

Capacity Theory as a Model of Cortical Behavior

Todd C. Handy

Dartmouth College

Abstract

■ Growing evidence suggests that a more complete understanding of cortical function requires developing cognitive models that are predictive of multivariate neural behavior (e.g., Raichle, 2000; Shulman et al., 1997). Towards this end, one approach is to interpret population-specific activity in cortex from the perspective of capacity theories of selective attention (e.g., Handy, Hopfinger, & Mangun, in press). In brief, the model is founded on the ideas that (1) processing capacity is limited and (2) different processes *may* draw on different capacities (e.g., Boles & Law 1998; Polson & Friedman, 1988;

see Kramer & Spinks, 1991). Testable hypotheses are then based on whether manipulations of process-specific load will lead to negative or positive covariation between different function-related clusters of activation in cortex—the predicted pattern depends on whether or not the clusters in question are assumed to share a common processing capacity. Expanding on these ideas, the current article addresses several recent issues that have arisen in the effort to apply capacity theory to the study of cortical function. ■

BACKGROUND

The central tenet underlying capacity theory is that processes can proceed only if sufficient “capacity” remains available (e.g., Wickens, 1980; Navon & Gopher, 1979; Norman & Bobrow, 1975; Kahneman, 1973). Translated into the neural domain, when the load on a cognitive process is increased—and the proportion of capacity “consumed” by that process rises—there is a corresponding increase in activation intensity in the cortical loci where the loaded process is implemented (e.g., Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Braver et al., 1997; Jonides et al., 1997; Just, Carpenter, Keller, Eddy, & Thulborn, 1996). Within this context, the consequences of capacity limits can be observed as either a ceiling on the activation of a loaded process (e.g., Handy & Mangun, 2000) or as a reduction in the activation of a second process that is in competition for capacity with the loaded process (e.g., Rees, Frith, & Lavie, 1997). Predictions of function-related covariation directly follow from this relationship between load and activation intensity: when the load on a process is manipulated, positive covariation between cortical loci suggests a sharing of processing capacity,¹ negative covariation suggests a competition for capacity, and no covariation suggests an independence of capacities (Figure 1).²

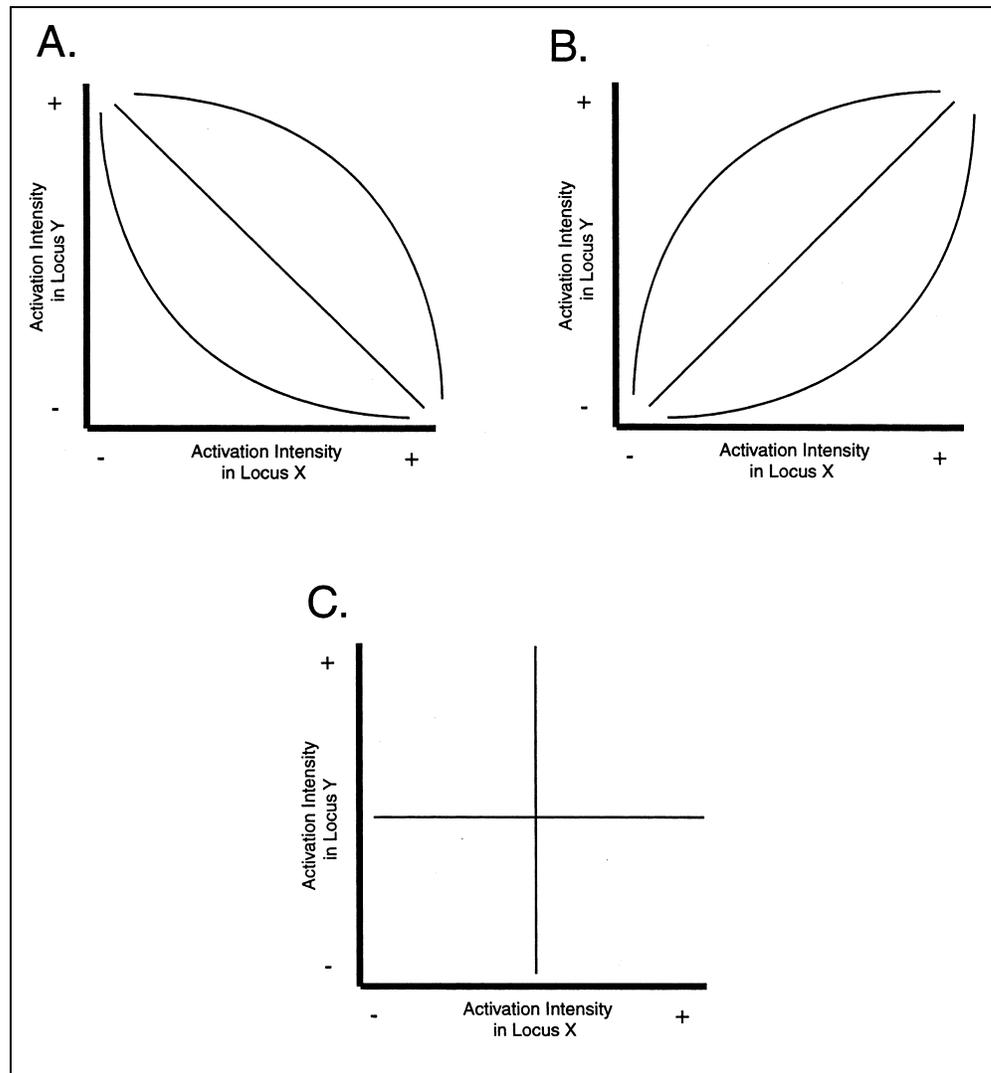
Like the use of structural cognitive theory for function localization (e.g., Posner, Petersen, Fox, & Raichle, 1988; Fox et al., 1986), the benefit of the capacity model is that it provides a framework for interpreting covariation in

