

Table R1. Views on four basic issues

relaxed. An object can be also be described by an imperfectly closed boundary together with constant texture or known structure.

Now, what is required for this? First, a possibility to group V1 cells without destroying their filtering properties, which is clearly provided by P&S. Second, the process must be cascable, that is, groups of groups must be possible. This is a bit more problematic, because the number of *different* synchronized groups at a time is very limited. For the system proposed here, this is not a serious problem, because the processors keep their RF properties intact, so the relevant cells for a whole object may be synchronized into one group without confusion. For implementing, for example, a graph structure like the one used by Lades et al. (1993) it might constitute a serious limitation.

If such object descriptions develop in a self-organized way based on the input image it should be relatively easy to match them with stored models of objects, although the integration of flexible matching and associative memory remains an open problem. Anyway, the target article opens a couple of interesting new routes of investigation.

Authors' Response

Progress toward an understanding of cortical computation

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Abstract: The additional data, perspectives, questions, and criticisms contributed by the commentaries strengthen our view that local cortical processors coordinate their activity with the context in which it occurs using contextual fields and synchronized population codes. We therefore predict that whereas the specialization of function has been the keynote of this century the coordination of function will be the keynote of the next.

We thank all of our commentators for producing thoughtful and insightful commentaries in the few weeks available. The commentaries come from five broad areas of expertise: neuroscience and neurology (13); computing, neural computing, and informatics (10); psychology (5); theoretical brain physics (2); and psychiatry (2). This diversity is a testament to the importance of trying to understand cortical computation. Anything common to such diverse sources of knowledge must reflect a deeper reality. We do not suppose, however, that all these perspectives can be boiled down to any single perspective, including that emphasized in the target article. Just as we suppose that cortical cells can cooperate so as to emphasize coherence while nevertheless maintaining their own distinctive contribution, so we suppose that different scientific perspectives can all shed light on a common underlying reality while nevertheless remaining distinct.

We first present a summary of the views taken on four central issues, and then discuss two of the most basic: the working hypothesis of common foundations, and the role of contextual coordination. The main body of the response is divided into nine sections. R1 to R5 discuss the five issues

Are common foundations for cortical computation likely?

YES Amit, Bower, Bugmann, Eckhorn, Floreano, Gregson, Grossberg, Haase & Diniz, Iacoboni, König et al., McCollum, Morasso et al., Niebur & Usher, Palm & Wennekers, Silverstein & Schenkel, Smyth, Tononi & Edelman, Treves, Wang, Wright, and Würtz.

NO
? Nunez, Stone.

Is the coordination of activity a fundamental goal?

YES Amit, Bugmann, Eckhorn, Floreano, Gregson, Grossberg, Haase & Diniz, Iacoboni, König et al., McCollum, Morasso et al., Niebur & Usher, Nunez, Silverstein & Schenkel, Smyth, Stone, Tononi & Edelman, Wang, Wright, and Würtz.

NO Treves.
? Bower, Palm & Wennekers.

Is the distinction between CFs and RFs useful?

YES Bugmann, Eckhorn, Floreano, Grossberg, Iacoboni, König et al., McCollum, Morasso et al., Silverstein & Schenkel, Smyth, Stone, Tononi & Edelman, Wang, Wright, and Würtz.

NO Niebur & Usher.
? Amit, Bower, Gregson, Haase & Diniz, Nunez, Palm & Wennekers, and Treves.

Does the cortex use synchronized population codes?

YES Bower, Bugmann, Eckhorn, Floreano, Gregson, Grossberg, Haase & Diniz, Iacoboni, König et al., McCollum, Niebur & Usher, Nunez, Palm & Wennekers, Silverstein & Schenkel, Tononi & Edelman, Wang, Wright, and Würtz.

NO Amit, Treves.
? Morasso et al., Smyth, and Stone.

listed in sections 6.1 to 6.5, and in the same order. R6 discusses possible additional foundations proposed by commentators. R7 discusses further issues raised by commentators. R8 takes up the invitation of one of the commentators to pursue the analogy between the scientific enterprise and cortical computation. Finally, R9 notes promising directions for future progress.

Table R1 classifies commentaries in relation to the views taken on four basic issues: (1) Are common foundations for cortical computation likely? (2) Is the coordination of activity a fundamental goal? (3) Is the distinction between contextual fields (CFs) and receptive fields (RFs) useful? (4) Does the cortex use synchronized population codes? Each commentary is classified as "yes," "no," or "agnostic" on each question. Most classifications are based on what is said explicitly, but in a few cases we inferred what seemed implied. Nevertheless, the classifications given are ours. There is no guarantee that commentators would agree.

On each of the four questions Table R1 classifies the majority of commentators as giving the same answers we

do. Few argue explicitly against the positions we take on these issues. They were not short of criticisms, of course, with the most prominent being as follows. **Amit** and **Treves** doubt any role for synchronization. **Bower** says that his biological models suggest a role for it, but a role that differs from ours. **Niebur & Usher** agree with us on the role for synchronization, but doubt CFs. **Palmer & Wennekers** think that synchronization is important, but criticize the computational studies for not modeling activity at the level of individual spikes. Some commentators see no role for information theory. There is thus no agreement between these criticisms, and much disagreement. Several commentaries call for more emphasis upon top-down processes. This is well within the spirit of our approach, and we agree.

All commentaries agree that it is worth searching for common foundations. This consensus does not show that view to be correct. There is no reason to suppose that those whose skeptical views were noted in sections 2.1, 2.2, and 2.3 are no longer skeptical. It is simply that their views are not represented here. It would help if they were, because their perspective suggests aspects of cognition that are unlikely to be directly comprehensible in terms of common foundations. Our search will be led seriously astray if it attempts to explain, without additions, aspects that require further capabilities. With respect to language, at least, the best supported hypothesis is that it does involve special capabilities (Pinker 1994). Whether these depend upon the common foundations, as our perspective suggests, remains to be seen.

Stone and **Nunez** both note that the hypothesis of common foundations is not well specified. We have not attempted any formal specification, simply using the word “common” to mean most or many, and not necessarily all. We do not see how this can be formalized. It is an empirical rather than a formal issue, so we keep our minds open as to what constitutes the range of cortical and cognitive processes to be understood under a common rubric. The more the better.

We now turn to views on the role of contextual coordination. We argued that functional specialization and contextual coordination together form two basic and mutually constraining principles of cortical organization (sect. 1.1). Functional specialization is undisputed. The issue is whether it is balanced against a need for coordination. **Tononi & Edelman** have argued elsewhere (Tononi et al. 1996), both formally and forcefully, that this is so, and von der Malsburg and Singer (1988) have shown how the emergence of global order from local cooperation is a very general property of physical systems composed of many distinct but interacting elements. The forms of contextual coordination emphasized in the target article include the selection of contextually relevant signals, their grouping into coherent subsets, and contextual disambiguation. Although most commentaries seem to agree with the need for such coordination, two raise important doubts. **Treves** argues for the value of dissonance and of letting cells be free rather than having them goose-stepping in synchrony. **Niebur & Usher** argue that as unexpected events can be both important for survival and highly salient, they constitute cases where our emphasis upon coherence is exactly the opposite of what is required.

