Emergence in the central nervous system

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Abstract “Emergence” is an idea that has received much attention in consciousness literature, but it is difficult to find characterizations of that concept which are both specific and useful. I will precisely define and characterize a type of epistemic (“weak”) emergence and show that it is a property of some neural circuits throughout the CNS, on micro-, meso- and macroscopic levels. I will argue that possession of this property can result in profoundly altered neural dynamics on multiple levels in cortex and other systems. I will first describe emergent neural entities (ENEs) abstractly. I will then show how ENEs function specifically and concretely, and demonstrate some implications of this type of emergence for the CNS.

Keywords Emergence · Internal viewpoint · Recurrence · Recursive · Gamma · Theta · Microcircuit · Mesoscopic · Mushroom body

There are several classes of problems which arise in investigating the neural correlates of consciousness (NCC). One class of such problems has to do with processing power, i.e., while single neurons are powerful processors, there are operations which they probably cannot perform (see, e.g., Koch 1999; Koch and Segev 2000). Another class, termed the “binding problem”, concerns the processes by which the various neural correlates of separate

experiences: sensations, memories, and others, can become united, since the experiences they correlate with are united. Yet another class of problems has to do, in effect, with the nature of the NCC: is it possible to go further than mere correlation, and describe causation? That is, can one pass from the physical characteristics of neural dynamics to non-physical abstractions through a causal chain with no breaks? This paper will address the first two problem classes, and hint at an approach to the third. This is a “proof of concept” paper which attempts to show that a particular neural dynamic, an “emergent neural entity” (ENE), is found throughout the central nervous system (CNS) at virtually all levels of scale. After describing this dynamic, I show that it is found at micro-, meso-, and macro-level scales in the CNS, and begin to elaborate on some implications.

1

We will start by addressing the idea of “emergence”. The concept of emergence is usually taken to relate to something like an unexplained or unexplainable appearance of an entity or property and/or something which is not “reducible” to well-defined interactions of other entities. This very vague notion has nonetheless been employed to justify why a variety of phenomena, ranging from biological entities and dynamics, through chemical interactions, to various mental phenomena, are useful or inescapable in creating explanations and experiments. The literature on emergence is enormous, and it ranges through fields from philosophy (e.g., Humphreys 2008a, b; Kim 2006) to computer science and modeling (e.g., Bettencourt 2009; Munoz and de Castro 2009), to more conventional sciences such as chemistry (e.g., Luisi 2002). Definitions of “emergence” are equally

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wide-ranging, and thus, generally, almost useless. If one wants to model, say, the behavior of flocks of birds, conceiving of emergence in terms of how “unpredictable” a phenomenon is (e.g., Crutchfield 1994) leads nowhere. Similarly, to claim that mind emerges from a biological substratum yet is “irreducible” to that substratum cannot lead to meaningful experimental investigations of that putative phenomenon.

Given this confusion, why even talk about something as vague and seemingly useless as emergence in the CNS? Even if emergence in the CNS could be quantized in some way, made precise, what practical significance could it possibly have (but see Gazzaniga 2010)? And can one show that there really is emergence, in some well-defined sense, in our nervous systems, and what function it might serve? To answer this question, I will describe below (section “1.2”) a type of emergence which is clearly defined, quantifiable, and which uniquely enables and describes particular processes.

To start with basics, I will employ the term “explained” in a reductionist sense, such that when something is explained it is put into terms which relate to simpler concepts, simpler in the sense that we have been able to understand and manipulate those latter concepts, i.e., we have been able to “think with” them, to employ them to construct other meaningful concepts. We might take McGivern’s description of the diffusion of something in water in terms of movement of particles through a lattice containing gaps as one example (McGivern 2008, p. 54), where one introduces the meaning of “diffusion” in terms of the known meanings of “particles”, “lattice”, “movement”, and “gaps”. There are many caveats involving this type of meaning of “explain” (e.g., McGivern 2008; Rueger and McGivern 2010), but I will take it to be a notion which encompasses most normal variants of the scientific endeavor (see, e.g., Carruthers 2004). Given the confusion I described above, I am going to simplify and restrict the term “emergence” to some particular types of systems and interactions. With these restrictions, we will find that it is possible to define emergence quite concretely and to draw definite and quantifiable conclusions about a fairly large class of emergent systems, which will include some structures within the CNS.

1.1

First, I will call any property “emergent” within a particular context if it is a property which cannot be further explained in that context, and I will also term such a property a “singular” property, and the entity a “singular entity” insofar as it possesses that particular property, in that context. This is therefore an “epistemic” or “weak” concept of emergence, i.e., it is dependent on knowledge

and viewpoint restricted to particular contexts. We can contrast weak and strong conceptions of emergence through, e.g., Delehanty (2005, pp. 725–726): “strong” emergence implies an inability to reduce explanations to simpler concepts, as in the example above. In contrast, “weak” emergence implies that complex systems possess properties which are not possessed by their parts, but that those properties *are* explicable in terms of those parts.¹ It is these latter complex entities which I am concerned with here, and which I term “singular entities”. It is easy, then, to find examples of singular entities, from various sciences at different historical periods, which have subsequently become reduced to sets of other singular entities. To take some examples from the history of science, heat, conceptualized as the entity phlogiston, was once conceived of as a singular entity. Molecules, e.g., water, before it was separated into hydrogen and oxygen, were at one point not merely regarded as, but were to all intents and purposes “atomic”. Atomic components such as protons and electrons were once thought of as irreducible, and thus their properties were at that point emergent, because at the time electrons and protons appeared to be singular, i.e., unanalyzable into components (for more details and examples, see Brown 2009, p. 225–238.).

When a “system”, that is, a set of interacting entities, gives rise to properties which cannot be analyzed into components within some context, then for the purpose of that particular causal relationship and that particular context, that system is a singular, irreducible entity, and those properties are emergent. This conception may seem odd at first, because some systems which are easily identifiable as consisting of components are thought to possess emergent properties in some circumstances. So-called “flocking” behavior is an example (Couzin 2009; Cucker and Smale 2007). Yet if we observe such a system only by observing the behavior of the flock, as such (as when, for example, the members are too small or too distant to be distinguished as individuals), we do indeed observe only a singular entity. A similar example can be found in Yokoyama’s recent paper (Yokoyama and Yamamoto 2011) involving groups (e.g., teams) of people.

Most examples of emergent behavior, or emergent systems, though vague, will fit into the above description, so long as one does not require those systems to always be opaque or singular, i.e., so long as the emergent property is not thought of as a “strong” emergent property. Thus, this is an epistemic conception of emergence (and see, e.g., Hosseinie and Mahzoon 2011 on this also... but it will be clear why I cannot agree with their conclusion that “the

¹ Not surprisingly, there are other, not too radically different, conceptions of strong and weak emergence (e.g., Bedau 2008; Chalmers 2006). I’ll stick with the one above in this paper.

concept of emergence is superfluous”: p. 5). For example, if one thinks of some aspects of the field of biology as best described only by the properties on the scale of structures such as e.g., mitochondria, rather than of the molecular components of those objects, then one may function perfectly well in many contexts by treating them as singular and irreducible, while realizing that although we may know that they are comprised of complex components, that knowledge and those components are irrelevant to the particular context.²

Similarly, in the CNS, it is possible to conceive of contexts where, say, dendrites, or dendritic spines, or areas of postsynaptic density, as singular objects, are sufficient to describe particular phenomena. It is however the other direction, towards increasingly large and complex neural ensembles (akin to what have been termed “cell assemblies” and larger), which is the subject of this paper. One can consider neural groups, on the one hand, as one considers flocks of birds, where individuals, cooperating in various ways, produce coordinated behavior. Various types of statistical correlation, brought about, for example, by near-simultaneous stimulation, will result in various spatial and temporal distributions of neural firings (e.g., “Mexican hat” distributions: Hamaguchi et al. 2005). Further, we may study a variety of neural groups whose excitations are closely enough coordinated that they arrive at near or actual phase-locked firing within some frequency distribution (e.g., “pulse packets”: Kumar et al. 2010, p. 621). There is a very large literature speculating on the functions of such groups (e.g., Canolty et al. 2006; VanRullen and Thorpe 2002, and many others).

Thus, a set of neurons might appear, under the right conditions, as a singular object to another neuron or set of neurons, outside of that first set. In other words, one question that will concern us here is not how such a group might appear to an external observer employing e.g., fMRI or electrodes, or even statistical analyses, but whether a neural grouping may function as a singular entity, “appear” as singular, internally, to other neurons or neural groups (see Parravano 2006; Angelo et al. 2011 for specific examples of this general idea purely in the physical realm, and, e.g., Cruse 2006; Cruse et al. 2009, for attempting more than a passing mention of this in the neural/mental realm). Among other things, then, this paper will attempt to introduce a means of approaching the problems inherent in this peculiar means of viewing neural functioning, i.e., from what might be termed the “internal” or “local perspective”

(borrowing Cruse/Parravano’s terminology): the viewpoint, so to speak, which is not that of an external observer, but is that of a member of the entities interacting. What conditions would make this possible, and what are the implications of a neural group which does not function as a statistical ensemble, but rather as a kind of unitary “virtual” object, a singular “emergent neural entity” (ENE) as “seen” by other parts of the CNS? The broad implications of such groups, I claim, is that they enable a first, tentative step from definite physical entities to abstractions which are nonetheless objects, if only in particular contexts (and see, e.g., Perry 2001; Howell 2009a, b for a more abstract treatment of this kind of idea, and Prinz 1992 for a different approach). A neural group (or indeed any group of physical entities) which interacts in such a way that it is effectively a single entity, in the context of and constrained by that interaction, realizes that single entity as a functional object, while outside observers may understand it in radically different terms. The functional or virtual object is thus in a sense a mere abstraction, yet one which, from the standpoint of the local group, is as real as any other entity that group interacts with, in the particular context supporting what I have termed (Brown 2009) the “reentrant emergent” (RE) state.