neural behavior that is grounded in long-standing cognitive theory. The empirical validity of the capacity approach, however, depends on three key factors: (1) controlling for the process that is loaded, (2) controlling for the degree of load placed on that process, and (3) identifying the mechanism of selection mediating the load-based effect. These are the points of concern raised here.

MANIPULATING LOAD

Operationally defined, a load manipulation can be based on either parametrically varying the load placed on a single process, or changing the actual process that is being loaded.³ In the former case, a task is held constant but the quantitative demands placed on processing associated with that task is varied. For example, in the typical working memory study the task—hold information in memory—remains unchanged, but the amount of information held in memory is parametrically varied (e.g., Manoach et al., 1997). In the latter case, load is manipulated based on qualitatively changing the nature of the processing demands. For example, studies using “feature” versus “conjunction” manipulations (e.g., Handy, Soltani, & Mangun, submitted; Lavie, 1995) require subjects to discriminate a single feature of a stimulus (e.g., shape *or* color) under low-load conditions, while under higher-load conditions a conjunction of two or more stimulus attributes must be discriminated (e.g., shape *and* color). The importance of mak-

Figure 1. Idealized scatter-plots representing predicted load-related changes in activation intensity in two different cortical processing loci. (A) Negative covariation between cortical-processing loci, a pattern suggestive of competition for capacity. (B) Positive covariation between cortical processing loci, a pattern suggestive of two loci sharing a common processing operation (see footnote 1). (C) No covariation between loci, a pattern suggesting that the two loci either draw on independent capacities or that one of the processes is not capacity-limited (see footnote 2).



ing this quantitative versus qualitative distinction is that the operational form a load manipulation takes directly constrains what will be revealed about capacity limits.

To adumbrate, in a recent study of perceptual selection in vision, Rees et al. (1997) found that the cortical response to task-irrelevant parafoveal stimulation (moving dots) decreased when the load of a task at fixation was increased. In the low-load condition, subjects discriminated whether or not single words presented at fixation were in all upper- or lower-case letters. In the high-load condition, the same words were presented, but subjects now had to discriminate the number of syllables in each word. These data suggest that linguistic processing can limit the cortical response to task-irrelevant motion. However, because there was a qualitative change in task demands between load conditions, the data are equivocal regarding whether the effect was due to (1) an overall increase in the consumption of a processing capacity that was shared by all processes involved, (2) switching from a task that did not share capacity with motion processing to a task that did share

capacity, or (3) a combination of both. The point here is that if a load manipulation is based on a change in the task being performed, one must consider whether confounding the consumption of capacity (a quantitative parameter) with an overt change in processing operations (a qualitative parameter) will limit the ability of the data to address the cognitive model in question (e.g., Handy et al., 2000).