Treves stressed the possibility that information transmission may be reduced rather than increased by synchrony. We will discuss evidence for synchrony as a cortical

code in section R3.1. Here we focus upon conceptions of the goals of cortical processing. Underlying Treves’s concern for squeezing as much information as possible out of cortical cells is the long and strong tradition that emphasizes the goal of recoding to reduce redundancy (sect. 1.2.1). If the goal is to transmit as much information as possible using a limited and noiseless channel, an optimal recoding will map activity into statistically independent variables. We agree that this perspective makes an important contribution to our understanding of cortical computation, but taken to the extreme it would lead to something worse than chaos. First, neither the external world nor the cortex are noiseless, so redundancy is necessary. More important, the transmission of as much information as possible seems to be a highly implausible goal for cortex. It is more plausible that it discovers what predicts what, including various aspects of reinforcement, and uses that to transmit information about just those variables that matter. This will emphasize signals that are coherently related, and thus reduce total information transmission.

Niebur & Usher note the sudden appearance of a predator as an example of the salience of “unexpected” events; they view this as evidence for the opposite of our emphasis upon coherence. We are well aware of the salience of abrupt changes. They were central to our studies of the detection of appearance and disappearance of single elements in random-dot arrays using psychophysical and physiological techniques (Phillips & Singer 1974; Singer & Phillips 1974). Gradients of change in both space and time are so crucial that they are central to RF specificity at all levels. This has long been clear, and it explains why contrast in either time or space (including higher feature spaces) is so noticeable. Does this imply that incoherent signals are more salient than coherent signals? Not at all. Consider a random-dot array in which two subsets of elements appear, one in some structured or familiar arrangement, the other at random. It is the structured or familiar subset that will be most salient, not the random one. The sudden appearance of a predator will produce activity across a wide array of cells in the visual cortex. Camouflage evolves so as to reduce the coherence of that activity, not so as to increase it. Thus, Niebur & Usher provide an excellent example that expresses at the intuitive and behavioral level our view that coherent patterns of activity, not incoherent ones, are most effective at the cellular level.

R1. Does the distinction between RFs and CFs have biological relevance?

R1.1. Niebur & Usher’s doubts

Most commentaries agree that this distinction is useful. **Niebur & Usher**, however, argue explicitly that it is not. Their grounds for this are that lateral interactions in the cortex can be explained by excitatory and inhibitory interactions alone, making no use of gain-control mechanisms. **Smyth** discusses the same phenomena as Niebur & Usher, but, in contrast, concludes that such lateral interactions support the RF/CF distinction and should be included in the CFs. Who is right? In section R1.7 we will outline a scenario in which they could both be partly right. Here we emphasize two more general points. First, CFs are primarily distinguished by the effects they have, that is, modulatory and synchronizing, not by the source from which they

come. They should not be identified with lateral interactions. Some long-range interactions may be concerned with computing RF features that require comparison with a large surround. RF features defined by comparing a center with a large surround are perfectly compatible with the contextual coordination of those features through CFs, however. Second, CFs are primarily distinguished by the effects they have, not by the mechanism producing those effects. Furthermore, although Niebur & Usher suggest a different mechanism for lateral interactions, they acknowledge elsewhere that voltage-dependent channels (e.g., NMDA) are common (Usher & Niebur 1996), and may play a role in "top-down attentional modulation." Thus, in our terms, they do assume a role for voltage-dependent CF mechanisms, suggesting that it is specifically intraregional voltage-dependent CFs that they doubt. If so, their view seems similar to that of **Grossberg** in this respect (sect. R1.7). The absence of such CFs is not yet clearly established. It cannot be established by showing that some long-range intraregional connections contribute to RFs, nor by showing that they may in part use mechanisms different from those we emphasized.

R1.2. How are RFs and CFs distinguished?

Given that this distinction is useful, how should it be drawn? At least five possible contrasts must be considered: (1) RFs have a driving effect (driving activity either up through excitation or down through inhibition); CFs are modulatory (producing either facilitative or suppressive gain-control); (2) RFs determine what information signals transmit; CFs help determine exactly when they are sent; (3) RFs determine what information signals transmit; CFs specify with which other signals they are to be grouped. (4) RFs determine what decision signals transmit whereas CFs help determine the confidence with which that decision is made; (5) RFs tend to be feedforward; CFs tend to be lateral and feedback.

Tononi & Edelman and **Eckhorn** cite further evidence that most of those contrasts are relevant. Our view is close to theirs but with a few differences of emphasis. **Tononi & Edelman** doubt the usefulness of distinguishing between decisions and confidence in those decisions. They rightly note the difficulty of making a categorical decision by distinguishing between active and inactive neurons. Our working assumption is that different outcomes of categorical decisions are represented by different groups of neurons with reciprocal inhibition between groups. The categorical decision could then be conveyed by the group transmitting more spikes or more synchronized ones, than the others, and the confidence by how much more. **Tononi & Edelman** put more emphasis on contrast 5 than we do. We propose that CFs are distinguished by the effects they have, not by the source from which they come. Nevertheless we agree that CFs are more likely to come from lateral and feedback sources. **Eckhorn** notes that there is little or no physiological evidence for suppressive effects between uncorrelated signals. This is a simple misunderstanding. The computational framework outlined in section 3 implies that CF connections will adapt so that they have no effect if they link streams between which activity is uncorrelated.

R1.3. Terminology for CFs

Given the similarities between our view of CFs and those of **Tononi & Edelman** and of **Eckhorn**, we explain briefly

why we use the terms we do, rather than those they propose. Calling the CFs reentrant connections puts the emphasis upon the source from which they come rather than upon the effects that they have. If it turns out that some bottom-up connections mediate contextual modulation, for example, to speed-up coordination, we could refer to them as feedforward CFs. Calling them feedforward reentrant connections would sound less coherent. **Eckhorn** calls the CFs association fields, as do **Field et al.** (1993). Although this has some appropriate connotations, it seems more appropriate to the retrieval of concepts. We therefore prefer to use the term associative connections to refer to the internal connections in attractor neural networks, such as those analyzed in detail by **Amit** (1989), **Hopfield** (1982), and many others.

R1.4. How could CFs produce synchronization?

It is noted by **Palm & Wennekers** that the computational theory outlined in section 3 does not show in detail how biological CFs could produce synchronization. Previous studies by many others have studied this in detail (sect. R1.9), however. An excellent example of the use of CFs in technological implementations is given here by **Wang**. His success in processing real images shows that CFs would be useful if they had biological reality. Further computational support for synchronizing CFs is provided by **Würtz** who notes that their use may overcome the problem of distinguishing multiple simultaneously active groups, which is a difficulty for the dynamic link architecture (DLA) (**Lades et al.** 1993). Thus, a system using CFs may be less flexible than the DLA, but closer to the biology.

R1.5. Is there a role for inter-regional feedback CFs?

There is an explicit call by **Tononi & Edelman, König et al., Grossberg,** and **Bugmann** for more emphasis upon top-down processes. We agree. Top-down sources for CFs are clearly shown in Figure 1c. Physiological evidence for such effects was cited in section 4, and their relevance to word perception was discussed in section 5.7.2. Nevertheless we understand why several commentators were misled about our views on this, because we did put more emphasis upon bottom-up stimulus-driven contextual coordination. This was not because we doubted the importance of top-down influences. Two classes of top-down effect must be distinguished, stimulus driven and strategically driven. There is clear physiological evidence for top-down contextual modulation that is stimulus driven (**Zipser et al.** 1996), and our computational studies have included such effects (e.g., **Phillips et al.** 1995a; 1995b). **König et al.** now provide evidence for strategic top-down coordination by showing that synchronization depends upon the current task and not just upon the current stimulus. We agree that such effects are important and could be mediated by CFs.