1.2

Before we can even consider how highly abstract entities might arise and function, we must investigate the details of their origins in relatively simple neural objects. What, exactly, characterizes an emergent group of any type, so that it may function, insofar as an observing entity is concerned, as a singular object? This question can be answered simply and precisely, as follows.

- (a) A “reentrant emergent” (RE) system may be characterized, in general, by faster internal relaxation times than those of another system’s interaction with that RE system.³ More precisely, if we take the example of two systems which are interacting, O (observing system) and S (system being observed), we can discriminate two classes of interactions: the interactions within each system (WO and WS), and the interactions (I) between O and S. In order for S to be RE relative to O, the relaxation time of any I must be longer than the totality of those of WS.
- (b) The components of an RE system are mutually interacting in the sense that every component will interact with every other component in the system, although that interaction may be indirect, i.e., through an intervening component within that system (and see

² My examples of emergent entities have been physical and not mental or cognitive for two reasons: first, this paper mostly deals with neurons and neural groups; second, problems with clarifying emergence in the realm of the mental makes the problems in the physical realm seem simple. I will attempt to deal more explicitly with the mental in the papers to follow.

³ See my earlier paper, Brown (2009, p. 227) for a detailed explanation of relaxation times.

Izhikevich 2006; Gollo et al. 2010, for similar conceptions, but without the emphasis on relative relaxation times). In addition, intra-systemic interactions (WS) are reentrant processes, in that the interactions of one component with others necessarily involves an interaction back to the original component. This physical recursion is analogous to, and is normally described by, the process of inductive recursion in logic or mathematics, but to cite even a fraction of that enormous literature is beyond the scope of this paper (however, e.g., Brattico 2010; Hammer 2002; Hammer et al. 2004; Voegtlin 2002; Kleene 1959; ... but for complications and implications of recursion, see Vitale 1989; Luuk and Luuk 2011).

- (c) The components of an RE system complete their mutual interactions (WS) before the RT of its interactions (I) with an external system. That is, the internal RTs of the RE system are sufficiently rapid relative to that of its interactions with an external system that they are complete before any single external interaction is complete. The concept of RT, then, is central to this conception of emergence (for a more extended explanation, see Brown 2009).

We might consider an example in the dynamics of molecules of water. If one water molecule hits another, the internal interactions between electrons and nuclei are usually extremely fast relative to the kinetics of water molecules, and each molecule is reacting not to any electron or nucleus in the other molecule, but to that molecule as a whole, simply because the internal interactions are fast enough that all the components interact before the external interaction is finished—a water molecule “sees” another as a molecular whole. If, on the other hand, another molecule was moving close to the speed of light, that is, at a speed comparable to the internal interactions in the second molecule, then it would not interact with that molecule as such, but would interact with whatever part of that molecule it impinged on, and not “see” a molecule at all, but perhaps the outer electrons of the oxygen, or a single hydrogen atom, simply because only those components had time to interact with it.

What does the ENE hypothesis imply, specifically, for groups of neurons⁴? Suppose we take a group of three

neurons, mutually interacting with each other. In this simple example, each neuron fires a train of impulses to one (or both) of the other neurons: a small mutually (and recursively) interacting group. Suppose there is a neuron (or neural group) external to this group, and it fires an impulse train to one of the neurons in the group. That train will cause an alteration in the latter’s signals to the other neurons in the group. The outside neuron has thus altered the totality of the inter-group signaling. Now, suppose that one of the neurons in the group sends a train of impulses to the outside neuron. If the delay between the initial impulses from the outside neuron to that response is long enough (or the external impulse train is long enough—the neural equivalents of the relative relaxation times above) that all the neurons within the group have been affected by the external signal, so that whatever processing that whole group has performed on the external signal is effectively finished, the result returned to the outside neuron is a recursive function dependent on the mutual interactions of the three neurons in the group. The three neurons in the group form a single object (perhaps like a single large virtual neuron) in this particular interaction, insofar as that neuron outside the group is concerned. That is, any signal to one member results in intra-group interactions which make the group output a complex recursive function of those interactions relative to an external neuron interacting with it as described. That group may well be the equivalent of a single large neuron, since evidence indicates that the below-threshold processing on a neuron’s soma may interact with intra-neuronal action potentials from its dendritic trees (Katz et al. 2009; Mel 1994). That is, for some neurons, single-neuron internal interactions include both spreading membrane de- (and hyper-) polarizations and spiking discharges. Since neurons in a group are connected solely through the latter, in order for such a group to be the functional equivalent of a large single neuron, single neurons’ long-range internal signaling must also at least in part consist of such discharges. It seems, then, reasonable to conceive of such closely connected groups as in some cases the equivalent of large “virtual” neurons. Such a group is not the equivalent of neurons mutually interacting in any linear fashion, because of the

⁴ One might compare the above with conceptions of interaction, e.g., “information integration” (II) such as Tononi and Koch (2008), Tononi et al. (1994), and indeed because of the necessity of mutual interactions balanced between sparse and total connectivity there would seem to be at least overlap between the two. However, to mention only one difference, Tononi’s conception is based solely on internal interactions within a system. That is, the measure Φ might well serve to characterize an ENE’s internal interactions, perhaps to optimize them, but the partitions employed to calculate Φ are not

Footnote 4 continued

designed to describe the creation of and interactions between those sets considered as unified entities. While joining these two theories seems quite possible, given the physical bases of the ENE hypothesis (e.g., its employment of temporal factors) this would be quite complex. In addition, it seems to me that some form of II is implied by the ENE hypothesis (since I am describing the creation of unified objects from interacting components), but not the other way around, since II does not follow the implication of those interactions: the effective creation of singular entities in particular contexts.

long delay of the outside signal relative to the intra-group signals.⁵

Since this (ENE) conception is a new one (but see Wickelgren 1999 and John 2005, p. 165 for similar ideas), at least in neuroscience, there have been no experiments that I know of specifically designed to find this type of group (although see, e.g., sections “2.2” and “3.1” for more on size constraints). With very few exceptions, one can at this point only show the feasibility of their existence. I will present evidence to that end, at all levels of the CNS, from microcircuitry, e.g., on individual cell bodies and between and within cortical columns, up to what might be termed “macrocircuits” uniting the neural dynamics of whole cortical modules (and see Van De Ville et al. 2010 for some tentative support for this idea). At the microcircuit level, ENEs may be understood as “virtual neurons”, as mentioned above, since many neurons may be united into a single functional processing entity which may extend conventional neural processing to recursive functions (see, e.g., Koch and Segev 2000, p. 1176, for a brief discussion of this limitation, but Cruse 2006, p. 103–104 and section “2.2” below, for a simple illustration of processing unique to such a group; also Sabatini et al. 2006 and Fortney and Tweed 2011), while those at higher levels may unite cortical modules. In summary, the characteristics of a neural

group functioning as an ENE would be (a) internal recurrence with fast relaxation times, (b) connections to other such groups (which themselves might have fast or slow internal relaxation times) which occur with relatively slower relaxation times. It is not enough, then, to find neural groups which form attractor basins (e.g., Cossart et al. 2003), or which are persistent (e.g., Durstewitz 2009), or which interact through internal recurrence (e.g., Douglas and Martin 2007); those characteristics by themselves are not sufficient for functional ENEs, although they indicate the possibility of ENE formation.

1.3

Now, above, I speak of “precision” and “quantization” without actually providing anything specific. Because this idea has not been explicitly investigated, I must merely indicate mathematical approaches used for other, hopefully similar, models. But this can be done. Thus, we can approach quantization and precision by considering something like an array of Hopfield networks, i.e., of perceptron-like neural networks with both feedforward and feedback links (with, or course, continuous values rather than merely 1s and 0s as in Hopfield’s original papers). Hopfield (e.g., Hopfield 1995, 1996, 2004) showed reasonably well that such a perceptron-like network (PLN) (a) would have a dynamic which included multiple attractors, (b) would have a number of attractors dependent on the size of the network, (c) would be able to discriminate between attractor states with unique neural frequencies, and (d) by including “action potential timing” (Hopfield 1995) could discriminate between sequences. Now, the above work concerned only one network (although Rojas briefly mentions that Hopfield networks can be considered “asynchronous recurrent networks of perceptrons”—Rojas 1996, p. 345). Suppose there are multiple networks, interconnected. Each network would have attractor states as described by Hopfield and others (e.g., Tegnér et al. 2002; Wang 2001; Wong and Wang 2006), and those states would interact. Thus, given that the individual networks could be discriminated as such, the attractor set would be the combination of the sets of the attractors for the individual (e.g., Abbott 2007). This number can be large, and in order to discriminate attractor combinations one would need another large network, or another set of networks designed for reception and discrimination. In order to realize the time delay which individual neurons realized in the original single Hopfield network, the set of discriminating networks would require an overall time delay in receiving and processing inputs from the attractor set. This is equivalent to the description of CNS emergence I have given, and most of this paper will be devoted to showing that the CNS does indeed

⁵ In addition, we can use the above temporally-oriented conception of epistemic emergence to generalize that latter concept. If we take the same kind of idea, applied to space rather than to time, we find that there may be spatial groupings which cannot be resolved by some particular means of measuring their spatial extent. Given the limits on spatial resolution, a particular group may also be taken as a singular entity. However in this latter case, there is nothing comparable to the recurrence in the temporal example, since recurrence requires temporality in the physical world (with the possible exception of entangled systems—although on this see e.g., Zurek 2009).