MEASURING SELECTION

In terms of perceptual selection, the data of Rees et al. (1997) suggest that when the load of a task at fixation is increased, there is a reduction in the cortical response to task-irrelevant parafoveal stimulation. However, it remains unclear how such effects are mediated: is it due to a narrowing of spatial attention under high-load conditions, or to a competition for capacity between task-relevant and task-irrelevant processing, with no intervening modulation by spatial selection? The question is of interest because it illustrates the two different

levels at which selective effects in population-specific cortical activity can be quantified.

In particular, selection can be measured as either a stimulus-specific or a process-specific effect. For example, our ability to covertly attend to visual locations is capacity limited. As a consequence, when the perceptual load of parafoveal targets is high, stimuli presented in attended parafoveal locations evoke a greater sensory-level response in visual cortex than stimuli presented in unattended locations, an effect of spatial attention that is absent when target load is low (Handy & Mangun, 2000). In this case, load-mediated selection is being measured in relation to what stimulus information is being selected under capacity limited condition, that is, stimuli at attended visual locations. On the other hand, selection can also be viewed in relation to the interactions that arise between processes when they compete for access to a common processing capacity. From this perspective, load-mediated selection is measured in relation to what processes are selected under capacity-limited conditions. For example, Lavie (1995, in press) has argued that in visual perception, task-relevant processing is selected when load exceeds capacity—a concept directly akin to the notion of dual-task interference, where increasing the load on one process can reduce the efficiency of a second process that relies on the same processing capacity (e.g., Pashler, 1993; Pashler & Johnston, 1998).

Given this distinction, the data reported by Rees et al. (1997) address selection measured at a process-specific level: motion-related activation in cortex decreases when a load is placed on linguistic processing. Whether this effect is actually due to selection for linguistic processing (at the expense of motion processing) rather than selection for information at fixation (at the expense of parafoveal information) remains an open question. A deeper interrogation of the capacity model suggests that the cortical response to motion should be measured as a function of (1) load at fixation and (2) the location of task-irrelevant motion—foveal versus parafoveal. If motion-related processing decreases with load independent of location, it would suggest selection for linguistic processing over motion processing. In contrast, if motion-related processing decreases with load under the parafoveal condition, but increases (or remains constant) with load under the foveal condition, it would suggest selection for information at fixation.

CONCLUSION

If systematically applied, capacity theory represents a viable cognitive model for predicting task-related, multivariate neural behavior. However, perhaps the even greater benefit to be gained by considering capacity theory is that it forces us to ask the difficult question: what *is* capacity? The implicit assumption here has been that, at the level of population-specific activity,

“capacity” is analogous to an activation “resource” (e.g., Just & Carpenter, 1992). While the concept of resources at the behavioral level has been historically contentious (e.g., Navon, 1984), the model may lead to more tractable questions when brought into the neural domain. For example, if two neuron populations are found to share a common processing capacity, does this suggest that the shared capacity might engender common effects at the single-unit level, in terms of modulating receptive field properties (e.g., Maunsell & McAdams, 2000; Desimone, 1999)? If so, can the single-unit effect be traced to a common underlying mechanism at the molecular level, such as a shared neurotransmitter system? Moreover, how are the limits on these capacities implemented at each level? These are hard questions of cortical function, but the capacity-based approach provides the necessary theoretical structure for integrating concepts across multiple levels of empirical analysis.

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Reprint requests should be sent to Todd C. Handy, Center for Cognitive Neuroscience, Dartmouth College, 6162 Moore Hall, Hanover, NH 03744. Email: tchandy@dartmouth.edu.

Notes

1. Positive covariation is also consistent with the notion of a “distributed neural system,” where a cognitive process is implemented across two or more functionally integrated loci (e.g., Friston, 1998); when a distributed process is loaded, the loci implementing that process should show positive covariation.
2. The discussion here is assuming capacity-limited, “non-automatic” processes are under study. Within the capacity framework, an “automatic” process would be capacity *unlimited*.
3. That is, a switch is made from loading Process A to loading Process B, or a switch is made from loading Process A to loading Processes A and B.

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