R1.6. Is there a role for internal sources of RF drive?

The flow of activity that arises from within the cortex itself is emphasized by **Tononi & Edelman,** and **Wright** suggests that intrinsic attractor dynamics be incorporated into the concept of a local-processor, and in such a way as to be seen as part of the RF. We see our approach as supporting both proposals. They rightly remind us that internal systems, for

example those concerned with plans and strategies, can provide a source of driving as well as of coordinating activity. Coordination of this internally generated activity is also crucial, however, because our thoughts and plans also need to be coherent (sect. R7.4).

R1.7. How are CFs related to long-range interactions in visual cortex?

The distinction between RFs and CFs is unnecessary, **Niebur & Usher** argue, because the effects of context can be explained without invoking a separation between the processing of context and content. It is not clear whether they are denying the functional distinction or proposing a different mechanism for it, however. Having denied the distinction, they then use it so that the sign of the effect of “context” depends upon the strength of the “input” (i.e., the RF input). If there were no difference between the processing of context and content then the sign of the effect of RF input should depend upon the strength of the context, and they do not claim that to be the case. It thus seems more likely that they are proposing a mechanism for the distinct effects of context. This interpretation is strengthened by their description of the physiological and psychophysical data to be explained as showing contextual modulation (Stemmler et al. 1995). The mechanism they propose is based upon the phenomenon of “stochastic resonance,” in which noise enhances detection of weak signals by increasing the gain at weak signal strengths (Stemmler et al. 1995). **Bezrukov & Vodyanov** (1997) have now proved that stochastic resonance can occur in voltage-dependent ion channels, however, so the mechanism that **Niebur & Usher** propose may be more compatible than they thought with the one we emphasized. If so, that would enable them to preserve their account of the relevance of stochastic resonance without having to explain away evidence that long-range intra-regional connections activate voltage-dependent channels (Hirsch & Gilbert 1991). Even that is unlikely to provide a complete account of long-range lateral interactions, however, because it is hard to see how enhancing the detectability of weak elements explains the figural grouping of high-contrast elements (e.g., as in Field et al. 1993).

Smyth, in clear contrast to **Niebur & Usher**, interprets the data on long-range interactions in V1 as evidence for CFs. **Kastner et al.** (1997) provide evidence for modulatory effects upon cells in visual cortex (V1). Their Figure 4a shows a cell with narrow orientation tuning. It is inhibited by a single central bar orthogonal to its preferred orientation. There is no sign of inhibition being produced by a surrounding array of parallel elements alone, but when they are presented along with an optimally oriented central bar they reduce firing rate from about 20 to about 5 spikes per sec above spontaneous. This is clear evidence for modulatory rather than driving effects, and **Kastner et al.** describe their findings in terms of effects upon “saliency.” This implies that they view the effects of the surround as not changing what is signaled, but as changing how effective that signal is at subsequent levels. This is in accord with what **Smyth** proposes.

The view just outlined allows for the dependence of context effects on the strength of the central stimulus. The hypothetical activation function used in section 3.1 of the target article produces smaller effects of context as target

strength increases, and in addition sect. 6.1 suggests that effects of context upon spike rate in cortex may reduce as target strength increases. Studies of context using visual evoked potentials show this to be so (**Polat & Norcia** 1996). Thus this aspect of “contrast-dependence” is catered for by the simple assumptions made in section 3, contrary to what **Smyth** may be taken as implying. The aspect that he intends to emphasize, however, is the change in *sign* of the context effects with changes in the strength of the central RF stimulus (personal communication with **Smyth**). We agree that this is not catered for in section 3.

For a broader view of long-range interactions it is crucial to distinguish several levels of processing. Two levels of analysis can be distinguished in the perception of textured stimuli such as those used in many of these experiments (**Sagi** 1995). At the lower level local features are computed, for example by anisotropic Gabor-like filters. At the higher level, further center-surround comparisons are used to compute gradients of change in the lower-level feature space (e.g., by isotropic Gabor-like filters with larger RFs than at the lower level). The model outlined by **Sagi** (1995) is concerned only with the basic feedforward RF architecture, so we need to add contextual coordination within levels and from the higher to the lower level. Detectors of distinct stimulus elements could therefore interact through modulatory CF effects at the lower level, but with their outputs being combined in RF computations at the higher level. At the higher level of analysis, however, long-range comparisons are used to compute gradients in feature space, and these are best thought of as being part of RF computation because information about the separate stimulus elements is lost (**Sagi** 1995). This is in keeping with the view expressed in section 1.3, except that it occurs in secondary rather than primary visual cortex.

This scenario may provide a reply to the second question that **Smyth** raises, that is, it shows how synchronization can have a role in input pre-processing. It allows for the dynamic sculpting of the exact extents of the effective RF centres and surrounds of cells in secondary visual cortex. These would otherwise be too rigid to reconcile, for example, the conflicting demands of segregation and integration (**Braddick** 1993). There is evidence that this involves top-down modulatory inputs (**Salin & Bullier** 1995), including those that are stimulus-driven (**Zipser et al.** 1996), as well as those that are task-dependent (**Maunsell** 1995). **Zipser et al.** (1996) found evidence for top-down contextual influences on V1 cells by showing that firing rate is increased by any of a variety of higher-level cues that made the features being signaled part of the figure rather than the ground. Synchronization of firing was not studied. Given the evidence for diffuse axonal bifurcation of the feedback connections (**Salin & Bullier** 1995), and given that pyramidal cells respond to synchronization over the relevant timescales (**König et al.** 1996), we predict that the outputs of V1 cells sensitive to different elements within the figure will tend to become more synchronized by the common top-down inputs that they receive.

An important difference between **Grossberg's** perspective and the one we outlined is that in his models top-down and lateral connections have very different roles, with only the top-down being analogous to our CFs. He states his conviction that the function of horizontal intraregional connections is to complete missing information, as over blind spots and retinal veins, but cites no evidence that

convinces us of this. It is hard to see how it could be the main part of the story, because lateral intraregional connections in V1 predominantly link cells with normal retinal input.

R1.8. What is the distribution of CF inputs?

Given the usefulness of distinguishing CFs from RFs, **Eckhorn** and **Morasso et al.** note that a major issue that arises is to map the distribution of facilitatory and suppressive CF inputs. We agree. Much relevant data concerning their distribution in V1 already exists (e.g., Kastner et al. 1997; Levitt & Lund 1996; Polat & Norcia 1996; Schmidt et al. 1997; Weliky et al. 1995; Zipser et al. 1996), but even there important issues await further clarification. In other regions there is much new territory to be explored, as Morasso et al. emphasize.

CFs are local in that each processor has its own particular set of direct CF inputs. All-to-all CF connectivity is neither possible nor desirable (**Wang**). If CF influences can be mediated through other processors, however, then each processor could be influenced indirectly by a much larger set. **Floreano's** simulation of mediated long-range contextual influences clearly demonstrates this possibility. He shows how activity in distant parts of the network can influence RF learning given a chain of intermediate CF connections. An important constraint on this possibility, however, is that the mediating processors in the chain must themselves simultaneously receive RF input. This is in striking agreement with the capabilities and constraints observed by Polat and Sagi (1994b) in their psychophysical studies of perceptual learning in human vision.