If we combine the temporal and spatial conceptions, we not only can specify the limits on what might be termed the “epistemic resolution” (and see, e.g., Hacking 1981 for somewhat similar arguments) of a given entity in some context, we can also begin to employ this conception to resolve more functional notions of emergence. For example, consider the molecular complex which drives the flagellum of the single-celled organism euglena. This is a “molecular motor”, a singular entity seemingly not because of any temporal or spatial limitations on observability, but because it “functions” as a motor only if all its components are properly placed in relation to each other and to its environment. Yet it is easily seen that if we decrease the spatial resolution too much, the motor disappears and we see only a moving flagellum, and conversely, if we increase that resolution too much, it also disappears, at least as a singular entity, and we see only moving atoms. Similarly, if the temporal window is too long, all we observe is a blur; and if too short, we cannot see the movement of the motor and thus its function, especially if this is combined with a very small spatial resolution. Observed function thus depends on the parameters of the observation. While this does not exhaust the analysis of an entity’s function, it delimits that analysis: within particular temporal and spatial limits, there is a molecular motor; outside of those limits, there are molecules or atoms in motion, or only a single-celled organism with a flagellum.

produce groups at least capable of generating both such attractors and temporal discriminations.

Specifically, consider the vector describing a minimal energy state in PLN (A). In order that another PLN (B) treats the first as a single entity, A must at least have that vector established across its output neurons in parallel in less time than the period in which network B interacts with A. That is, in the case of much of the CNS, the iteration period in the first resonance network (and see also Rojas 1996, p. 338) must establish the vector at faster than theta frequency (of which I will have much more to say below), and more or less in phase with that frequency. To put it another way, the delay must be roughly equivalent to the theta period. This is the first requirement for emergence when two networks interact at theta frequencies, and this is the parameter which this paper will primarily investigate. Later (section “5.1”), we will see that there is a logical extension of the fundamental Hopfield temporal interval integration to a spatial integration model which has similar spatial implications to Hopfield’s temporal implications (e.g., Hopfield 1995, p. 34).

Even more specifically, we might look at Eq. 14.1 in Rojas 1996, p. 374, as an example of what the temporal treatment might look like, where the change in the excitation of unit i must be periodic with period corresponding to the theta frequency. This more complex treatment might also serve to modify something like Eq. 3 on p. 34 of Hopfield 1995. The treatment in this paragraph will enable temporal discrimination and summation of the outputs of a group, and that group can be treated just as any single neuron would be, after such a summation.

2

We will now proceed to investigate whether the CNS can actually support such a dynamic. The investigation will move from the smallest to the largest levels of the CNS. Beginning, then, we find that at the level of individual neurons, there is not sufficient data at this point to show that ENEs can form on the membranes of individual cells (although see Migliore et al. 2008; Migliore and Shepherd 2008; Soucy et al. 2009). The implications of the enormous extent of some dendritic trees and the complexity of their processing (e.g., London and Häusser 2005; Mel 1994; Poirazi et al. 2003a, b; Spruston 2008; Bollmann and Engert 2009; Grimes et al. 2010, p. 877; Huhn et al. 2005; Branco and Häusser 2011), might imply the possibility of ENEs at this level. Perhaps the most directly relevant studies are these: Bloodgood and Sabatini (2007), Remme et al. (2009, 2010), Chalifoux and Carter (2011), which strongly indicate that there do exist reciprocal intra-dendritic and dendritic/soma interactions capable of complex

single-cell integration and computations, and perhaps of micro-level ENEs.

We shall therefore start by investigating (1) the evidence for small neural groupings whose interactions are consistent with the formation of ENEs, then (2) the evidence that these groupings interact differently with neurons outside their groups than internally.

2.1

There is a great deal of evidence supporting the existence of small neural groups capable of creating ENEs. The idea that recursion exists and plays a part in the microcircuitry of the CNS is not a new idea by any means. Most generally, some neural groups are distinguished from their surroundings by measures of connectivity, forming small-world networks (e.g., Bullmore and Sporns 2009; Földy et al. 2005). Small-world networks are characterized by a structure in which nearby elements are closely connected, with sparser connections to farther elements. Given this preponderance of close connections, structures consistent with ENE formation are quite conceivable. In addition, there is explicit evidence for connectivity close and reciprocal enough for ENEs to exist (e.g., Buzsáki et al. 2004; Haider and McCormick 2009; Morgan and Soltesz 2008; Silberberg 2008; Silberberg et al. 2005; Takahashi et al. 2010) in cortical microcircuitry. These few papers are merely the tip of the iceberg in a large literature. The next step is also non-controversial: data supporting the existence of very specific recurrent microcircuits, and theories about their functions, have proliferated in the last several decades.

Harris summarizes evidence from multiple studies which indicates that firing patterns in hippocampus are most likely to arise from recurrent microcircuits (e.g., “Observations that are often interpreted as evidence for temporal coding might instead reflect involvement of [recursive] cell assemblies in ICPs” Harris 2005, p. 405). Shu et al. have shown not merely the presence of recurrent microcircuits in the cortex, but have described in detail how they arise and are stabilized through GABAergic connections (Shu et al. 2003, p. 291), as has Tegnér et al. (2002). Douglas et al. estimate that in the cat visual cortex, spiny stellate neurons receive between roughly 50–120 recurrent connections (Douglas et al. 1995, p. 982). In this case, recurrence is employed to amplify and denoise visual signals. Roberts has determined that the length of recurrent loops will probably not exceed three neurons (Roberts 2004). The above chain of data provides a brief indication of the possible scope and size of recurrent microcircuits in the cortex. Yet these papers, and the works they reference, do not give a hint of the extent in topics and time of the enormous literature on neural recurrence (see, e.g., Amit 1995 for an extensive list of only the pre-1995 literature).

It is not straightforward, even in theory, to extrapolate to the conditions required for 2, i.e., different interactions with neurons outside the group. Assuming constant propagation velocities, we might simply group a few neurons together, like balls and strings, with one ball hanging outside, “observing”.⁶ Thus, the sum of the distances between the neurons in the group divided by that velocity plus the sum of the times for the neurons in the group to reach firing threshold needs to be smaller than the distance to the “observer” neuron, plus the duration of its spike train to and from the group, plus the time for that neuron to reach threshold. This is the easiest, and probably the least accurate way to look at neural groups, in which one assumes that the relevant processing aspect of a neuron consists only of a small cell body. However, since attention lowers firing thresholds (e.g., Buehlmann and Deco 2008; Chelazzi 1999; Desimone and Duncan 1995; McAdams and Maunsell 1999; Müller and Kleinschmidt 2007; Noguchi et al. 2007; Vuilleumier and Driver 2007; Womelsdorf et al. 2008), the result of attention directed to specific areas of the cortex will tend to create areas with particularly low thresholds. This decreases the time to firing for those groups, effectively decreasing the conduction time between their neurons, and ENEs may be more easily formed relative to unattended areas. In addition, the nearly ubiquitous center-surround phenomenon, which is found throughout the cortex (Blair et al. 2008; Carr and Dagenbach 1990; Devor et al. 2005; Huang et al. 2007; Olsen and Wilson 2008; Schwabe and Blanke 2008; Simola et al. 2009; Sur 1980; Tadin et al. 2006; Thielscher and Neumann 2007), effectively increases the distance to nearer groups by raising their thresholds because of surround inhibition, even at the level of adjacent cortical columns (e.g., Helmstaedter et al. 2009; Lubke et al. 2003). To further complicate the picture, if the length of the spike trains linking members of a group is much longer than those from outside the group, that group may effectively be broken apart. It does not seem possible, then, without future investigations, to analyze this dynamic in any decisive way (e.g., see Douglas and Martin 2007).

However, even given the above, it is possible to say that in reasonable scenarios, ENEs can be realized at the level of cortical microcircuitry. Given cortical columns of widths approximating 400 μm and approximately 10–20 neurons across the width of a column (e.g., Amir et al. 1993, p. 36; Douglas and Martin 2004, p. 430), all other things being equal, the relaxation times and transmission distances, based solely on these numbers, are within the same order of magnitude for neurons within and without the columns, allowing ENEs to form. Thus, groups which, insofar as neurons interacting with them are concerned, act

effectively as large single cell bodies, can form with very few neurons. Similar structures can be traced as far back as Ashby (1960), but this type of circuit may make possible something like Koch’s more recent idea of “a small network” of neurons carrying out computations requiring “more than two recursive nonlinear interactions” (Koch and Segev 2000, p. 1176).

