with the earlier mapping evidence from owl monkeys by Newcombe & Allman (1980). However, the concept of VP and V3d as separate visual areas, with VP representing only the upper visual field, and V3d only the lower visual field, seemed improbable to some (Kaas, 1993b; Zeki, 2004), and other proposals emerged, including the concept that different parts of the territory of V3d are subsumed within several visual areas, DM, DI, and M (e.g., Allman & Kaas, 1975), or that VP continues onto the dorsal surface of the cerebral hemisphere to form a somewhat smaller representation of the lower visual quadrant (e.g., Rosa et al., 2005). As this issue of cortical organization has not been fully resolved, some depictions of visual cortex organization in macaques and humans continue to illustrate a ventral VP and a V3d (e.g., Grill-Spector & Malach, 2004; Rottschy et al., 2007), while others include a V3d and V3v (e.g., Brewer et al., 2002; Vanduffel et al., 2014).

The concept of VP requires reconsideration, as there is now compelling evidence that both the V3v/VP territory and the V3d territory have interconnections with V1 in topographical patterns that conform to the proposed retinotopies of V1, V3v, and V3d. Such patterns of connections have been revealed for macaque monkeys (Lyon & Kaas, 2002b), four species of New World monkeys (Lyon & Kaas, 2002c) (Lyon & Kaas, 2002c), and a prosimian primate (Lyon & Kaas, 2002a). Such injections of tracers in various retinotopic locations in V1 produced dense foci of labeled neurons (and axon terminals, depending on the tracer) in retinotopically matched locations in V2 and a corresponding retinotopic location in V3d or V3v. Less dense foci of labeled neurons and axon terminals were consistently found in the middle temporal visual area, MT, and the DM visual area. The labeled foci for V3v and V3d were similar in magnitude, but clearly less in magnitude than those in V2. The same injections produced somewhat smaller magnitudes of label in MT and even less in DM. These results provide strong evidence that V3v and V3d receive similar inputs from V1, and that together, they constitute a complete representation of the contralateral visual hemifield. In addition, the foci of label in the DM region seem to reflect a complete representation without any involvement of the territory of V3d, as injections separately labeled the DM and V3 regions, as well as MT. Finally, there is no evidence from these studies that prosimian primates, New World monkeys, and Old World monkeys differ in any major way in having or not having a complete V3 representation. These three areas appear to be basic to the primate visual system, as there is considerable retinotopic fMRI imaging evidence for the existence of V1, V2, and V3 in the visual cortex of humans (e.g., Larsson & Heeger, 2006; Abdollahi et al., 2014; Vanduffel et al., 2014).

While any theory of visual cortex organization in primates will need to account for the anatomical observations on V1 connections, it remains important to account for the proposed differences in the single neuron response properties of neurons and in cortical architecture for the V3v and V3d region. Previously, we have suggested that such observations may be unreliable because of uncertainties that recordings were completely from equivalent parts of V3d and V3v, or were restricted to V3d or V3v (Kaas & Lyon, 2001; Kaas, 2005b; Lyon, 2013; Lyon & Connolly, 2012). It is also the case that the proposed modular organization of V3 (Lyon & Kaas, 2001; Xu et al., 2004; Fan et al., 2012) could bias recording results by favoring one type of module over another and could influence the architectonic description of the V3 territory. But real differences in response properties of neurons in V3v and V3d, and cortical architecture, could exist, possibly reflecting the different requirements of upper field and lower field vision (Previc, 1990) or forcing another interpretation of visual cortex organization (see below). There may be architectonic differences in V3d and V3v as well, but there is little agreement on this (Lyon & Kaas, 2001; see; Lyon & Connolly, 2012). For example, in characterizing neurofilament protein patterns, Hof and Morrison (1995) concluded that “there was no difference between the staining patterns of the dorsal and the ventral parts of area V3”. We now consider the other strong evidence for V3 as a single complete visual area.