R1.9. What synaptic receptor channels do CFs use?

Doubts are expressed by **Niebur & Usher** about whether NMDA-receptor channels can mediate synchrony at short-time scales. NMDA channels have long been thought to have time constants of more than 150 msec, but it is now known that there are also fast components to the NMDA response with time constants closer to 15–50 msec (D'Angelo et al. 1990; Hestrin et al. 1990; Monyer et al. 1994). Although the fast components of the NMDA response are not well known, they have been used in models of STM (Jensen et al. 1996; Lisman & Idiart 1995). None of this implies that there are no other mechanisms for synchronization, and there is evidence for others (e.g., Cobb et al. 1995; Traub et al. 1996).¹

R2. Does the distinction between RFs and CFs (and/or synchronization) have psychological relevance?

In section 5 we argued that cognitive and neuropsychological evidence from a wide variety of paradigms supports our approach. Few of those arguments were questioned. Overall, commentaries did not subtract much from the psychological case presented, but, with one notable exception, neither did they add much. This suggests that a great deal remains to be done to foster facilitatory interactions between psychological and neurobiological studies of contextual coordination. The encouraging exception is provided by **Silverstein & Schenkel**. They have long used a variety of cognitive psychological paradigms to study perceptual

grouping and other forms of contextual coordination in schizophrenia and conclude that it is selectively impaired in a distinct subset of patients. If so, studies of such states could provide new insights into the broader psychological significance of contextual coordination and of its pharmacological bases. Their suggestion will be considered closely in section R7.4.

R2.1. What is the role of top-down contextual control in cognition?

Internal sources of RF drive are dominant over external sources, **Tononi & Edelman** argue. This contrasts with the greater emphasis in the target article upon stimulus-driven effects. We agree that this is a major issue, and that the contextual modulation provided by strategic control may have much import for psychology. Perhaps the balance between internal and external sources varies, with the balance shifting too far toward external sources in some cases (e.g., attention deficit hyperactivity disorder, frontal lobe damage), and too far toward internal sources in others (e.g., psychotic delusions, dream states). They also argue for the importance of global context as provided by diffuse ascending systems. We agree, but emphasize that they do not carry semantic information and differ anatomically, pharmacologically, and functionally from mechanisms for local contextual coordination.

König et al. also emphasize the importance of internal strategic control variables, and show that they are amenable to combined electrophysiological and behavioral study. Their results indicate that such control uses similar CF synchronizing mechanisms as do stimulus-driven effects, and thus suggest promising new directions for future research. Section 1.4 in the target article notes several prior theories with similarities to our approach, including that of **Grossberg**. We did not specifically relate his work to these issues, however, and he has now done that better than we could have done. Instead, we put more emphasis upon relations to other theories that are closer to ours in spirit, and to the neurobiology in detail. Nevertheless, it is encouraging that Grossberg also sees important roles for synchronization and contextual modulation, for example in the top-down matching process of ART. **Bugmann** also makes a good case for top-down task-dependent contextual effects. We agree, but note that this does not imply the absence of bottom-up stimulus-dependent contextual effects. We await with interest for further developments in the use of CFs in computational models of strategic control.

R2.2. Are there modulatory interactions in word perception?

The relevance of contextual modulation to word perception is called into question by **Niebur & Usher** on the grounds that the effects of context and target are independent until additively combined at the final stage of response selection (Massaro 1989a; sect. R7.1.1). There are four replies to these doubts. First, Movellan and McClelland (1995) show how the data suggesting independence is compatible with interactions between streams even in the case where those interactions are mediated by driving excitatory and inhibitory connections. Second, even Massaro acknowledges an asymmetry in the effects of context and target, because it is only the target that determines the alternatives between

which choice is made. Third, Samuel (1996) shows that there are conditions where the signal detection measures used as evidence for independence do show effects of context upon signal detectability, even though these effects are small and fragile. Fourth, and most importantly, measures of signal detection are not equivalent to measures of information transmission. Changes in bias can have large effects on information transmission, so other measures are needed to test for the interactions that we propose. The appropriate conditional mutual information measures are presented in Smyth et al. (1996). We do not know of any studies applying these measures to context effects in word perception, but possible paradigms for doing so were outlined in section 5.7.2.

Iacoboni summarizes data showing that interhemispheric priming effects are mediated by the corpus callosum, as most theories would predict. This could reflect interhemispheric contextual modulation, but more direct evidence is required. In particular, measures that distinguish modulatory from driving effects (e.g., Smyth et al. 1996) would have to be used in order to show that the interhemispheric priming is indeed modulatory. Until then, a *prima facie* case for the hypothesis can be made on the grounds that response selection is determined by the target, with cross-hemispheric context predominantly influencing the RT.

R.3. Does the cortex use synchronized population codes?

R3.1. The doubts of Amit and Treves

Both **Treves** and **Amit** doubt that synchronization is used. This question can only be resolved experimentally. Spurious synchronization in Amit's models in no way detracts from the many observations of stimulus-dependent synchronization in real animals. Treves's use of information measures may well help analyze this data, but it is not just the transmission of information in general that must be measured, but information about the particular stimulus relations that affect synchronization. Stimulation paradigms have to be used that require response selection and grouping, and evidence has to be obtained that the result of these operations is signaled by changes in synchronization rather than by changes in discharge rate. Such evidence is available. Whether neurons with spatially segregated RFs are activated with a single continuous contour or with two different stimuli is reflected by the degree of synchronization rather than by rate changes in the cat retina and LGN (Neuenschwander et al. 1996), cat area 17 (Engel et al. 1991; Freiwald et al. 1995; Gray et al. 1989), for groups of neurons distributed across area 17 of the two hemispheres (Engel et al. 1991; Munk et al. 1996), or across areas 17 and PMLS (Engel et al. 1991), in area MT of awake monkeys (Kreiter & Singer 1996), and in primary auditory cortex (deCharms & Merzenich 1996). In amblyopia, a developmental disorder associated with deficits in contextual grouping, the only detectable abnormality in primary visual cortex was drastically reduced synchronization among responses conveyed by the amblyopic eye. There were no differences in discharge rates between neurons driven by the normal or the amblyopic eye even when these responses were evoked by gratings whose spatial frequency was so high that they could no longer be resolved by the cats when

viewing with the amblyopic eye alone (Roelfsema et al. 1994a; 1994b). Finally, dynamic selection of responses, such as occurs during binocular rivalry, is associated with changes in synchrony but not discharge rate in area 17 of awake cats experiencing rivalry. Upon introduction of a rivalrous stimulus, neurons responding to the eye which won the competition increased their synchrony while neurons responding to the losing eye did the reverse (Fries et al. 1996).

R3.2. Should external (stimulus-locked) and internal synchronization be distinguished?