2.2

However, insofar as I can determine, there is virtually no evidence nor theorizing about details of the dynamics of groups of neurons relevant to how, while connecting within a group recurrently, (a) they interact stably with other such groups similarly to the above description of ENEs, and (b) how that interaction functions from the “local perspective” (see section “1.1”). Given normal activations in most cortical modules, it cannot reasonably be claimed that there is only one such recurrent group at any time in all cortical modules (where “module” refers, roughly, to functionally different parts of the cortex, e.g., visual versus auditory, and within the former, V1 versus V2, and so forth). How do these groups interact? Studies of stochastic resonance, for example, form a field of their own, yet they (e.g., Boccaletti et al. 2005; Makarenko and Llinás 1998; Hipp et al. 2011; Foss et al. 1996; Hoang 2011; Klinshov and Nekorkin 2011, are a very small subset of examples in this field) are largely concerned with elements which might be taken as such groups, becoming, in effect, united into one large resonating array (although see, e.g., Okamoto et al. 2007). But to be taken as a singular object, an ENE cannot be the only resonating group, and the “observing” group must be resonating at a different rate. In addition, such uniform arrays, even if present in the cortex, cannot be the only dynamics; if they were, how would there be degrees of salience both between and within modules? The literature touching on non-uniform cortical activations, for example, the so-called “Mexican hat” distributions (e.g., Moser et al. 2008, p. 74; Boehler et al. 2009; Taylor 2003, p. 430), and others (e.g., McNaughton et al. 2006a, b; Samsonovich and McNaughton 1997), also provides evidence and theory contrary to that idea, but that literature (with the exceptions of Moser and Taylor above, and the notable exception of Gong and van Leeuwen 2009) is basically concerned with single groups, or, if multiple, do not deal except in very rudimentary fashion with the interactions between such groups. Yet it is precisely such interactions which are of concern if the existence of ENEs in microcircuitry is to be confirmed.

There are some few studies which seem, very tentatively, to investigate some characteristics of the dynamics of interactive neural groups. Thus, Zahid’s work on asynchronous coupling indicates that in such a regime, the

⁶ But see the explanations and references in Sections 1.3 and 5.2.

“dynamic richness of the output” is greater (Zahid and Skinner 2009, p. 125) than in synchronous arrays. A group forming an ENE might be synchronous with other groups, but only as whole groups, not as individual neurons. Xie has studied neural groupings arising from lateral inhibition of neurons outside the groups, but only as a means of isolating attractor basins (Xie et al. 2002). However, this type of grouping per se, as I have noted, will not result in ENEs. But Xie’s general formulations for neural groupings (e.g., p. 2629–2630) seem nice starting points (although the assumption that groups do not overlap does not seem realistic in the CNS—e.g., Padberg et al. 2009; Tudusciuc and Nieder 2007).

Wang describes a system of two interacting recursive circuits (Wang 2002, p. 956), which might otherwise model ENEs, and he and others employ similar ideas in their models of memory through attractors (e.g., Constantinidis and Wang 2004; Lo et al. 2009; Miller et al. 2003; Renart et al. 2003; Wang 2001, 2002; Wong and Wang 2006; Wong et al. 2007). The interactions, and the neural groups, are limited by Wang’s intent to model memory by employing attractor basins in which individual neurons interact with other individuals in a different group. That is, the combination of slow internal (within-group) excitation and external (between-group) inhibition ultimately results in one of the groups being inhibited, while the other “wins” (e.g., Wang 2008, p. 220) and remains in its attractor basin. The scale of these groups vary. If his model were such that the between-group interactions were functions of the overall state of the group resulting from its internal recursive dynamics, then he would indeed be modeling a type of ENE. However, even with his current approach, Wang shows that recurrent interactions could result in quite different dynamics than in a rival (non-recurrent) diffusion model (e.g., p. 221). An additional limitation, so far as this present paper is concerned, is that Wang et al. do not concern themselves with the local perspective of the groups.

Gong and van Leeuwen consider both multiple groups and group interactions, but not from the viewpoint of ENEs; rather, their work is reminiscent of some of the early work in the field of neural computation (e.g., McCulloch 1970, p. 32; McCulloch and Pitts 1990; Rumelhart and McClelland 1988, p. 423–429; and later, Shepherd 2004, p. 17, 547), in which attempts were made to duplicate Boolean logic and circuitry with neural net interactions. Gong and van Leeuwen’s efforts (see, e.g., Gong and van Leeuwen 2007; Gong and van Leeuwen 2009, p. 5–6) are much more sophisticated insofar as neural modeling and neural data go, but basically attempt the same thing. Similarly, Buzsáki’s recent paper (Buzsáki 2010) does indeed describe a type of ENE. However, I will argue in a following paper that this type of approach,

generally similar to that of Gong and van Leeuwen, does not take a particular aspect of the structure/function of cortical networks sufficiently into account, and therefore must fail in its goal of accurately modeling neural processing at that level. That is, I will argue (in a later paper—see Footnote 5) that neither “words”, as Buzsáki terms them, nor Boolean circuits (a more limited case of the same symbolic paradigm), accurately capture cortical functioning (i.e., abstractly, one might relate this to the so-called “frame problem”—e.g., Dreyfus 2007; Fodor 2001).

We have seen, then, that recurrence in groups will result in at least two different types of interactions. First, the processing possible by such a group can be more complex than without recursion, as can be seen from the examples and references above. Second, the results of that processing may be “seen”, i.e., interacted with, as if the group is a simple, singular object, as in Cruse (2006). That is, although the output values of the system Cruse describes (p. 103) can temporarily hold any value between 1 and -1 , the system eventually settles in one of states (1, -1) or (-1 , 1). The internal interactions in his “neuroids” will not be observed if the observing group’s interactions are relatively coarse; only the long-term, relatively stable outputs resulting from the internal interactions of the group will affect the observer. Thus, another system interacting with that system, if, roughly speaking, it interacts slowly enough, will only see outputs of (1, -1) or (-1 , 1). This is a simple example of the principle I described earlier involving RE and local perspective. In addition, the ENE may function similarly to the “time delay” elements described by Hopfield (e.g., Hopfield 1982, p. 2556; Tank and Hopfield 1987), in that the internal reentrant interactions may produce delays either internally, as the group “absorbs”, so to speak, inputs, effectively storing states within the group, or externally, by delaying output to another group.

However, there are still no studies that I know of which take the local perspective approach to between-group neural interactions, and neither does Cruse take this perspective in his example. Yet it may be that such an approach will lead to very interesting results: e.g., van Swinderen’s study of discrete versus continuous choices in *drosophila* with and without mushroom bodies (van Swinderen 2005, p. 325–326). Thus, in *drosophila* without recursive interactions between the circuitry in the mushroom bodies and their visual maps, visual choices are continuous, not what would be expected in an attractor basin model. In those with mushroom bodies, however, their visual choices are discontinuous, which is what one would expect if an attractor basin model were applicable there (and see sections “4.5”, and “5.1” and 5.2 for further discussion of this).

2.3

In addition, in most of the examples, I have described ENEs which originate through what might be termed horizontal interactions, i.e., between neurons in the same cortical layer, or at least in the same cortical area, connected through horizontal circuits. However, a different generating mechanism, a vertical one, may also be responsible for ENEs. Grossberg, for example, describes processes involving several cortical areas interacting with thalamus which seem to result in neural groups similar to, or identical with, ENEs (e.g., Grossberg and Versace 2008, p. 3–7). The top-down/bottom-up resonance (“adaptive resonance”) he describes as selecting neural groups (p. 3) in order to recognize stimulus patterns seems another means of generating sustained recursive groups, as Grossberg himself notes (e.g., Grossberg 2003, p. 427). Although his groups are conceived as resonating vertically (i.e., between more and less abstract processing, so to speak), that does not seem incompatible with the above picture. This type of ENE could occur as a three-dimensional entity over several cortical areas, rather than the more restricted entities described above (and see section “3.1” on “bubbles”). Given the resonance phenomenon modeled by Grossberg, one might expect, with the vertical extent of the group, somewhat less horizontal extent, since specificity is a point of Grossberg’s model. Total group size, then, could remain roughly the same as horizontal ENEs. But this is pure speculation.

Given this, and given that external success triggers internal reinforcement which builds circuits to maintain that success (e.g., Edelman’s “neural Darwinism”: Edelman 1993), it would seem that the existence and maintenance of internally recursive neural groups on the micro-scale is justifiable both theoretically and from existent data.

3

The previous section investigated ENEs formed both on and from individual neurons, where the latter comprised relatively small groups. In modeling, the groups were usually under 50 neurons in size, and in experimental studies they might be up to several hundred neurons. In this section, we will see evidence for groups ranging from hundreds to thousands of neurons, and in addition we will attempt to look at possible local interactions between such groups, where “local” in this case refers to interactions which might take place up to roughly a few centimeters. I will assume that these groups operate in part to maintain neural excitations performing some particular function, and that the persistence of such a group is related in part to the persistence of a process. We will look within neural

modules with similar functions, e.g., hippocampus, parietal cortex, various visual modules, and so forth, which require fairly persistent activity of roughly the same group of neurons in certain circumstances. Again, I will look not merely for groups which have repeated or sustained firing, but for groups with such firing caused by internal recurrent connections.