Microelectrode mapping and functional imaging evidence for V3

The other impressive evidence for a V3 with a systematic representation of the complete visual hemifield, in primates, stems from the early microelectrode mapping of V3 in macaques byGattass et al. (1988); (see Rosa et al., 2000 for New World Cebus monkeys). Gattass et al. (1988) revealed a single overall representation of the contralateral visual hemifield in V3, split along the representation of the horizontal meridian, from peripheral vision of the lower visual quadrant to foveal vision, and then to peripheral vision of the upper visual quadrant in a sequence of recording sites from DM cortex to dorsolateral cortex to ventromedial cortex in parallel but with a mirror reversal of the retinotopy of V2. A similar organization for V3 has been demonstrated repeatedly with fMRI techniques in monkeys and humans (e.g., Tootell et al., 1997; Brewer et al., 2002; Wade et al., 2002; Orban et al., 2004; Kolster et al., 2009; Kolster et al., 2010; Vanduffel et al., 2014), and other microelectrode mapping results in monkeys have been consistent with the proposed organization of V3v (Newsome & Allman, 1980; Newsome et al., 1986; Rosa & Tweedale, 2000). In addition, the expected retinotopy of V3d has been revealed in optical imaging studies of V3d organization in prosimian galagos (Fan et al., 2012) and New World owl monkeys (Lyon et al., 2002; Kaskan et al., 2009), where V3d is exposed on the dorsal surface of the brain. However, most of the recent, alternative proposals for the organization of visual cortex in primates have been concerned with cortex in the V3d region, where there is microelectrode mapping and connectional evidence for some of the rostral border region of V2 being directly adjoined by part or parts of the representation of the upper visual quadrant, not the lower visual quadrant, as proposed for V3d. It is this evidence that we consider next.

Microelectrode recording and anatomical evidence for one or more upper visual quadrant representations along the V2d rostral border

In an early microelectrode mapping study of visual cortex organization in owl monkeys, Allman and Kaas (1975) found evidence for both representations of parts of the upper and lower visual quadrant in the cortex just rostral to V2d. The upper and lower quadrant representations were combined to define a new visual area, the DM visual area, which has been subjected to considerable further study (e.g., Krubitzer & Kaas, 1993; Beck & Kaas, 1998; Beck & Kaas, 1999; Rosa & Tweedale, 2005; Rosa et al., 2005; Lui et al., 2006; Rosa et al., 2009). More medially in cortex rostral to V2d and extending onto the medial wall of the cerebral hemisphere, Allman & Kaas (1976) provided evidence for a second representation of the upper visual quadrant as part of another complete representation, the medial visual area (M), an area in the relative location of what is likely the same visual area in macaques (Colby et al., 1988) and Cebus monkeys (Sousa et al., 1991; Neuenschwander et al., 1994) renamed the parieto-occipital area. Other microelectrode...
mapping studies have found evidence for the representation of parts of the upper visual quadrant along the rostral border of V2 in marmosets (e.g., Rosa & Schmid, 1995; Rosa & Tweedale, 2001; Rosa et al., 2005), and this led to proposals for various arrangements of visual areas along the border of V2d, including DM (also see, Jeffs et al., 2013). Microelectrode recordings just rostral to V2d in prosimian galagos also revealed evidence for a representation of part of the upper visual quadrant in the territory of V3d (Allman et al., 1979; Rosa et al., 1997). Although some of these results may reflect recordings rostral to V3d (For review, see Lyon & Connolly, 2012), it is difficult to dismiss all of these observations.

In addition to this physiological evidence, the existence of an upper quadrant representation along the rostral border of V2d is supported by evidence from studies of cortical connections. Injections of tracers near the proposed V2/V3 border or in the proposed territory of V3 sometimes reveal connections that differ from those expected for V3d, especially those with parts of V1, V2, and other visual areas representing the upper visual quadrant. (e.g., Knobitzer & Kaas, 1990, 1993; Beck & Kaas, 1998; Rosa et al., 2005; Jeffs et al., 2013). Other injections in the V3d territory next to V2d, but attributed to DM, reveal patterns of connections with V2d and V1 that are highly consistent with the V3d concept (discussed in Lyon, 2013; also see Fig. 2). The difficulty in accurately identifying the rostral border of V2 and the width of V3, adds to the problem of interpreting such results. Additionally, cortex along the rostral border of V2d represents the region of the horizontal meridian, including a narrow strip of the upper visual quadrant (Jeffs et al., 2013). Thus, injections in V3d that include the V2d/V3d border zone could label neurons in the V2v/V3v border zone, as well as other places, and such patterns of label could be taken for evidence of a more extensive upper quadrant representation along the rostral border of V2d. Nevertheless, the possibility that some of these injections are revealing a representation of a large part of the upper visual quadrant next to part of V2d should be seriously considered.

