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Placing Area MT in Context

Abstract: *In this article I raise empirical challenges for the claim that area MT/V5 is the neural correlate for visual experience as of motion (Block, 2005). In particular, I focus on the claim that there is matching content between area MT, on one hand, and visual experience as of motion, on the other hand (Chalmers, 2000; Block, 2007). I survey two lines of empirical evidence which challenge the claim of matching content in area MT. The first line of evidence covers new results in neuroscience which emphasize the ongoing dynamics in cortical activity. The second line of evidence focuses on results regarding area MT in particular (Maier, Logothetis and Leopold, 2007; Cohen and Newsome, 2008). Together, the empirical results indicate that neural processing is context sensitive in a way that challenges the attribution of content to local areas of the cortex, to area MT in particular. In the final part of the article I explore alternative approaches and discuss remaining issues.*

1. Introduction

This article is a study in the search for the neural correlates of consciousness (NCC). Area MT/V5 has been the topic of a great deal of research in cognitive neuroscience, and a particular kind of activation in this area is a strong candidate for being the neural correlate of the experience ‘as of motion’ (Block, 2005). The purpose of this paper is to evaluate the claim that area MT activation is the neural correlate of the experience as of motion in light of some new trends in neuroscience. In particular, I will review evidence which points to the *context sensitivity* of neural processing and investigate how this evidence challenges strong claims about the representational content of area MT. The evidence motivates a more subtle view of the role that MT plays in conscious visual experience. In particular, the evidence casts

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doubt on stronger claims about the representational content of area MT. First I will explore the general emerging themes of context sensitivity in neuroscience, then I will focus on evidence regarding area MT. The paper closes with a discussion of the consequences for these new results for theories of consciousness.

First I should motivate the topic of this paper. I am investigating the claim that activity in area MT is the neural correlate for experience as of motion with special attention to the question of content. I choose area MT as my topic because there is a strong case that area MT is an NCC.¹ If one were to make a case for any area of the cortex being an NCC, area MT would be a good choice. In an influential article, Ned Block outlines the case for MT being the neural correlate of experience as of motion by appealing to a number of different lines of evidence (Block, 2005, p. 46). Here is a summary of the evidence as Block presents it. Studies using fMRI in humans show that there is an increase in activity in MT during motion perception (Heeger *et al.*, 1999), during the perception of ‘implied motion’ in static images (Kourtzi and Kanwisher, 2000), and during after-images of motion (Huk, Ress and Heeger, 2001). In monkeys, microstimulation to area MT can influence the monkey’s judgment of the direction of motion (Britten *et al.*, 1992). Lesions to MT in humans can result in the inability to perceive motion visually (Zihl, Von Cramon and Mai, 1983). Finally, transcranial magnetic stimulation (TMS) applied to area MT in humans can disrupt moving after-images (Théoret *et al.*, 2002) and can bring about the experience of moving phosphenes (Cowey and Walsh, 2000). The evidence is sizeable; area MT is one of the strongest purported instances of a local NCC. If there are problems for the claim that area MT is a local NCC then it is plausible that the problems generalize to other candidate NCC areas as well.

The evidence cited by Block clearly indicates that area MT is important for visual perception of motion. There are a number of different ways to understand this claim that area MT is an NCC. My focus here will be on the more ambitious understanding of the neural correlate that can be found in the main philosophical literature. As Alva Noë and Evan Thompson (2004) have argued, many consciousness researchers, following Chalmers (2000), are committed to a *match in content* between neural areas and conscious experiences. For instance, Chalmers writes, ‘We require that the content of the neural

[1] The claim being investigated here is that area MT is a ‘core’ NCC, not a ‘total’ NCC. As Block explains, ‘The core NCC is the *part* of the total NCC that distinguishes one conscious state from another — the rest of the total NCC being considered as the enabling conditions for that conscious experience’ (Block, 2005, p. 47).

state in question match the content of consciousness' (*ibid.*, p. 23). Block has explicitly affirmed his commitment to matching content:

...the Phenomenal NCC is the minimal neural basis of the *content* of an experience, that which differs between the experience as of red and the experience as of green. (Block, 2005, p. 46)

and

Mere correlation is too weak. At a minimum, one wants the neural underpinnings of a match of content between the mental and neural state... (Block, 2007, p. 483)

In what follows, I will be exploring empirical details which cast doubt on matching content in the case of MT. The more ambitious position about NCCs goes beyond mere correlation to make a claim about matching content, but I hope to show that mere correlation may be all that the empirical evidence justifies.