Stimulus-locked and internal synchronization are distinguished by **Tononi & Edelman, Eckhorn, and Wright**. We agree. In both cases synchronization is exploited for binding. Psychophysical evidence suggests that stimulus-locked synchronization is used for figure-ground segmentation if figure elements are presented with temporal offset relative to background elements. The temporal precision of this segmentation is better than 8 msec and the temporal information is provided by the magnocellular pathway (Leonards et al. 1996; Leonards & Singer 1997; but see Kiper et al. 1996 for a different result). This grouping by external timing can be overridden by internal grouping, however. If the figure is defined by textual coherence of its elements, detection is not impeded by false temporal conjunctions. If two different figures are defined, one by temporal cues and the other by texture cues, there is rivalry and the figure defined by the more salient cues is perceived.

R3.3. What are the time-scales of synchronization?

Questions concerning the relevant time scales of synchronization are raised by **Palm & Wennekers** and **Nunez**. One of the main advantages of synchronization is that it can operate on a much faster time scale than selecting responses by increasing their rate – provided that it is possible to synchronize responses rapidly. If responses are selected by rate increases, a cell has to integrate over a sufficiently large number of incoming EPSPs before emitting a response in order to assume that the response is actually generated by the selected input and not by accidentally arriving EPSPs or nonselected inputs. The required duration of this safety interval depends on average firing level and can be set by modulating the membrane potential (i.e., the distance to threshold and the membrane time constants). Assuming response frequencies of cortical neurons in the range of 50 Hz and postulating summation over at least 4–5 EPSPs before reaching a decision amounts to transmission times per processing step of at least 80 to 100 msec. This is far too slow. Input selection by spike synchronization is much faster because it does not rely on temporal summation. Coincident EPSPs can reach firing level within a few msec, thus reducing transmission times to near the synaptic delay. The speed of selection is thus primarily constrained by the time required to obtain synchrony. Contrary to earlier models, which generated synchrony by coupling harmonic oscillators, more recent models based on spiking neurons (i.e., relaxation “oscillators”) indicate that synchrony can be obtained very rapidly (**Wang; Somers & Kopell** 1993). This is supported by experimental evidence. In the retina, responses to coherent stimuli are

synchronized within milliseconds after their onset (Neuenschwander et al. 1996).

In the cortex, it is much more difficult to determine experimentally the time required for the alignment of spikes by cross-correlation analysis because the windows must have a minimal duration to obtain sufficient entries, and because response onset is not well defined when moving stimuli are used. The data suggest that newly induced oscillatory responses synchronize right away once oscillatory patterning develops (Singer & Gray 1995). As cortical activity has a complex oscillatory structure (Arieli et al. 1996) and as oscillatory modulation of the membrane potential shifts spike timing, feature specific synchronization may occur very rapidly. The rate at which different assemblies can be organized successively without merging depends critically on the integration time constants of cortical neurons. Here views diverge, ranging from estimate of less than a millisecond (König et al. 1995; Softky 1995) to tens of milliseconds (Shadlen & Newsome 1994). Data on echo location and spatial location of sound sources show that neurons are capable of very precise coincidence detection (Yan & Suga 1996). Whether this is also true in the cortex remains to be seen, but recent evidence on action potentials backpropagating into dendrites (Stuart & Sakmann 1994) and other regenerative events in dendrites (Connors & Gutnick 1990) may lead to a drastic change in views on the timescale of dendritic integration.

R3.4. What is the role of oscillation?

Questions are raised by **McCollum**, and **Haase & Diniz** concerning the relation between oscillation and synchronization. Experimental observations indicate a close relation between oscillation and the precision of synchrony (König et al. 1995). Also, there is evidence that cortical neurons engage in synchronous oscillations in the beta and gamma frequency range across visual, association, somatosensory, and motor areas when the animal focuses its attention in the preparation of a visuomotor reaction; this synchronization increases in a task-specific way during execution of the task but collapses upon completion (Roelfsema et al. 1997). This suggests that oscillatory modulation helps synchronize responses, facilitating handshaking among neurons that need to be bound together for the execution of the task. Whether this frame-setting oscillatory modulation of membrane potential is due to oscillatory input from inhibitory or excitatory sources is not crucial for the principle and requires experimental testing.

Oscillatory patterning may be advantageous for rapid synchronization of discharges because it allows for temporal shifting of responses to synaptic input in both directions. The duration of the possible shift intervals is determined by oscillation frequency, and in the range of about a half-cycle. An assembly defined by synchronized discharges need not necessarily extend over many oscillation cycles. In some cases it may be sufficient to organize a single volley of synchronized discharges and have a new assembly at the next processing stage as proposed by Abeles (1991). In that case different assemblies can be organized on successive cycles. However, oscillatory patterning can also serve to generate the same synchronous volleys over several cycles, thereby refreshing assemblies that need to be stabilized for a while. The advantage over stabilizing assemblies by simple rate increases would be that it reduces the possibility

of getting false conjunctions if several assemblies need to be maintained within the same array of neurons, as false bindings are avoided if unrelated assemblies do not fire in synchrony. This does not require fixed phase shifts, as it can be achieved by interactions that modulate the regularity of the respective oscillations.

R4. What forms of learning occur within the cortex?

R4.1. Can the abstract learning rules discover higher-order variables?

There is a recognition by **Stone** of the potential of using context to guide learning to variables that are statistically related to variables of significance to the organism, including, but not limited to, reinforcement. We agree that this can include temporal as well as spatial structure. The algorithms that use temporal constraints to discover statistical structure (e.g., Becker 1996; de Sa & Ballard 1997; Stone 1996a; 1996b) are sufficiently similar to those outlined in section 3 that ways in which the two constraints can be used together merit further study.

Floreano shows that the learning rules outlined in section 3.3 can discover nonlinear transforms. The example used is stereo depth. He studies the possibility that this is guided by contextual input from other cues to depth. As there are usually multiple cues it may be that those that are either genetically specified or more easily learned guide the discovery of others. Floreano assumes that different depth cues are processed in different streams, and this is also plausible because different cues are not always in agreement (e.g., depth of a picture plane versus depth in the picture). The success of Floreano's simulation in sometimes discovering stereo depth using such an internal teacher is therefore encouraging. It did not do so reliably, however, and although his suggestion as to why that was so may be part of the story, the capabilities and limitations of this whole class of learning algorithms remain unclear.

R4.2. Does unsupervised learning in the cortex discover higher-order variables?

In section 6.4 we asked whether there is any evidence that self-organization in the cortex can discover nonlinear variables such as XOR. No such evidence was offered in the commentaries, nor have we yet found any from other sources. The continued failure of such evidence to appear suggests that reliable discovery of such nonlinear variables may not be a fundamental capability of cortex.

R4.3. Is there a floating threshold for LTP, and if so what are its determinants?

Sections 3.3 and 6.4 note converging evidence for learning rules of the BCM/ABS type (Artola & Singer 1993; Bienenstock et al. 1982; Hancock et al. 1991a). A central feature of these learning rules is a non-monotonic dependence of synaptic change upon post-synaptic activity with a threshold (that may be movable) below which synapses are weakened (LTD) and above which they are strengthened (LTP). **Grossberg** notes that some of his learning rules have a similar form, and **Stone** also notes their importance. A major goal for the neurobiology of learning is therefore to

find out whether the threshold for LTP does move and if so what it depends upon.²

R4.4. Does SMA modulate sensorimotor learning in PMdc?