**Does V3d have a gap?**

We are left with results that seem to support conflicting schemes of visual cortex organization. Earlier proposals argued that the territories of V3d and V3v formed complementary representations of the upper and lower visual quadrants or interpreted the ventral and dorsal territories of V3 as parts of two visual areas, V3d and VP. This controversy now seems to have been resolved in favor of V3v over VP. Thus, Abdollahi et al. (2014) have recently concluded that “V3d and V3v are now widely regarded as subdivisions of a single retinotopic area”. Nevertheless, the previously well-accepted concept of V3d remains in question. Attempts to resolve differences in interpretations and accommodate contradictory results have included renaming VP as VLP and extending VLP dorsally to include much of the territory of V3d, thereby forming a visual area with representations of both the upper and lower visual quadrants (Rosa & Tweedale, 2000; 2005). Other similar proposals have been made to accommodate the proposed locations of upper visual quadrant representations along the rostral border of V2d (Jeffs et al., 2013). Our alternate approach is to retain the overall concept of V3d but with a gap for part of an upper quadrant representation in the middle of V3d (Fig. 1) and at another location at the DM tip of V3d for area M.

Our recent optical imaging and microelectrode mapping study provided more evidence for V3d in prosimian galagos (Fan et al., 2012), while possibly allowing for such a gap. The optical imaging mapping results revealed the expected retinotopic organization of V3d, with a seemingly modular organization of orientation selective or nonselective neurons. Visual stimuli that were effective when placed in the lower visual quadrant were completely ineffective in the upper visual quadrant in activating cortex we defined as V1d, V2d, and V3d, including the possible gap region of V3d. In addition, a 100-electrode array with equally spaced electrodes was used to simultaneously record from neurons in fixed positions across V1, V2, and V3 in a strip of dorsal visual cortex as the neurons were activated by various visual stimuli. As expected, recordings from each of the three visual areas were clearly distinguished by receptive field locations and sizes, so that the receptive fields were smallest in V1 and largest in V3. All of the neurons in the sampled region of dorsal cortex had receptive fields in the lower visual quadrant, although some of the large receptive fields for neurons in the proposed V3 territory extended slightly past the zero horizontal meridian into the upper visual quadrant. These results provided further evidence for a V3d, adjoining V2, but no direct evidence for a representation of the upper visual quadrant in cortex next to V2d. However, the complete border region of V2d was not investigated with the 100-electrode array, and a gap in V3d could have been missed. Overall, the results based on injections in V1 and these other mapping results based on optical imaging or microelectrode recordings lead us to propose that V3v (VP) and V3d are closely matching parts of a single visual area, V3, as proposed by Zeki (1969) and Gattass et al. (1988). Yet, it also seems possible that the data reviewed in support of V3d are compatible with some of the data that argue for one or more upper visual quadrant representations extending near or to the rostral V2d border. Thus, we consider modifications of the V3d concept that are compatible with the overall V3 concept while allowing for discontinuities in V3d.