Before presenting problems for the claim that there is a match in the case of area MT, it will be helpful to consider what the matching claim is supposed to mean. Chalmers is not proposing that we should look for a match in the sense that matching neural states and mental states ought to have the same properties; obviously he is not suggesting that, say, a neural state needs to be blue in order to match a blue sensation. Rather, as I understand it, Chalmers is saying that neuroscientific research can motivate the attribution of content to particular neural states and that such content should match the content of the correlating mental state. If the content matches, then we would have a systematic — rather than arbitrary — correlation between mental and neural. Such a situation could then enable us 'to predict the presence or absence of phenomenal features that may not have been present in the initial empirical data set' and would help with 'finding a mechanism and a functional role for the NCC that match[es] the role we associate with a given conscious state' (Chalmers, 2000, p. 23). If there is no match, 'things would be much more untidy' (*ibid.*). One of the goals of this paper is to show how the neuroscience of the last few years reveals that things are indeed much more untidy than Chalmers (and Block) had hoped.

2. Empirical Problems with MT Content Matching the Visual Experience as of Motion

One motivation for my criticism of matching content in area MT comes from recent trends in neuroscience, trends that have not yet been incorporated into empirically oriented philosophy of mind. What

I mean here in particular is an increasing emphasis on the ongoing dynamics in the cortex as creating a kind of context sensitivity in neural processing. First I will make a few quick comments about these general trends and then I will present some recent work which focuses on area MT.

2.1. *General issues*

Neurons are tuned to respond strongly to particular properties or stimuli. It is well known, though, that there is variation in neuronal response to the same stimulus over trials. Traditionally this variation has been understood as noise in the system. Within the last decade or so, neuroscientists have been developing a more sophisticated understanding of this variation, and increasingly regard this variation as being meaningful. In one of the first articles representing this trend, Amos Arieli and colleagues showed how neural responses to stimuli are sensitive to the ongoing activity in the cortex:

...these findings indicate that old notions of what is ‘noise’ in brain activity may have to be revised. Because the ongoing activity is often very large, we would expect it to play a major role in cortical function. It may provide the neuronal substrate for the dependence of sensory information processing on context and on behavioral and conscious states. (Arieli *et al.*, 1996, p. 1870)

This theme, that the ongoing neural dynamics in the cortex are meaningful for the organism’s mental life, is gaining more and more attention. The idea is not terribly new (Llinas, 1988; Freeman, 1999), but it is starting to gain more widespread acceptance in recent years. Of course, the issue of distinguishing signal from noise in the brain is a terribly difficult one. Here I only mean to indicate that there are emerging reasons to cease treating ongoing activity as mere noise.

A first point in favour of taking intrinsic dynamics seriously comes from a consideration of metabolism. The brain uses up a disproportionate amount of the body’s energy, and this high energy consumption does not increase much in particular areas — only about 5% — as tasks change (Raichle, 2010, p. 180). Thus, claims based on fMRI evidence that a cortical area is activated during a particular task, such as some of Block’s claims about area MT (Block, 2005), can be misleading. All cortical areas are always active: ‘activation’ as detected using fMRI really means a slight increase in this metabolic activity. The main point here is that most of the brain’s energy use is intrinsically driven, and not task dependent. This fact is leading more neuro-

scientists to pay serious attention to the nature and function of the brain's intrinsic activity.

A second reason to take intrinsic dynamics seriously comes from neurophysiology. In the visual system, the number of feedback connections is equal to or greater than the number of feedforward connections (Kveraga, Ghuman and Bar, 2007, p. 148). In addition, the information which is fed forward from the retina is degraded as it progresses into the brain (Raichle, 2010, p. 181). It seems as if much of the information with which the brain represents the visual world does not come directly from the visual world: it is either intrinsically generated or it is feedback.