3.1

On this middle scale, which has been termed “mesoscopic” (e.g., Freeman 2003a, p. 2496), that of, for example, cortical modules, small-world networks can support the formation of recursive neural groups, that is, of neural groups, rather than single neurons, which are reciprocally interacting, similarly, at least, to ENEs. This is due to the combination of low path length and high clustering in such networks, facilitating local recursive circuitry (e.g., Kwok et al. 2007; Masuda and Aihara 2004; Rubinov and Sporns 2010, p. 1062). Modeling indicates that small-world networks may in fact emerge spontaneously in neural systems (e.g., Gong and van Leeuwen 2004; Kwok et al. 2007).

One might also recall Wang, et al. here, since his model describes recursive interactions on both the microcircuit scale and on the mesoscopic scale (e.g., Wang 2008, p. 220–223) as a basis for decision-making, as described in section “2.2”.

There are two categories of studies which support ENEs on this level. One is a theoretical literature concerned with models of the cortex. This literature describes “bubbles” or “packets” of activation in the cortex which are modeled as recursive groupings. The other literature is mainly empirical, and is concerned with explicating the dynamics of cell-assemblies in various cortical areas, particularly in hippocampus. I will cover the former first, because it is perhaps the more questionable and certainly the more limited in terms of clear empirical evidence. The term “bubble”, implying a three-dimensional structure, is somewhat of a misnomer, since these packets, corresponding to the “Mexican hat” distribution mentioned above (in 2.2), are hypothesized to occur mainly on the cortical surface. Many neural net models employ this packet dynamic, which seems to be traceable to a mathematical model by Amari (1977—although see also Beurle 1956). Thus, Kohonen mentions these (Kohonen 1995, p. 137) and so does Taylor in multiple papers (e.g., Taylor 1999, 2003), but none of the above authors cite clear evidence for those constructs, relying instead on plausible models. There are many papers in this area which similarly either assume that these packets will form, or derive them from mathematical models (e.g., Fleischer 2010; Fuhs and Touretzky 2006; Lehar 2003; Ménard and Frezza-Buet 2003, 2005a, b; Ménard et al. 2004; Mikkilainen et al.

2005; Pashaie and Farhat 2009; Sirosh and Miikkulainen 1996; Tsuda 2001; Ursino et al. 2009; Wilson et al. 2010). However, as far as I know, there are very few papers in this particular literature which actually show strong empirical evidence for neural dynamics which might be inferred to correspond to the activation packets modeled, and most of those are inferences from work with electrodes on rabbit cortex by Freeman (e.g., Freeman and Schneider 1982). Markounikau has recently investigated this experimentally (Markounikau et al. 2010), and found that modeling actual retinotopic activation (in cats) with “Amari-type” parameters fit the data reasonably well (p. 8). But aside from very few studies, hard data in that area seems quite sparse. In addition, it is not clear that these packets are recursive, i.e., are self-maintaining, nor, indeed, chaotic (and see, e.g., Calude et al. 2010, on the theoretical difficulty of determining this latter). The models assume recurrence, and Freeman assumes that these are chaotic attractors (e.g., Freeman 2005), but the data could either support this or a dynamic in which they are maintained by long-range (e.g., thalamic) bottom-up excitations, or a combination of bottom-up and top-down, as in Grossberg’s ART model (e.g., Grossberg 1976a, b—in which case “bubbles” might be an accurate description), rather than by internal (and largely horizontal) recursion. Thus, although this literature employs complex models to make precise claims, the assumptions underlying those models are usually not investigated in depth (although Balaguer-Ballester’s recent paper: Balaguer-Ballester et al. 2011, is a notable exception), and in consequence few experimentalists draw upon these papers to support or inspire their investigations.

3.2

There is, however, indirect support for mesoscopic ENEs in areas of the empirical literature. Because there are very few experimentalists explicitly looking for such resonant packets, empirical corroboration is largely incidental, but when these studies are combined, they seem to indicate the existence of these groups. Thus, in Weliky et al.’s studies of retinotopic mapping, we find pictures of activations which seem to capture these packets, i.e., areas where “retinotopically integrated activity closely echoes the underlying local image contrast structure” (Weliky et al. 2003, p. 711), and similarly with Whitney et al. (2003). Chen shows similar patterns in the somatosensory cortex (Chen et al. 2003), and Carrillo-Reid in the striatum (e.g., “Experiments... demonstrated the existence of robust nonrandom cell assemblies... with *recurrent* [my Italics] and alternating activity” Carrillo-Reid et al. 2008, p. 1443). Ponzi has modeled striatal networks and found hierarchies of such assemblies (Ponzi and Wickens 2010, p. 5901). Ikegaya notes that small groups of neurons (in slices from the

visual cortices of mice and cats) which reactivate themselves through reentrant firing form larger patterns which themselves are recurrent: “When examining the temporal pattern of repeated sequences on larger time scales, we noticed that series of sequences could be repeated in the same sequential order” (Ikegaya et al. 2004 p. 562). Cossart found similarly “synchronized neural ensembles” in cortical slices (Cossart et al. 2003, p. 284, 286). Thus, the microscopic groups form mesoscopic groups with, it seems, similar recurrent activations. Whether these groups at either level are actually ENEs is uncertain, but the structures capable of forming them are clearly present. A similar phenomenon is shown in sequences of motor neuron group firing. For example, Ben-Shaul demonstrates that replicating sequences of population firing accompany movements (Ben-Shaul et al. 2004): “the direction of a movement and the sequential context in which it is embedded may be simultaneously... encoded” (p. 1759). That population encoding of sequence may be similar to the above studies. Evidence for “synfire chains”, i.e., sequences of small numbers of neurons firing which “build complex representations out of simpler parts” (Abeles et al. 2004, p. 180; and see also Abeles et al. 1993; Arnoldi and Brauer 1996; Masuda and Aihara 2004; Miller 1996; Vadia et al. 1995) also supports this type of what might be termed “dynamic fusion”. In addition, it seems reasonable to infer that there is a connection between this type of phenomenon and that of chaotic resonance, which does explicitly involve recursion, but the only person exploring that relationship to any extent, as far as I know, has been Tsuda (2001, 2009), although Freeman (2003b) notes it. However, empirical support for that latter connection is sparse.

3.3

In addition, there is a large literature concerning the neural basis of working memory, and this literature does seem to have accrued a good deal of evidence for the recurrent neural groups which may be responsible for this phenomenon. Many in this field assume that these groupings are not necessarily identically recurring neural excitations, but rather supersets of neural attractor basins, a neural dynamic which can entail recurrence of subsets of neurons active both within a larger stable set and within a parameter space of neural dynamics, rather than the repeated activation of identical neural sets. Although there is some ambiguity in the literature, I will take it that the term “attractor basin” indicates a superset of neurons, within which subsets, if not the same identical neurons, are actively recurring across any of the attractor’s single periods. That is, working memory may be realized either by the self-sustained activity of a small set of neurons or by attractor dynamics

per se (and see, e.g., Daelli and Treves 2010, for a brief presentation of both sides of this issue). This dynamic is quite compatible with the ENE conception if there is recurrence within such a basin fast enough relative to outside groups. However, the attractors described in much of this literature are usually more suitable to the micro-level analysis of ENEs, since they are assumed to be (and in some cases have been found to be) fairly small sets of neurons, especially in the hippocampal grid maps. But studies taking into account the temporal aspect of those maps, e.g., those of rats running mazes and/or recalling that maze-running (e.g., Dupret et al. 2010), must account for the evidence of “path integration”, where animals take into account the whole path in their memories and/or predictions. Path integration, then, necessitates a combination of whatever components of the maze have been remembered, and what is anticipated, into a single entity, and this whole, if indeed it is treated as such, will be a mesoscopic ENE if the hypothesis in this paper is correct.

Support for this viewpoint includes work by Buzsáki (2005, 2006, 2010), Durstewitz (2009), Durstewitz and Seamans (2006), McNaughton et al. (2006a, b), McNaughton and Morris (1987), Samsonovich and McNaughton (1997), also Becker (2005), Colgin et al. (2010), Conklin and Eliasmith (2005), Daelli and Treves (2010), Pastalkova et al. (2008), Zylberberg et al. (2010), and many others. One finds quotes such as, “The place cell... is bidirectional because it is under the control of multiple assemblies.” Buzsáki (2005, p. 832), where the “assemblies” are recurrently activated neural groups formed over the neural correlates of “sequential places” and “travel distances” (p. 831) mapped in the hippocampus and cortex, and have a lifetime of about 10–25 ms (p. 833). Durstewitz speaks of “active memories” (Durstewitz 2009, p. 1190, realized by “reverberating feedback excitation in recurrently coupled neural networks” (p. 1190). The reverberations may last at least as long as a theta period (e.g., p. 1198), and possibly much longer (Durstewitz and Seamans 2006, p. 126). McNaughton’s idea of “a continuum of cell assemblies” (McNaughton et al. 2006a, b, p. 665), in which “activity bumps” maintain working memory, is similar. One can see, however, that although the case for mesoscopic ENEs seems strong, there is very little direct support for ENEs in this literature, not at all comparable to what is found on the micro level.