Neuroimaging evidence is outlined by **Iacoboni** showing that activity in the supplementary motor area (SMA) provides a contextual input that guides the learning of a sensorimotor mapping from the rostral sector of dorsal premotor cortex (PMdr) to the caudal sector of dorsal premotor cortex (PMdc). We agree that this may be so but other explanations of the results are possible. One way forward may be to show that activity in both PMdr and PMdc is necessary for learning, but that activity in SMA is not, even though it has a guiding effect when present. Experiments of this sort are now under way (Iacoboni, personal communication).

R5. To what extent do these processes provide a representation of the external world?

One of our central suggestions is that local processors could lay foundations for representation and meaning by discovering commonalities across diverse data sets. This is because CFs provide a means whereby local processors can select the relevant information. **Morasso et al.**, **Stone**, **Tononi & Edelman**, and **Wright** all supported this suggestion and no one argued against it. **Amit**, **Eckhorn**, and **McCollum** all overlooked this suggestion, however, calling for a notion of relevance as though we had not addressed the issue. We must thus reiterate our suggestion, which is essentially a simple one. If local processors receive only RF input then we can see no way in which they could distinguish the relevant from the irrelevant. If they also receive CF input, then they can do so by, for example, selectively transmitting only the RF information that is statistically related to the context. Thus, in clear contrast to what **McCollum** assumes, this does involve information loss, and crucially so.

In section 6.5 we asked whether the processors we propose could help form proper intentional representations of the external world. We suggested that while they might contribute they could not be sufficient. We have so far not been very precise as to what "external input" means. In relation to the simulations it simply means external to the network being simulated. For most local processors in the cortex this is analogous to input from another cortical subsystem, and not to input from a world external to the system as a whole. To make this distinction the system must have some notion of "itself." **Wright's** insightful suggestion that the ability to discover coherence in multiple sources of activity could apply to sources from within the organism may be relevant here, but philosophical clarification of the issues involved would also be helpful.

R6. Additional computational foundations suggested by commentators

We proposed functional specialization and contextual coordination as two fundamental and mutually constraining foundations of cortical computation, expecting thereby to

provoke proposals of additional or alternative foundations. Few others were forthcoming. **Grossberg** refers us to his neural network models. **Tononi & Edelman** suggest a perspective from which the predominant information flow is between sources internal to the cortex, with the main role of external input being to modulate that flow. We agree that the distinction between internal and external sources is important, and that the balance between them is a topic of fundamental importance (sect. R2.1). It is clear that at the level of local circuits **Tononi & Edelman** emphasize just the same two fundamental principles as we do.

In keeping with an emphasis upon internal sources, **Wright** notes that local processors may be organized so that they are autonomously active and with an intrinsic dynamic. In this case they cannot be adequately described only in terms of a transfer function. We agree that in this case such sources should be seen as being included within the total set of primary RF inputs, and that developments of the kind he suggests are well worthwhile. **Haase & Diniz** and **Stone** note that structure in time is as important as structure in space, so an ability to process temporal sequence is also crucial. This seems compatible with our emphasis upon both coherence and synchrony. Indeed, as **Haase & Diniz** note, precision in temporal sequencing may be well served by the use of synchronized population codes (**Abeles** 1991). Overall, functional specialization and contextual coordination still appear most prominent as fundamental principles of cortical computation.

R7. Further issues raised by commentators

R7.1. What mathematical formalisms are useful?

We take it for granted that if there are common foundations then it must be possible to describe them in abstract terms that are independent of any specific content.

R7.1.1. Is information theory useful? We can ask, echoing **Amit's** questions concerning synchronization "Is information theory necessary to an understanding of cortical function?" and "Is it sufficient?" To both we answer with an unequivocal "No." **McCollum** identified our methods with information theory and neural network simulations. Given our backgrounds in experimental psychology and neurophysiology, and the allocation of only 20% of the target article to computational studies we do not see that as being accurate. Nevertheless, it is justified to ask "Is information theory useful to an understanding of cortical function?" and "Are other formalisms useful?" To both we answer with an unequivocal "Yes." Of the commentators, **Stone**, **Tononi & Edelman**, **Treves**, and **Wright** also find information theory useful, but **Gregson**, **Eckhorn**, **Nunez**, and **McCollum** do not. These differences may be due to a misunderstanding of the uses proposed for information theory, so we will try again to make them clear.

Three uses are exemplified in the target article and commentaries. First, there is its use for job specification, that is, to provide a conception of the essential information processing operations performed by local cortical circuits. In clear contrast to **Grossberg's** perception of the target article, its central concern is with general principles. In using information theory to formulate a conception of the goals of cortical computation we are in a long (e.g., **Atneave** 1954; **Barlow** 1959) and still strong (e.g., **Intrator & Cooper**

1995a; Olshausen & Field 1996) tradition. The goals of information compression, data reduction, and sparsification are relevant to the concerns rightly raised by **Gregson** and by **Eckhorn** in relation to metabolic constraints. In accord with the work of **Stone** and of **Tononi & Edelman**, a central aim of the target article is to extend these conceptions to include the challenging task of information *selection* (sects. 1.2.1, R5).

Second, and also in accord with the work of **Stone**, we have used the information theoretic job specification to derive a learning algorithm that changes connection strengths to better approximate the goal, given the statistical structure within the input received. Our description of the goal as maximizing the objective function specified (sect. 3.2) may mislead some commentators, for example, **Amit**. There is no reason to suppose that in any realistic situation perfect optimization is either necessary or possible. All that is required for the learning to be useful is that it more closely approximates the system to such a state. Although it may not be necessary to use information theory to understand learning, should synaptic plasticity be found to have a dynamic threshold for LTP that moves as specified by one of the abstractly derived learning rules (sect. R4.3), then many will wish to understand better how that rule was derived.

Third, information theory can be used for data analysis, for example, to measure information transmitted, as emphasized by **Treves**. We agree that such measures are useful (sect. R3.1). In addition, we use information theory to tackle a problem that no commentator discussed, that is, to provide an adequate specification of what should count as "context." There was agreement that context is important, but this means little unless we can give an adequate account of what can count as context.

Consider a psychophysical experiment in which there are two cues to texture segregation and that both influence performance, although subjects are asked to base their judgments on just one of them. We could call the specified cue the target, and the other the "context," thereby hoping to provide evidence for the relevance of context. Though common, this conception of context is wholly inadequate. On that conception "target" and "context" are distinguished simply by what experimenter and subject call them. It may be that both cues contribute in essentially the same way to the observed responses, so that dividing them into target and context is arbitrary.

This is exactly what is implied by Massaro's (1989a) fuzzy logic model of perception. Perceptual channels are independent until they all contribute in essentially the same way to response decision. In such a system there is no need to distinguish target from context. Either an input variable contributes to response or it does not. The same can also apply to the cellular level; either an input effects output or it does not. If it does, it is part of the cell's RF, and if not, it isn't. From this viewpoint there is no need to distinguish RF influences from CF influences (Gilbert, personal communication). Thus, in contrast to what **Amit** assumes, the case for "context" does have to be made. Our use of information theory to specify what can count as context is developed further in Smyth et al. (1996), and is being used at Stirling to analyze the interaction of cues to texture segregation by human subjects (thus addressing **Gregson's** doubts about the empirical validity of the transfer function used in the

computational theory). We hope to put the study of contextual coordination on a sounder basis than is provided either by showing that variables other than those that the experimenter calls the target can affect subjects' responses, or by showing that cellular activity is affected by more than what the experimenter calls the classical receptive field.