A final reason that intrinsic activity is gaining attention is the discovery of the so-called 'default mode network' (DMN), which is a network of cortical regions that is *less* active during a large variety of tasks than it is during a resting state (Raichle *et al.*, 2001). This network reveals 'a dynamic interplay within and between large, spatially distributed systems representing opposing components of our mental lives' (Fox *et al.*, 2005, p. 9677). If there really is a 'dynamic interplay' going on, then it is plausible that such an interplay would have some impact on the representational content of areas such as MT.

What is most relevant here is that this new conception of neural activity as primarily, or at least partially, driven by intrinsic dynamics is in tension with some versions of the search for various neural correlates of consciousness. If spontaneous² ongoing activity makes a meaningful contribution to low-level sensory processing, then it would be imprecise to assign coarse-grained content (as of motion) to neural activity in parts of sensory cortices (such as MT). For example, perhaps the goals or the bodily positions³ of an organism are reflected in the ongoing activity. Then it would not be right to say that the ongoing activity merely modulates sensory activity. Instead, it would be better to say that the ongoing activity adds content and context to the low-level sensory activity. Such content might be attentional (whether a particular stimulus is relevant for the organism's current goals), sensorimotor (whether the motion of an object could interfere with one's own bodily trajectory), or something else entirely.

If the spontaneous activity does make a meaningful contribution to low-level sensory processing, then it may not be correct to claim that stimulus properties are represented *simpliciter*. One alternative to this

[2] By 'spontaneous' here I mean stimulus free, but I do not mean to imply that the activity is random or arbitrary.

[3] Noë and Thompson make a related point (2004, p. 13).

claim would be that sensory processing in the cortex also includes content about whether or not the stimulus is relevant for the organism. This point has been developed by Kathleen Akins (1996), who has argued that sensory systems may be ‘narcissistic’ and not ‘servile’. That is, sensory systems are concerned with whether the stimulus means anything given the state and goals of the organism. Sensory systems are not ‘servile’, to use Akins’ term, by which she means that sensory systems do not represent ‘the world as accurately as possible, without embroidery or fiction, given the information available’ (*ibid.*, p. 344). New results on the ongoing dynamics of the cortex can be understood as offering more evidence in favour of Akins’ position.

2.2. *Focusing on MT*

Much of the literature mentioned above is concerned with properties of the cortex overall, but the topic here is area MT. Here are some of the results which complicate and challenge the claim that there is matching content between MT and visual experience as of motion.

A number of studies have shown context sensitivity in the response of MT neurons. Here I will outline the results of two such studies. Maier, Logothetis and Leopold (2007) used single-cell recording in macaque monkeys in a binocular rivalry paradigm, which means that each eye receives a different stimulus. Rather than seeing a mix of the two stimuli, subjects — both humans and monkeys — experience only one of the two stimuli at a time. Maier *et al.* used a technique called flash suppression to control which of the two stimuli was consciously experienced at any particular time. Previous research using binocular rivalry and single-cell recording had found that about half of the directionally tuned neurons in area MT fire in a way which reflects the stimulus, and that the other half fire in a way which reflects the conscious percept (Logothetis and Schall, 1989). A plausible hypothesis which would explain this finding is that there are neurons in MT which are devoted to representing the stimulus, and that there are other neurons in MT which are devoted to transmitting the disambiguated percept (Koch, 2004). Such an hypothesis, if correct, would provide the kind of systematicity that Chalmers had advocated as a goal for NCC research (Chalmers, 2000, p. 23). Maier and colleagues tested this hypothesis and the evidence speaks against it. They discovered directionally tuned neurons which sometimes respond as if representing the stimulus, and sometimes respond as if transmitting the consciously experienced percept. The very same neuron can take on a different functional role depending on, Maier *et al.* suggest, the exact

nature of the conflicting stimuli.⁴ Since the functional role of the neurons in MT tended to change even across very similar stimulus conditions, they claimed to find ‘the same visual percept emerging despite grossly different patterns of underlying neural activity’ (Maier, Logothetis and Leopold, 2007, p. 5624).