A subset of the working memory studies also provides indirect support for mesoscopic ENEs: the investigation of conscious visualization (where “visualization” here includes the self-induction not only of visual images, but of sounds, motor kinesthetics, and so forth). There has been controversy as to whether visualization employs the same areas as sensation, and whether visualization does indeed involve images comparable to sensation at all (see e.g.,

Kosslyn 2005 on this), but at this point I believe these issues have been resolved at least to the extent that visualization has been shown to involve the induction of sensations, and to employ at least many of the same cortical areas that are involved in sensation. Tackling that controversy is beyond the scope of this paper, and I will assume that Kosslyn is correct in his claims to this effect (and see, e.g., Bakker et al. 2008 for further support of this in the realm of motor imagery). Given that, visualization becomes another source of self-maintaining neural activations which may be realized as ENEs.

Thus, Slotnick et al. found that with active visualizing, cortical regions “had sustained activity” (Slotnick et al. 2005, p. 1579, and see p. 1580) which was, importantly, not merely due to sustained visual attention. de Lange has found activation in parietal and premotor cortex accompanying motor imagery (de Lange et al. 2008). Ranganath has found that “human neuroimaging studies report inferior temporal activation during maintenance of visual objects” and that the fusiform face area “exhibits persistent activity when faces are maintained across memory delays” (Ranganath and D’Esposito 2005, p. 175, 176). They also find that while other areas, notably the prefrontal cortex (PFC), seem necessary to control these sustained activations when presented with distractors, they may also help to maintain them. Thus, Mechelli et al. find that the PFC seems necessary for the maintenance of visualizations (Mechelli et al. 2004).

Given the above, there is at least weak evidence for ENEs during various types of visualization. However, the activations found in these imaging studies are usually more extensive than those in single cortical areas, which I termed “mesoscopic”. Activations in visual imagery extend from PFC to temporal and fusiform cortex, and in the motor imagery studies, can include parietal, PFC, premotor and other areas. Kleber et al. (2007) found similarly widespread activation during “imagined singing” (i.e., aural imagery). This leads to the next section on “macroscopic” ENEs, i.e., those spanning large areas of the cortex (and other brain areas).

3.4

Before I proceed to the analysis of macroscopic groups, however, I would like to highlight some functional differences between micro- and mesoscopic ENEs, those treated in the sections above. We saw that microscopic ENEs could extend, in effect, the processing power of single neurons. In addition, the recursion inherent in that type of grouping opens the analysis of neural interactions to a variety of nonlinear and perhaps chaotic systems, where the elements of such systems may be either individual neurons or ENEs. However, I have hardly touched

on the original motivation for deriving the possibility of ENEs, that of the generation of virtual objects and reifying abstractions. On the micro level, these aims will not, I believe, be realized to any significant extent, because there is no function, no point, at that level, to those latter entities. The micro level is the closest to the parallel processing/network paradigm developed in the last century, and still being elaborated successfully today with neurons, roughly speaking, as its elements. ENEs may function at this level as virtual recursive processors, but they are not, by and large, conceived as reifications of abstractions (speculations as to ENEs themselves functioning as elements—analogue to individual neurons—in virtual networks which form virtual maps and functional areas, are irrelevant here). On the next two levels, however, the situation is different, because neural groups are employed not merely as processors but as entities. That is, it is common to speak of “memories”, “sensations”, “concepts”, and so forth, in the field of neuroscience while actually referring to the neural correlates of such entities. One merely has to look at the literature, some of which has been cited here. That literature commonly equates “working memories” and “attractors”, or “visual imagery” and “cortical activations”, and this points out a major difference in the way neural groups are conceptualized (and, it seems, function) on the medium and large scales from the way they are understood on the small scale.

On the middle level, then, I have indicated that there are neural groups (more accurately, stable neural dynamics) which are consistent with the dynamics of ENEs, which occur within various cortical areas, and that they may be treated, at one end of a spectrum, as something like ripples or vortices (e.g., Freeman, section “3.1”), and at the other end as stable resonant dynamics, all or some of which may correspond to units or elements of thought and to phenomenal experiences.

4

Now, before viewing any data, let us employ purely theoretical considerations and extrapolate briefly as to what large-scale (“macro-level”) ENEs should look like and how they should function. We have seen that ENEs are virtual objects, in that they are single entities only relative to their interactions with other entities. In order to function thusly, the internal interactions should be faster (pace Footnote 5) in some way than the external interactions of the group, and entities outside the ENEs should, roughly speaking, interact more slowly with the ENE grouping, in some manner, than those internal interactions. We would expect, then, that if there were neural groups functioning as ENEs on a macroscopic scale, that multiple ENEs, over

various cortical modules and areas, would be somehow united into large, single objects: ENEs comprised of groups of ENEs. That would imply that those latter groups would interact quickly internally, and in addition, would interact quickly between groups in order to unite ENEs over large cortical areas. However, that resultant unification would not function as a singular entity unless it was interacted with by some system “outside” of that set of groups, which interacted relatively slowly with that set. So if the general hypothesis is correct, we would expect to find systems in the brain, preferably in the cortex, whose dynamics reflect this structure: many activation areas which interact quickly among themselves, “seen” by one or more other areas interacting slowly and more-or-less simultaneously with the former (and if the latter are multiple, then they also must interact quickly among themselves—see 4.1 and following).

4.1

As it happens, we do find such systems.⁷ I will present data showing that the sensory, motor, and other cortical areas interact in just such a manner with at least three “control” areas: parts of the prefrontal cortex, the hippocampus, and the parietal system. Specifically, while activations within and between such areas as visual, auditory, and kinesthetic normally occur with gamma frequencies (which can go as high as 250 Hz: e.g., Ojemann et al. 2010), the interactions of those areas with, for example, the hippocampus, normally occur at much slower (roughly 5–100 times slower) theta and other, notably beta frequencies (and see Siegel et al. 2008; Donner and Siegel 2011, for summaries of this literature). If the coarse maps on the hippocampus need to evoke objects which consist of the unification of (the NCCs of) multi-modal sensations and abstractions (that is, if when we remember something, we remember how it looks, feels, sounds, etc., simultaneously), then if the hypothesis in this paper is correct, we would expect something like within-cortical gamma (or similar)-united activations interacting at theta (or similar) frequencies with within-hippocampal gamma-united maps—which is, in fact, what is found (e.g., Doesburg et al. 2005, 2010). Similarly, if the PFC is in part an “executive” which in some manner manipulates concepts, and if those concepts entail neural unifications over multiple sensory areas, then we would

⁷ In this following section, I will not attempt to explicitly distinguish between neural activations and phenomenal experiences; I have done that above, and one may take it that I am aware that “neural activations” and “sensations” or “thoughts”, etc., are at this point no more than correlated, and that when I speak of them I am speaking of their neural correlates—NCCs, since I take it that for a neural activation to be “phenomenal” we must be conscious of it (although of course see Block 2008).

expect such a relationship (theta or comparably relatively slow frequencies) between PFC and other areas of the cortex in particular contexts. If the parietal cortex is necessary for our focusing on particular objects (in contrast to general arousal – see e.g., Fuller et al. 2011; Gollo et al. 2010; Ribary 2005, on the possible role of gamma interactions between cortex and thalamus, and recent evidence that the thalamus generates theta in normal waking states—e.g., Tsanov et al. 2011) and these objects also entail such multiple neural activations, then, again, we should find this kind of neural dynamic between parietal areas and cortex. Further, if those three areas are themselves united (i.e., if we experience memory, sensation, and prediction simultaneously in a “phenomenal moment”—see, e.g., Husserl 1991, for an extended analysis of temporal experiences, and p. 54: Section 24—specifically on this point), they should interact through fast processes (and see also Lou et al. 2010, p. 186, and Doesburg, above, for similar ideas, and e.g., Tamber-Rosenau et al. 2011, for support of the general argument above). In addition, there is a literature concerning the phenomenon of “ignition” (e.g., Dehaene and Changeux 2005; Del Cul et al. 2007, 2009; Fisch et al. 2009) over the cortex, which supports, at the minimum, the fast interactions between cortical modules. However, while there is much support for widespread cortical activation in conscious states, ignition is usually described as widespread activation which is recurrent and self-maintaining. There is, however, little experimental evidence that these latter properties hold, although they have been found in neural models.

It should be clear, since strict synchronization is not necessary for the above dynamic, that I am also proposing a somewhat different mechanism for what is termed “binding” (e.g., Engel and Singer 2001) than the usual. However, one should note that while strict synchronization is not necessary, it is certainly relevant to the dynamic I am describing (e.g., VanRullen and Thorpe 2002).

I will begin by taking the components separately: cortical sensory areas first. I will briefly (because of the enormous extent of the literature on this subject) cite some few papers illustrating that these interact both internally (within-module, as we have seen above) and between-module with fast processes. I will then show that hippocampus, PFC, and parietal cortex, also interact internally with fast processes, and that they may interact with each other with such processes. Then I will show that the former interact with the latter three (or four) with slow processes. None of this, of course, is written in stone, and it is far beyond the scope of this paper to explain the enormous variation in processing speeds and extent which occurs within these modules. However, the above dynamics are common enough that there is sufficient evidence to build a case supporting them.

