

Neural Mechanisms for Response Selection: Representation Specific or Modality Independent?

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Is response selection a unitary central cognitive mechanism? Some information processing theories assume it is (Pashler, 1994; Welford, 1959); whereas others suggest it may not be (Meyer & Kieras, 1997). This question was addressed by two studies using functional magnetic resonance imaging (fMRI) published in this issue of the *Journal of Cognitive Neuroscience*. Schumacher, Elston, and D'Esposito (2003) manipulated response-selection difficulty in two visual-manual tasks using spatial and nonspatial stimuli. They found that largely distinct brain regions mediated response selection for the two tasks; with right dorsal prefrontal, and bilateral premotor and superior parietal brain regions subserving spatial response selection and left dorsal prefrontal, ventral parietal, and temporal brain regions subserving nonspatial response selection. These results led these authors to conclude that the neural mechanisms for response selection are specific to the type of information processed. Jiang and Kanwisher (2003a) reached a different conclusion. They manipulated response-selection difficulty in visual-manual, auditory-manual, and visual-vocal tasks. Like Schumacher et al., Jiang and Kanwisher observed fronto-parietal activations for spatial response selection. Contrary to Schumacher et al., however, Jiang and Kanwisher found activation in these same brain regions for nonspatial response selection. These results led Jiang and Kanwisher to conclude that response selection is a modality-independent unitary process. That is, the same neural mechanisms mediate response selection across a variety of tasks and modalities. Is there a way to reconcile the results of these two studies, which address the same question with similar designs, yet reach opposite conclusions?

DIFFERENCES IN PROCESS IDENTIFICATION

Although both studies address the same question in a similar way, methodological differences may at least partly explain the discrepant results. Schumacher, Elston, and D'Esposito parametrically manipulated response-selection difficulty in both their tasks. They identified brain regions related to response selection by identifying those regions showing a monotonic increase with their parametric manipulation. In contrast, Jiang and Kanwisher tested two levels of response selection difficulty and

identified response selection related regions as those that showed more activity for the hard than for the easy response-selection condition. By testing only two extreme levels of response-selection difficulty, Jiang and Kanwisher's comparison may be more powerful than Schumacher et al.'s, but it may also include brain regions related to task processes not strictly necessary for response selection. For example, brain regions showing a difficulty effect but no corresponding monotonic increase at intermediate levels of response-selection difficulty may reflect changes in working memory processes required to retain the more complicated stimulus-response (S-R) rules rather than response-selection processes required to apply them.

This difference in the authors' approach for identifying the neural mechanisms for response selection may reflect a difference in the authors' operational definitions for this process. Schumacher, Elston, and D'Esposito were interested only in the minimal set of brain regions involved in applying S-R rules. Jiang and Kanwisher, on the other hand, were interested in identifying a larger set of brain regions affected by manipulations of response-selection difficulty more generally.

The difference in the way response-selection related regions were identified cannot, however, explain all the discrepancies between the results presented in the two articles. After excluding voxels not showing a monotonic increase in activation with response-selection difficulty, Schumacher, Elston, and D'Esposito's reported activation should be a subset of Jiang and Kanwisher's. This appears to be the case for spatial response selection. In the nonspatial task, however, Schumacher et al. reported activation increases with response-selection difficulty not found by Jiang and Kanwisher (e.g., left middle temporal gyrus). Furthermore, like Jiang and Kanwisher, Schumacher et al. also compared activation between the extreme levels of their response-selection manipulations. Even this comparison identified distinct brain regions for the spatial and nonspatial tasks. Thus, the discrepancy between the two studies, especially for nonspatial response selection, does not seem to be driven entirely by differences in the method for identifying response selection regions.