R7.1.2. What other formalisms are useful? We do not expect to squeeze all of cortical function into a single mathematical formalism. We agree with **Gregson, Nunez, McCollum**, and **Morasso et al.** that others are needed, and non-linear dynamic systems analysis in particular. They complement rather than supplant the uses just listed for information theory, however. The challenge for such formalisms is to give rise to revealing experimental paradigms and to make their findings more comprehensible than they would otherwise have been. Having tried to do that for what are perhaps some of the more basic and intrinsically comprehensible aspects of cortical function, we know how big a challenge that is.

R7.2. What is the role of modeling?

None of the uses listed in section R7.1.1 for information theory can be described as "modeling." Simulations are outlined in section 3.4 but they are not models of biological systems. As **Bower** indicates, they are "proof of concept" simulations, being designed to explore the abstract goals, transfer functions, and learning rules. **Würtz** also understood this, and thought our focus on simple computational concepts a distinct advantage. Nevertheless, **Palm & Wennekers's** attempt to interpret the simulations as models of spiking neurons, and then criticize them for not being so. Their attempt to interpret the simple demonstration whose results are shown in Figure 10 of the target article shows that they misunderstood it in several ways.³ Palm & Wennekers ask questions that are not pertinent to any of the uses made of the computational theory, but they could be asked of a biological model, or more pertinently still of the biological system itself (sect. R3.3).

Bower continues to argue for the relevance of detailed biological models. We agree that they are useful, but their limitations as a primary focus for research are well revealed by Bower's commentary. Necessary responses to the question posed in his title are "What details?" and "To what is their relevance being assessed?" If they matter, they are not details. If we were trying to discover how birds stay up in the air it would be counterproductive to try to include all details of bird structure and physiology. The "details" that matter are those essential to aerodynamic lift. Bower implies that the details that matter in the case of cortical computation are those in his models. **Grossberg** also describes his models as being biologically realistic, but they are not the same as Bower's and are used to support different conclusions. The most convincing way to test the relevance of a theory to biology is to test it on real organisms, not on models that try to replicate them. We therefore direct our efforts towards seeking a conceptual understanding of cortical computation that can be tested and developed through investigations of real brains and real people, as exemplified here by **König et al.** and by **Silverstein & Schenkel**. As the role of computational theory is still so widely and deeply misunderstood Table R2 compares it

Table R2. *Relations between theory and biology*

	Bird flight	Cortical computation
Goal ¹	Stay up	Coordinate activity ²
Strategy	Use aerodynamic lift	Use contextual information
Formalization	Aerodynamic equations for lift, drag, moment, etc.	Transfer functions and information theoretic objective functions, etc.
Mechanism	Wings ³	Contextual fields ³
Testing the strategy	Wings in wind tunnels ^{4,5}	Neural net "simulations" ^{4,5}
Biological testing	Do bird's wings have the required aerofoil section? Is air velocity adequate?	Do cortical cells receive contextual input? Does it affect output as required?

1. Only one goal is considered in each case. Both bird flight and cortical computation have other goals but separate goals are best considered separately.

2. The goals of cortical computation are far less obvious than those of flight. Discovering what they are is part of the problem we have to solve.

3. Wings and CFs are neither necessary nor sufficient for their goals.

4. The theories are best tested using versions of the mechanism that are as simple as possible yet consistent with achieving the goal in accordance with the theory.

5. The mechanisms tested are real. The wing in the wind tunnel generates lift. The "simulated" net computes. Thinking of them as models of something else does not contribute anything to their role in testing the strategy.

with the role of aerodynamics in the study of flight, in the hope that that will clarify our views on this issue.

R7.3. What is the role of CFs and/or synchronization in motor control?

The possible relevance of CFs and synchronization to motor control is discussed by **Iacoboni, McCollum, and Morasso et al.** The selection of particular motor responses raises combinatorial problems similar to those raised by scene segmentation. The number of different constellations of muscle contractions needed for the execution of different movements is very large. As the same muscles are used in different combinations for different movements, the commands for their contraction have to be bound in ever different constellations. Representing every possible movement by a command unit that distributes its output to the appropriate constellation of motor neurons leads to the same combinatorial explosion as representing every distinguishable object by a pontifical cell. The analogy with scene segmentation and object representation is obvious if one equates motor units with elementary features and a motor program with an object. This predicts that one should observe oscillations and synchronization during the initial selection phases of motor programming and a sequence of successively structured synchronized assemblies of the type ABCD etc. during execution. The findings of Murthy and Fetz (1996) are compatible with such a view.

R7.4. Is contextual coordination deficient in schizophrenia?

Contextual coordination, **Silverstein & Schenkel** suggest, may be impaired in particular schizophrenic states. *Prima facie*, this has an intuitive appeal. If there are specialized mechanisms for contextual coordination, fragmentation will result from their impairment. If these mechanisms are widely distributed across cortex, disorganized perceptions, thoughts, and actions are all possible consequences. Many studies of cognition in schizophrenia can be seen as evidence for such disorganization. Silverstein & Schenkel's suggestion is further strengthened by evidence for under-activity of NMDA-receptor channels in schizophrenic states (Olney & Farber 1995) and for the psychotomimetic effects of ketamine (Krystal et al. 1994), which blocks NMDA-channels. This is in keeping with our hypothesis that contextual coordination is achieved via CFs that exert gain control, for example, via NMDA-channels. It thus becomes of paramount importance to understand the basic pharmacology of coordinating gain-control channels, because that may advance our understanding of schizophrenia in a way that directly links molecular mechanisms with their cognitive consequences.

Attempts to understand schizophrenia have been plagued by finding a task on which patients are impaired, and then building a grand explanatory model on that (Ronan O'Carroll, personal communication). A particular problem that arises here is that the "contextual coordination" that is impaired in schizophrenia may have little or nothing to do with the "contextual coordination" for which the target article presents evidence. We therefore first consider studies of perceptual grouping in schizophrenia, then note unresolved issues that arise.

Silverstein et al. (1996a) review many studies of perceptual grouping in schizophrenia beginning with those of Cox and Leventhal (1978) and Place and Gilmore (1980), and present further evidence using the Banks and Prinzmetal (1976) paradigm to study the effect of visual grouping on visual search. All these studies suggest that in severe schizophrenic states perception is more fragmented than normal, with reduced effects of processes that group the stimulus elements into larger units. The evidence suggests that both stimulus-induced and top-down attentional processes may be involved in this impairment. The impairment is indicative of schizophrenia (Knight 1992; Silverstein et al. 1992), and correlates with the severity of other psychotic symptoms (Silverstein et al. 1996c). Using Navon's (1977) terminology, these patients have a tendency to see the trees before the forest, whereas control subjects have a tendency to see the forest before the trees. The evidence cannot be dismissed as being due to a general impairment of performance for at least two reasons: (1) The altered processes involve a reversal in the relative difficulty of conditions as compared with controls (Silverstein et al. 1996a); (2) This patient group performs *better* in tasks where it is advantageous to see the trees, not the forest (Place & Gilmore 1980; Rabinowicz et al. 1996). These perceptual disorders thus fit well with those to be expected, given impairments to the processes of contextual coordination hypothesized in the target article, however several unresolved issues then arise.