4.2

In the cortical sensory areas, the evidence for fast interactions, including synchrony, not merely during, but underlying, processes which necessitate the unification of different types of sensations and concepts, is simply enormous. The claim that gamma-frequency interactions unite cortical areas is hardly controversial at this point, dating back at least 40 years (e.g., da Silva et al. 1973). Given that large-scale ENEs are necessary, not so much to generate such unity but to embody it, we would expect to find this dynamic. More recent studies of such large-scale fast interactions include Buzsáki (2010), Buzsáki and Chrobak (1995), Buzsáki and Draguhn (2004), Crone et al. (2001, 2011), Del Percio et al. (2011), Doesburg et al. (2010), Fries (2009), Gollo et al. (2010), Miltner et al. (1999), Pockett et al. (2009), Pockett and Holmes (2009), Pockett et al. (2007), and Singer (2001), to name just a few in addition to the papers cited in previous sections. Canolty also finds long-range coupling in near-gamma (beta) frequencies (Canolty et al. 2010, p. 17360) related to behavior. There may be, in addition, some evidence that beta and alpha frequencies may participate in a hierarchical organization of network dynamics (e.g., Canolty, above; Jin et al. 2012; and Donner and Siegel, above), where inter- and intra- modular interactions may proceed through beta/alpha and gamma interactions, respectively (unfortunately, neither Jin et al. nor Donner and Siegel, above, looked for such hierarchies). If this is true, the stability of the alpha and alteration of the beta bands might be evidence for a hierarchical ENE structure even on the macro level.

4.3

Given the overwhelming evidence for the point (i.e., internal fast cortical interactions which are necessary, but not, if I am correct, sufficient, for “binding”) above, I will move to the hippocampus. The rationale here, as I mentioned, is that when we remember, our memories consist of a *set* of evocations which may include sound (aural imagery), vision (visual imagery), kinesthetic feel (kinesthetic or bodily imagery), scent (odor imagery), and so forth. Since we remember these simultaneously (although the gestalt changes with time), we would expect the corresponding areas of the cortex to be activated simultaneously, unless the hippocampus were itself a duplicate of the cortical maps (when I refer to “cortex” or “cortical” in this context I am of course referring to sensory modules, in contrast to the hippocampus). Yet this latter cannot be the case, and there is another literature detailing the locations and dynamics of memory formation and access, beyond the scope of this paper (see, e.g., Marr 1971; Becker 2005; Wang and Morris 2009), which shows that. Since the

hippocampus is comprised of coarse maps which evoke, i.e., which serve to stimulate (activate), the relatively fine sensory (and other) maps of the cortex (after memories have consolidated), then in order to evoke those memories, we should expect a relatively small area of the hippocampus to activate multiple large areas of the cortex. This is what happens, and those large areas, by the reasoning above, should be activated simultaneously, and further, if the hypothesis in this paper is correct, they should be “seen”, i.e., interacted with, as single objects, if that is how we experience them. In order for that to occur, one can extrapolate from characteristics of ENEs, and expect that the hippocampus should employ relatively slow “scanning”, so to speak, of the fine cortical maps, which latter should meanwhile be interacting internally much more quickly (than that scanning). That would force the unification of (“bind”) the fast interactions within a single interval of the hippocampal pulse or activation frequency. That is, recalling the epistemological basis of the ENE, the “unification”, above, is virtual, i.e., only such because of the slower hippocampal theta. What is “forced” is the effective grouping because of that temporal difference (gamma vs. theta). Thus, hippocampal scanning must occur at (something like) theta frequencies, and cortical interactions at gamma, roughly speaking, in order to produce a unification of memory components relative to the hippocampus (which hints that the shortest conscious moment for memories should be the theta period; and see, e.g., Doesburg et al. 2009, for experimental support of this inference).

Chrobak et al. (2000) elaborate and attempt to explicate hippocampal interactions with cortex and neocortex. From the above, one might expect that input from cortex, since that latter must be unified by coarse hippocampal maps, would be at high frequencies, with the hippocampal frequencies receiving them low, while internal hippocampal frequencies themselves should be comparable to internal cortical frequencies (e.g., gamma), so that the hippocampus itself would contain united groupings. This is what was found (p. 457–459). Hippocampal output, however, should induce gamma firing in the cortex for specific memories comprised of separated cortical groupings. We might expect something like widely-aimed (to cortical areas involved in the specific content of the specific retrieval) bursts of near-simultaneous cortical activation, and this seems to be the case with the “sharp wave bursts” found as hippocampal output (e.g., Buzsáki et al. 1992, p. 1025–1026; Chrobak et al. 2000, p. 461–463, and see Sullivan et al. 2011 for more details on such bursts).

Bastiaansen et al. (2002a, b) investigation of Treves and Rolls’ theory of hippocampal function (Treves and Rolls 1994) found supporting data: increased theta power during both memorization (encoding) and retrieval of memories,

with greater power during the latter (p. 1882–1883). And their explanation for theta increases (and decreases) in terms of Rolls’ theory of “cortical reactivation” (p. 1891) is consistent with the ENE hypothesis.

If we assume primacy of the theta oscillations originating in the hippocampus with respect to memory retrieval, one would expect that theta would tend to entrain the cortical gamma frequencies in that context, as I mention above. The literature does support this prediction. Insofar as phase-locking and frequency constraint are concerned, Mormann et al. (2005) and Canolty et al. (2006) summarize and extend much of the work pre-2006. This is also supported by the work of Burgess (Burgess and Ali 2002), who not merely showed theta modulation of gamma, but differences in gamma amplitude with recollection versus familiarity. And recently, Manning et al. (2011) have found evidence that hippocampal activation does indeed reinstate (“when recalling an item, the pattern of neural activity exhibits graded similarity to the neural activity measured during the encoding of items studied in neighboring list positions”, p. 12896) the cortical activations corresponding to the memories.

4.4

Interactions between the PFC and cortical modules are probably more complex than those between hippocampus and those modules, since executive functioning depends, at a minimum, not only on concurrent control but on prediction. Examining possible mechanisms of control is beyond the scope of this paper, but since control can involve, similarly to the hippocampus, some induction of activation in the cortical modules, one would expect similar types of interactions at least part of the time. However, executive control does not necessarily imply the sensory activation that recall entails, and thus that activation, and/or accompanying motor activation, can neither be as ubiquitous nor as automatic as the induction and recall of memories. Despite this, there does exist suggestive data in this area.

4.5

Take the issue of language learning. According to de Diego-Balaguer et al. 2011, data indicate that there are two major strategies, found in good and poor learners. The former infer rules from the data, while the latter primarily use memorization of specific examples. If we assume that the former strategy employs inferential and executive systems, while the latter mainly employs more localized systems, we might expect that good learners would have to connect prefrontal and parietal systems with the local temporal language modules, while poor learners would not

have this type of long-range connection so prominently. This would imply that for good learners, prefrontal and parietal should mutually interact with gamma (to unite the controllers), and with either theta or gamma (depending on how the controllers interact with the language modules) to the temporal modules. With poor learners, we might expect less long-range gamma between those modules and more local gamma, with theta perhaps to the hippocampus and/or to the controllers (given increasing but non-specific effort). De Digeo-Balaguer states: “Poor learners displayed greater local neural synchrony in the gamma band, mostly at bilateral fronto-temporal electrodes, whereas Good learners engaged long-range synchronization between frontal, parietal, and temporal electrodes.” (de Diego-Balaguer et al. 2011, p. 3116). A temporal analysis showed increases in long-range theta in poor learners and, in contrast, with long-range gamma in good learners (e.g., p. 3113–3114). If poor learners must exert more effort, one might expect wider controller activation, whereas good learners would need less controller and would have more local activation. But without more detail about the above processes, this must remain speculative.

Bastiaansen has investigated language retrieval and processing as they relate to theta and other frequencies (Bastiaansen et al. 2002a, b, 2005, 2008, 2009). Given syntactic violations, theta increased (but see below, this para, for a more nuanced picture), and Bastiaansen’s rationale is consistent with the hypothesis in this paper: “We proposed that a possible candidate process underlying the phasic increase following individual words in a sentence could be the synchronous activation of a neuronal population corresponding to some aspect of the processing of the word, either in isolation or in its sentence or discourse context.” (Bastiaansen et al. 2002a, b, p. 1480). “Synchronus” is of course of relevance for the ENE hypothesis, and that activation should occur at gamma or comparable frequencies. In a later publication (Bastiaansen et al. 2009), Bastiaansen addresses the complex issue of frequency/processing interactions. Let us suppose that correct sentences evoke richer and more complex experiences than do incorrect sentences, for the most part. In that case we would hope to find more gamma in associative areas and more theta in prefrontal and/or linguistic processing areas when sentences are correct. This kind of activity was found (p. 1341–1342), with the opposite for incorrect sentences. Since Bastiaansen relates beta frequencies to “syntactic unification operations” (p. 1335), one might expect that either beta is interacting with theta as above, or that beta is interacting with gamma to produce larger ENEs relating to syntactic unification. Although beta and theta are fairly close frequency bands, ENEs might still be formed, since beta (13–18 Hz) and theta (4–7 Hz) differ sufficiently for small ENEs to be generated. Further, the

interrelationship between the various frequencies (alpha, beta, and gamma) may support my earlier speculations concerning hierarchical ENEs. However, without more data on exactly where the various kinds of linguistic processing occur, and what that processing consists of, one can go no further here.⁸