Similarly, Cohen and Newsome (2008) recorded from neurons in area MT in monkeys who had been trained to perform a direction discrimination task. They recorded under two different conditions by changing the axis of motion that the monkey was instructed to discriminate. For instance, in the first condition, the monkey would have a forced choice between up and down motion in the random dot display, and in the second condition, the monkey would have a forced choice between left and right motion in the display. The stimulus stays the same, but the task changes. They then selected two neurons in MT which were tuned to a particular direction of motion such that these neurons would ‘cooperate’ under one condition, but ‘compete’ under the second condition. To illustrate these conditions using the upright clock position, one can imagine one neuron which fires most strongly in response to motion towards 2 o’clock and a second neuron which fires most strongly in response to motion towards 10 o’clock. If the forced choice is between up and down motion, the two neurons would cooperate. If the forced choice is between left and right motion, the two neurons would compete.

Cohen and Newsome recorded from such pairs of neurons while randomly changing the axis of motion that the monkey was supposed to discriminate. They measured changes in ‘noise correlation’, which is ‘the correlation of trial-to-trial fluctuations of visual responses to a given visual stimulus’ (*ibid.*, p. 162). They found changes in noise correlation in cases when the stimulus was the same. They conclude that context, which in this case is the changing axis of the motion discrimination task, changes the functional circuitry within the visual cortex. They suggest that the changes in noise correlation ‘must be due to changes in functional inputs of central origin’ (*ibid.*, p. 170). Besides these two studies, which both use single-cell recording, task sensitivity for MT activation has also been explored using TMS by Treue and Maunsell (1996) and Ellison *et al.* (2003), as well as with MRI by O’Craven *et al.* (1997) and Shulmann *et al.* (1999).

What do the results of these two studies mean for the claim that activity in area MT matches the content of the conscious experience as

[4] Perhaps another possibility is that the activity of the neuron changes as a result of intrinsic ongoing activity in the cortex. Maier *et al.* (2007) do not mention this possibility.

of motion? Both studies show that neurons in MT can do more than detect (or represent) motion. From the Maier *et al.* study, we have evidence of MT neurons which can switch functional role between reflecting properties of the stimulus, on the one hand, and transmitting perceptual interpretation, on the other hand. From the Cohen and Newsome study, we have evidence of MT neurons which respond differently depending on the nature of the task. This result challenges the notion of matching content because the activity of the neurons seems to reflect more than just ‘as of motion’. The neural activity is sensitive both to the stimulus as well as the task. Both Maier, Logothetis and Leopold (2007) and Cohen and Newsome (2008) show cases in which it is not at all clear what kind of content to attribute to neurons in area MT. If the content of MT is not clear, then claims about matching content with area MT become less convincing.

These findings expose some of the general difficulties with attributing content to neural activity. It would be reasonable to expect *some* variation in neural activity across brain states with the same content. But if, as in these cases, the variation appears to be functional, rather than mere noise, then we should consider the possibility that the neural variation reflects differences in content. The variation in response is not noise in an otherwise informationally encapsulated Fodorian module. *Contra* Block, the modularity of the early visual system is not a Fodorian modularity (Block, 2007, p. 481; Fodor, 1983; Spivey, 2007, Chapter 5). Instead, the variation in neural activity could be interpreted as MT receiving and processing information that is somehow meaningful and relevant for the organism.

The first conclusion from these studies is that we need to be very careful about attributing content to neural activity. The evidence indicates that things are untidy and dynamic in the cortex, at least as far as functional role or representational content is concerned. Secondly, from what I can tell, we do not have strong evidence about what these functional variations in neural activity might mean for conscious experience. The results from Maier *et al.*’s flash suppression paradigm suggest a many-to-one mapping, rather than a match, between neural states and visual percepts. But even a many-to-one mapping would require decisions about the individuation of conscious states, decisions which may prove difficult (Noë and Thompson, 2004). The proper way to individuate conscious states is not obvious — neither for human nor for macaque consciousness. These two conclusions suggest, at the very least, that it is overly ambitious at this point to claim that we have found matching content.