1. This patient group shows no deficits in grouping under conditions where there are either strong stimulus cues to

grouping (Knight 1992) or a strong push to allocate attention to global properties (Silverstein et al. 1996a). The hypothesis must therefore be expressed in terms of a reduced *tendency* to use grouping, and this needs further conceptual clarification and empirical testing. Gestalt grouping processes may not be at all impaired, either because they are genetically specified, or because if they are acquired or refined by visual input then the input correlations upon which they depend are so overwhelmingly present in natural input that they are learned to asymptotic levels even by an impaired learning mechanism. The acquisition of new assemblies at higher levels is not based upon such strong statistical structure, however, so impairments in acquiring and using those may be associated with impaired binding and reduced synchronization both within and between regions.

2. As **Silverstein & Schenkel** note, the evidence suggests impairments of perceptual learning as well as of perceptual processing, and this is in keeping with other perspectives on this disorder (e.g., Gray et al. 1991). An unresolved issue that arises here is whether it is only CF learning (i.e., assembly formation) that is impaired and, if so, how this can be reconciled with the hypothesis that CFs guide RF learning.

3. Some of the top-down attentional effects on perceptual grouping that have been shown to be impaired in schizophrenia clearly involve episodic and working memory processes (Silverstein et al. 1996b). The framework as presented in the target article would therefore have to be extended to show how it is related to higher level processes such as attention and episodic and working memory, if it is to be applicable to such findings. The value of such an extension is also emphasized by **Bugmann, König et al., and Tononi & Edelman** (sect. R3).

4. It is easy to see how an impairment in contextual coordination could produce symptoms of disorganization, but it may at first seem less easy to see how it could account for the positive symptoms, such as hearing voices. One approach would be to seek a separate explanation for these positive symptoms. Alternatively, we could speculate that they may reflect: (1) reduced modulatory control by external input of the flow of activity arising from internal thoughts; and (2) reduced knowledge of the source of internal speech and percepts because of reduced inter-regional binding.⁴ The pharmacological evidence encourages the search for an integrated explanation because drug-induced psychoses that reduce NMDA activity mimic both positive and negative symptoms (Krystal et al. 1994).

Silverstein & Schenkel's hypothesis thus survives close scrutiny well and, as they argue, it opens important directions for further work. One possibility may be to study the effect of drug-induced psychoses on perceptual learning and inter-regional synchrony using local field potentials. More broadly, this hypothesis should encourage physiological, psychological, and neuroimaging studies of contextual coordination in schizophrenic and drug-induced psychotic states using both human and animal subjects.

R8. Science as a search for coherence

It is suggested by **Treves** that if the commentaries "turn out not to be fully synchronized" (by which we assume he means not in full agreement) then they will contribute to the population response but by means other than synchronizing

it. We agree that it may be both revealing and entertaining to draw an analogy between the outputs of local cortical processors and scientific writings. Each paper written tries to convey something that is both distinctive and relevant. Relevance does not imply agreement, however. Different members of a group can have opposing effects at a higher level of analysis. The primary code used by *BBS* to signal mutual relevance is simultaneous publication of target articles and associated commentaries, that is, grouping through synchronous transmission. This is not because synchrony is necessary to grouping, but because it makes it a lot easier for readers to process them as a whole.

This analogy is also useful for another reason. By seeing science as a continuation of the search for coherence, by means beyond the reach of any algorithm possessed by mammals in general, we are reminded that local processors should be seen as moving toward that goal, not as reaching it (sect. R7.1.1).

R9. Promising directions for future progress

Specialization of function has been the keynote of this century. Coordination of function may be the keynote of the next. This will require more attention to contextual interactions, synchronized population codes, and fast dynamics. We believe that future research must emphasize relational codes rather than focusing only upon response properties of single cells. The relevant relations can be detected only by analyzing simultaneously recorded activity. We shall have to look at the outputs of any processing level in the same comprehensive way as it is looked at by the subsequent processing stages to which it projects. This requires analysis of mutual dependencies among the responses of a large number of neurons, and hence the study of ensemble dynamics. There is thus a logical progression from early studies of the topology of brain functions, to the functional analysis of individual neurons located in different compartments, and now to the attempt to understand the spatio-temporal patterns of coordinated neuronal activity. In conclusion, then, our prediction is that the temporal organization and coordination of brain activity is as sophisticated and subtle as is its topological organization, the former being an emergent property of the latter.

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NOTES

1. Indeed, if NMDA receptor activation is combined with oscillatory modulation of the membrane potential, latency of responses is shifted as a function of oscillation phase and output phase is locked to input phase (Volgushev et al., submitted). This can synchronize discharges within a single oscillation cycle with high temporal precision because of the voltage-dependent gating of the MG^{2+} -block, which allows for very rapid activation and inactivation of NMDA-receptor mediated input.

2. Evidence is becoming available that it is not the absolute level of postsynaptic depolarization or the absolute level of the postsynaptic Ca^{2+} -surge alone that determines whether a particular synapse undergoes LTP or LTD. The actual state of the synapse, that is, the actual release probability with which it operates (Volgushev et al. 1997) and the rate with which it is activated during induction of the modification also matter (Hansel et al., in preparation). Thus synaptic changes are affected by information stored locally at each synapse, and this makes complex

learning rules such as those of Phillips et al. (1995b) and Kay et al. (in press) less implausible.

3. The simulations assume four levels of organization: cells, units, local processors, and layers. They operate at the level of units, but assume them to be composed of stochastic binary elements. The simulation shown in Figure 10 is intended to be analogous to the perception of an ambiguous figure, such as the Rubin vase, where alternative perceptions emerge successively, even though the external stimulus does not change. Thus, in contrast to what Palm & Wennekers assumed, the input cannot represent direct input from the external stimulus. Instead, the processing layer to which the simulation relates is assumed to be some layers distant from the external stimulus. Its inputs from the previous layer fluctuate because processing is stochastic. Palm & Wennekers suggest that the simulation in Figure 10 would work in the same way if the graded response units were replaced by single binary units. This is not so. If outputs are restricted to their extremal values, the CFs have no effect, in which case the outputs in at each iteration in Figure 10 would simply be identical to the inputs. We should therefore have made in clear in section 3.1 that the apparent insensitivity of performance to such a replacement refers only to the learning, with which most of the simulations were concerned. The two sets of 3×3 units with internal coherence in the study of grouping shown in Figure 10 represent the two alternative percepts. CFs were therefore positive within and negative between these two alternative groupings. The background elements received no CF input. The first six iterations show the simultaneous emergence from the background of all elements in one of the two alternative groupings. Thus, contrary to what Palm & Wennekers conclude, this demonstrates the role of internal grouping processes, because the coherent sets of elements are distinguished from the background only by their CFs. To show the successive emergence of alternative percepts activity in the units was stopped and restarted after six simulations. The cortex is not short of mechanisms that would have such an effect, so there is no need for either it or a simulation to become stuck in the stationary state to which Palm & Wennekers refer. The choice of six iterations was arbitrary, but by varying it in an appropriate way periodic or other temporal structure could easily be introduced to the simulation. That would not change the effects with which it was concerned, however.

4. The latter possibility was suggested to us by Frith's (1992) interpretation of psychotic hallucinations as being due to a failure of self-monitoring. Words activated within the articulatory-loop can arise from either internal or external sources. Their source may therefore be unknown if they are not bound to activity in the other cortical modules from which they arise.

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Letters "a" and "r" appearing before authors' initials refer to target article and response, respectively.

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