Sauseng et al., following up Ishii’s et al. (1999) and others’ work, dissociated frontal-midline theta relating to attention from that relating to memory, and found increased theta in “frontal-midline ROI [regions of interest] only in the condition where complex novel sequences (COMPLEXNOV) had to be performed” (Sauseng et al. 2007, p. 588). When tasks are more demanding in terms of complexity and novelty one would expect that more processing areas would be activated simultaneously, and that the perceived complexity would be greater. Widespread “interregional” theta is associated with increased memory load, while more localized theta is associated with complex tasks, as above. Suppose we hypothesize that tasks with increased memory load need both increased control and increased memory retrieval. We have seen that increased memory retrieval entails increased hippocampal theta interacting with various cortical gammas, and we see from the above that the control of demanding tasks may require frontal theta. We might conclude, then, that tasks which are both demanding and memory-intensive would require both controllers, which could result in “interregional” theta, similar to what Sauseng found. Similar results were found by Sammer et al. (2007), who noted that theta increased with mental arithmetic workload not only in hippocampus but in “widespread cingulate activation, frontal superior, and cerebellar activation”, and goes on to hypothesize that “Hippocampal-cortical networks emerge theta band oscillations representing a binding process of widely distributed cortical assemblies. This binding process may form the source of surface-recorded EEG theta.” (p. 802), in line with the ENE hypothesis. Indeed, Klimesch et al. (2005), cited by Sammer, above, also comes extremely close to this aspect of ENE hypothesis (p. 105). Kaller et al. have also found theta involvement (i.e., the effects of theta-frequency TMS) in the speed of planning to be asymmetrical over right versus left prefrontal cortex (Kaller et al. 2011).

⁸ Beta and/or theta-beta relationships, where the frequencies are fairly close, may reflect only (or mostly) unconscious processes which do not necessarily require the construction of emergent groups. That is, “syntactic unification operations” are not usually conscious. Notice, however, that I am not merely relating the gamma-theta interaction to the activation and/or control by one area of multiple areas, I am also assuming that this interaction may relate to consciousness, i.e., that some ENE generation (thus, “binding”) is tied to conscious experiences (but see, e.g., Zmigrod’s findings on unconscious binding—Zmigrod and Hommel 2011). Since much of linguistic processing is in fact unconscious, there may be processes in which relationships such as gamma-theta are unnecessary.

Given that their task (solving the Tower of London problem) was primarily a logical one, one might speculate on the differential effects of the disruption (and/or stimulation) of theta generation on such (usually) lateralized abilities, but that is beyond the scope of this paper. Thus, the recent paper by Benedek et al., indicates (with Bastiaansen, above) that perhaps the theta band alone is too narrow, and that alpha (up to 12 Hz) may also be involved in ENE generation in control processes (Benedek et al. 2011).

Caplan et al. (2003) and Manns et al. (2003) investigated theta originating in the brainstem and thalamus which entrained theta and gamma across the cortex during periods of motor learning and maze running in humans and rodents. The finding that thalamic-generated theta is present in waking conditions and seems not merely correlated with memory formation in hippocampus but with task complexity seems to contradict many studies of Llinás et al. (none of which Sauseng, Klimesch, Sammer, Caplan or Manns cite) in which thalamic theta typically occurs during slow-wave relaxation in normal subjects and not during waking states (e.g., Llinás et al. 1999; Llinás and Steriade 2006; Llinás et al. 2005; Steriade and Llinás 1988, to cite only a few). One can thus only speculate that earlier studies did not take into account, e.g., theta generation in the anterior thalamus, or that instrumentation is simply better today.

5

The above at least gives an indication that the ENE hypothesis is viable. But I have inadequately pursued the question of what it means to say that some set of neurons, or its “dynamic”, “sees” another set as a “whole”, in the last few sections. The examples given of ENEs of other types, from physics and chemistry, are too straightforward to answer this satisfactorily for neural dynamics.

5.1

However, if we return to Cruse (2006), in 2.2 above, we can begin to approach this question. There we saw that a simple recursive circuit, which could be realized by a small group of neurons, could appear to have discrete outputs if an “observing” group interacted with it slowly enough, so to speak. If we apply that to van Swinderen’s findings (2005) in *Drosophila*, we see a similarity in the behavior of fruit flies with and without mushroom bodies, the parts of their brains which add recursion (at a minimum) to visual and other circuits (p. 325, and see also Cruse and Hübner 2008). Flies with mushroom bodies will respond to salient/nonsalient stimuli with all-or-nothing behavior: as a

stimulus changes gradually, the flies’ behavior does *not* change until some threshold is reached, upon which it will change abruptly. In contrast, a fly with damaged or incomplete mushroom bodies will exhibit gradually changing behavior as the stimulus changes gradually. This seems analogous to the behavior of a circuit “observing” or responding to the loops in Cruse’s example above. A suitably structured circuit will, then, present itself differently depending on how and by what it is observed. If observed “externally”, by an experimenter, it can present as continuous dynamics. If observed “internally”, by another circuit within the totality of the neural structure, it can present as such, or as a discrete set of states (see also Tang and Guo 2001; van Swinderen 2005, p. 585; van Swinderen 2009) if the temporal parameters are suitable. The “observation” of a subset of the dynamic continuum (perhaps one attractor) as a single state, “binds”, then, the continuity of states within that attractor into one virtual object, but only, it must be emphasized, within particular parameters of that interaction. The fruit fly responds to, “sees”, that internal dynamic as a single virtual entity—a constant stimulus, a primitive gestalt, in effect—and does not, when it is neurologically intact, behaviorally indicate that there is a *continuum* of states in its visual maps which are the lower-level neural responses to multiple stimuli. The analogy with e.g., the theta/gamma interactions between hippocampus and cortex is clear. Just how similar the phenomena are is of course a question that cannot yet be answered.

5.2

More generally, it is possible to extend Hopfield’s temporal summation and discrimination through “action potential timing” (Hopfield 1995) to a spatial dynamic. Let us imagine two neural groups, one (A) which has as output a 2-dimensional array of neurons in various states, and the second (B), which interacts with A through a slow (e.g., theta) interaction, and then has its own internal interactions at periods similar to A (e.g., gamma). In order to do this, the input neurons (the outputs of A) must be treated as a spatial array leading to another corresponding array, as with the Wöhler and Anlauf (1999) model. In this way spatial arrays can be discriminated. Now, suppose the second module was connected to a single neuron instead of to an array; “single neuron” implies that any feedback from the former module to the neuron, whether it is in one or multiple parallel channels, is treated as a single process. This single process must occur over the spatial distribution of the first entity’s outputs as well as over their temporal period. In order for that to occur, according to extant models (e.g., Wang 1999; Wöhler and Anlauf 1999), there must be parallel

inputs to the second module which correspond to the spatial distribution of the outputs of the first module. We do find this in the cortex, and this implies, first, that cortical modules must be internally connected (i.e., the parallel modules which are the map columns corresponding to different locations) at gamma frequencies (assuming, as above, that the inputs proceed in something like theta periods), in order to make them *effectively* parallel. However, this is not sufficient to unify the inputs in a sense analogous to Hopfield's temporal unification that we saw in section "1.3". Consider how that latter was accomplished: a varying subthreshold voltage served to impose differences on different input sequences, which could then be combined in some fashion and effectively discriminated. The analogous spatial variation can be imposed if the cortical modules (B) receiving the 2-dimensional arrays from A vary *spatially*. A continuous and organized spatial variation in the reception of a pattern on B will serve to make spatially similar but differently oriented (for example) patterns received as intrinsically different, just as a temporal variation does the same for temporally similar (e.g., different patterns summing to the same over some temporal interval) patterns. But this is just a description of what is found throughout the cortex: i.e., the cortical maps. In fact, a fine-to-coarse (from A to B) mapping will serve to further unify patterns in B. However, once a spatial pattern is imposed on a map, and that pattern remains, through some type of resonance, for at least a theta period, the fast gamma of the receiving module can effectively unify that input through its internal interactions, even if there is no convergence to a coarse map.⁹

Returning to van Swinderen, above (5.1), it is now easier to see why the fruit fly might respond both with different orientations and more holistically to a directionally varying stimulus; if that variation were accomplished through the formation of two attractor basins, each unifying a set of stimuli at *both* different locations and times on the fly's visual map, any single basin could unify a series of temporal/spatial stimuli until some threshold was reached. The jump to the other basin does not then merely imply another temporal unification, but a unification located in another position on the map of the fly's visual space.

Cortical maps, then, might be conceived of as supportive and even vital to the type of emergence described in this paper. The literature on the formation of cortical maps is enormous, and I will not even attempt to speculate, here, on any sort of chicken and egg dynamic re emergence and those maps, nor on the functioning of emergent groups on

those maps. That is for the next paper, to which this last Section can serve as brief introduction.

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⁹ I would like to point out that the logic above derives, from first principles which do not assume maps, a reason for their existence; the principles of emergence in this series *predict* cortical maps.

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