3. Remaining Issues

The focus of this article has been on the claim that activation of area MT is the neural basis for the content of experiences as of motion (Block, 2005; 2007). The empirical considerations here give a good motivation to refine, or even abandon, claims of matching content for area MT. Since area MT is a strong candidate region for a local NCC, it is not unlikely that the problems sketched here will generalize to other NCCs. If the problems generalize, then we could end up with a motivation to abandon claims of matching content for all local NCCs.⁵

Crucially, though, the search for NCCs need not be committed to matching content and localization. There are at least four alternative options available: no neural content, global content, vehicle externalism, and mere agreement. First, the *no neural content* approach would be, no surprise, to avoid attributing content to neural states at all. This sort of approach may strike some as extreme, but it finds support in live, albeit not dominant, philosophical traditions (Bennett and Hacker, 2003; Zahavi, 2008). Second, the *global content* approach would involve expanding the vehicles of content to include larger neural areas (Freeman, 1999; Baars, 1997). A promising variation on this second approach would include Giulio Tononi's information integration theory (2004). On this theory, the contribution made by activity in particular areas of the brain is determined by 'the informational relationships both *within* each area and *between* each area...' (*ibid.*, p. 7, emphasis in original). In contrast to a view in which local activity directly gives rise to content, Tononi's theory posits that the relationship between local areas of activity plays a role in determining content. This feature of the theory may be especially accommodating to concerns about context sensitivity.⁶ *Vehicle externalism* involves the claim that vehicles of content can include parts of the body and environment (Hurley, 1998; Noë, 2004; Menary, 2007; Rowlands, 2010). This move would allow for more flexibility in accounting for the contribution from ongoing dynamics in the cortex as well as sensorimotor relations between the body and the environment. Finally, for those interested in attributing content to localized neural activity, the best option may be to settle for *mere agreement*, rather than a match, in content (Noë and Thompson, 2004; Hohwy and Frith, 2004). As Noë

[5] On the other hand, due to global processing of larger areas of the visual field, it is possible that area MT has more context sensitivity than some other brain regions. The way in which context sensitivity might generalize to other areas remains an open question. I thank an anonymous referee for this point.

[6] By the global content approach, I mean something like the approaches in the authors cited. I do not mean that content is distributed across a local population of neurons.

and Thompson explain, a photo of birds in flight and a verbal report that there are birds in flight agree in content, but there is no match. The photo contains information about the formation and colour of the birds but the verbal report does not. Likewise with area MT. One might want to describe MT activity as making an important causal contribution, or even a necessary contribution, to the experience of motion, and one could also claim that there is agreement between what seems to be represented in MT and what is represented in experience. The problems arise with the additional claim that the representational content of area MT *matches* experiential content.⁷ This option has the advantage of modesty, but the disadvantage of losing the systematicity that Chalmers was seeking.

All of these approaches are better able to accommodate the results discussed above because they avoid the attribution of matching content to local areas in the cortex. The results sketched above indicate that cortical processing is influenced by ongoing dynamics and is context sensitive, neither of which can be localized in a straightforward manner. Since it is not clear that localized content can accommodate these results, it may be more fruitful to consider these alternatives.

In addition to matching content, another central interpretation of NCC research is the hunt for the minimally sufficient conditions for producing particular conscious states (Chalmers, 2000; Metzinger, 2003; Koch, 2004; Block, 2007). It is important to note here that these two concerns — matching content and minimal sufficiency — are independent of each other. That is, one can claim that a particular physical system is minimally sufficient for producing a particular conscious experience without thereby claiming that the physical system is the vehicle for any representational content. Likewise, one can claim that a neural system is the one and only vehicle of matching representational content without claiming that such a neural system is the minimally sufficient core realizer for an experience. Therefore, any problems for matching content in area MT are not necessarily threats to the search for minimal sufficiency (although the search for minimal sufficiency encounters practical problems of its own; Fell, 2004).

To sum up, a strong candidate for the neural basis of experience as of motion in humans is area MT. In the interest of finding a systematic correlation between the neural and the mental, it would be helpful to go beyond mere correlation and claim that the experienced content as

[7] Although the critical target here is the matching claim, I should also point out that there is no developed account of the ‘agreement’ relationship, either. Thomas Metzinger’s concept of a partial relational homomorphy may turn out to be helpful here (Metzinger, 2003, p. 348).

of motion matches the representational content of area MT as well (Chalmers, 2000). I hope to have demonstrated that this more ambitious claim runs counter to recent empirical results, results which reveal the context sensitivity of activity in area MT.

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