One further argument for V3 is the evidence that sensory areas in general tend to have congruent borders (e.g., Grill-Spector & Malach, 2004). Thus, receptive fields for neurons near the border between adjoining areas are similar in location on the sensory receptor surface. The reasons for this are unclear, but one area may serve as a template for the development of others, with the added benefit of allowing shorter interconnections (Van Essen, 1997). Whatever the reason, V3 thereby forms the expected representation along the V2 border with a reversal retinotopy. Because of similar constraints, a similar V3 may have evolved independently in carnivores and primates and perhaps other taxa (Rosa & Manger, 2005). Yet, a progression in representation from the lower visual quadrant of V2 into the upper visual quadrant in the territory of V3d would seem to be a possible alternative, as the rostral border of V2 represents the horizontal meridian that separates the lower and upper quadrants, and the border zone of V3 and V2 already represents parts of the upper and lower quadrant along the horizontal meridian (Jeffs et al., 2013). The argument against the V3d concept is based on the evidence for a gap or disruption in V3d by the intrusion of the representation of part of the upper visual quadrant, possibly as part of DM or some other visual area, or even as a separated fragment of a representation. In addition, there is good evidence for the visual area M, at the medial end of V3d that has an upper quadrant representation next to V2d (Allman & Kaas, 1976). A small disruption or gap in V3d would not necessarily be apparent in studies of V1 projections to V3, and such a gap might not be obvious in the retinotopy of V3d as revealed by optical imaging due to the modular organization of V3d (Lyon et al., 2002; Xu et al., 2004; Kaskan et al., 2009; Fan et al., 2012). Alternatively, small regions of cortex that are not activated above threshold in such studies may represent the upper visual quadrant, rather than being insensitive to the specific visual stimuli. In the optical imaging studies of V3d noted here,
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area DM was not activated above threshold. This is not a surprise as higher order visual areas are more depressed by anesthesia than early visual areas, such as V1, V2, and V3. Thus, the lack of optical imaging evidence for an upper quadrant representation within the V3d territory does not rule out the possibility. Conclusive evidence for the presence of such a gap would require that the description of V3d be modified, perhaps as in Fig. 1B. The alternative of a VP or VLP that extends along the rostral border of V2v and then curves rostrally away from V2d while being displaced by other visual areas (e.g., Rosa et al., 2009) does not seem consistent with the anatomical evidence of V1 connections to V3d and V3v that are in expected topographic locations relative to V2 and clearly greater in magnitude than those to DM.

Differences in the V3 region across primate taxa

Differences in the organization and functions of the V3 region of primates are likely to exist across taxa, especially those that have been in separate lines of primate evolution for many millions of years. As a clear example of a difference in extrastriate cortex, V2 of prosimian galagos does not have a well-developed banding structure in cytochrome oxidase and myelin preparations as in New and Old World monkeys, reflecting perhaps the over 60 million years of separation of prosimian and simian branches of the primate radiation (Xu et al., 2004; Fan et al., 2012 for review). Similar differences may exist in V3 across taxa, but there have been only limited attempts to investigate the modular organization of V3.
Additionally, there have been few attempts by members of the same laboratory using the same procedures to study a range of primate species.

Conclusions

In our opinion, the bulk of the data supports the conclusion that a single visual area, V3 with dorsal and ventral halves, forms most of the rostral border of V2 in primates. For us, the evidence that V1 is retinotopically interconnected with the total V3 region across primates is particularly compelling. In brain sections, cut parallel to the surface of flattened cortex, the border of V1 (area 17) with V2 (area 18) is clear, and one can see where the injection in V1 is located and see the relevant patches in the proposed territories of V2 and V3. The projections to the DM region are not confused with the V2 and V3 patches as the DM connections are reduced in magnitude compared to the V2 and V3 connections. We have placed injections of tracers in V2d and V3d that reveal the connections expected for V3d, but these results are more questionable because the borders of V2 and V3 are estimated and somewhat uncertain. Injections in V3v are difficult to place and can miss V3 altogether, wrongly leading to the conclusion that V3v does not interconnect with V1. Microelectrode mapping results are limited by difficulties in accurately defining receptive fields, especially when responses are weak or variable and by the problem of defining functional borders. Furthermore, subjectively determined receptive field results may be unintentionally influenced during collection, and such results may be selectively illustrated. Such difficulties can be reduced by the use of fixed electrode arrays, such as the Utah array of 100 electrodes, so at least the arrangement of recording sites is fixed. In our hands, recording with such an array from the dorsal V1, V2d, V3d region in galagos revealed receptive fields only in the lower visual quadrant, and consistent size differences in receptive fields for recording sites architecturally identified as in V1, the V2 region, and the V3 region (Fan et al., 2012). Finally, optical imaging results from the exposed V3d region in owl monkeys and galagos, together with the fMRI results in macaque monkeys and humans all present a similar picture of the global organization of cortex that supports the V3 concept. Evidence in conflict with the V3 concept seems much less compelling.

Nevertheless, it remains possible that V3d does not form the complete border of V2d in at least some primates. This possibility would remain compatible with most of the evidence that supports the V3d concept, while allowing for some of the data that seem to be in conflict with the V3d concept. More specifically, the middle part of V3d may have a gap in which part of the upper visual quadrant is represented as part of another visual area. The identity of this hypothesized visual area is uncertain, but the candidate area, DM, is represented as part of another visual area. The identity of this part of V3d may have a gap in which part of the upper visual quadrant seems much less compelling.

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