DIFFERENCES IN TASK MANIPULATION

Another important difference between the two studies is the way response-selection difficulty was manipulated. Jiang and Kanwisher manipulated S-R compatibility in

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each of their three experiments. Schumacher, Elston, and D'Esposito manipulated S–R compatibility only in their spatial experiment. They manipulated S–R numerosity in both their spatial and nonspatial tasks. S–R compatibility is a prototypical factor influencing response selection (Kornblum, Hasbroucq, & Osman, 1990). S–R numerosity also affects response selection (Schumacher et al., 1999), but may affect stimulus-encoding processes as well (Sternberg, 1969). Thus, at least some of the activation found by Schumacher, Elston, and D'Esposito in their nonspatial task may be related to encoding rather than selection processes (e.g., extrastriate).

These differences in the choice of response-selection manipulations raise an interesting possible interpretation of the results. Both S–R compatibility and S–R numerosity have been used in the cognitive literature to affect response-selection difficulty, however, these current results may suggest that these factors have different neural substrates, and thus may influence different cognitive processes. Although both manipulations vary the difficulty of mapping a stimulus to a response, the difficulty in the S–R compatibility manipulation is primarily due to selecting the task relevant, but less prepotent, S–R mapping. In contrast, the difficulty in the S–R numerosity manipulation is primarily due to the increasing number of potential S–R rules to be considered before selection.

Thus, the distinct brain regions identified by Schumacher, Elston, and D'Esposito may reflect a dissociation between response-selection processes required for selecting between prepotent and relevant S–R rules versus response-selection processes required for selecting among an increasing number of S–R rules. Conversely, Jiang and Kanwisher may have found overlapping activation in brain regions not because response selection is a unitary process, but because one type of response selection—affected by S–R compatibility—is modality independent. A full understanding of the discrepancy between the activation patterns between the Schumacher, Elston, and D'Esposito and Jiang and Kanwisher studies requires a better understanding of the cognitive mechanisms affected by these different manipulations of response-selection difficulty.

DIFFERENCES IN PROCESS INDEPENDENCE

A second paper by Jiang and Kanwisher is also included in this issue of the *Journal of Cognitive Neuroscience* (Jiang & Kanwisher, 2003b). This study is conceptually similar to a previously published study by Schumacher and D'Esposito (2002). Both studies report a selective influence of a perceptual difficulty manipulation on neural activity in occipital cortex. Other results, however, differ between the two experiments. Schumacher and D'Esposito report a selective influence of response-selection difficulty on neural activity in dorsal prefrontal and superior parietal cortices. Jiang and

Kanwisher, conversely, report an effect of both perceptual and response-selection difficulty on neural activity in prefrontal and parietal cortices.

Can *these* discrepant results be reconciled? Jiang and Kanwisher study included more participants than did Schumacher and D'Esposito, thus the failure of Schumacher and D'Esposito to find an effect of perceptual difficulty on prefrontal and parietal activity may be due to a lack of statistical power. However, their perceptual difficulty manipulation did influence activity in a number of other brain regions so additional hypotheses should be considered.

One additional possibility is that the overlap in activation reported by Jiang and Kanwisher is not related to an overlap in perceptual and selection processes specifically, but rather the activation overlap may be caused by additional cognitive processes required to perform these tasks. Schumacher and D'Esposito reported an effect of perceptual difficulty in the anterior cingulate and lateral premotor cortices—regions not usually associated with perceptual processing. Activity in these regions may suggest that their perceptual-difficulty manipulation did not solely affect stimulus encoding (e.g., response monitoring, response programming, and so on). Perhaps the perceptual-difficulty manipulation used by Jiang and Kanwisher affected cognitive processing even more broadly than did Schumacher and D'Esposito's. Consistent with this interpretation, the effect of the perceptual difficulty manipulation used by Jiang and Kanwisher was much larger than the one used by Schumacher and D'Esposito, producing roughly 20% and 3% accuracy decreases, respectively.

RECONCILIATION

Perhaps the conclusions (i.e., representation-specific vs. modality-independent response selection) offered by each of these studies are too extreme. Schumacher, Elston, and D'Esposito provide evidence against the conclusion that *all* response-selection manipulations affect the *same* neural substrates. Jiang and Kanwisher, on the other hand, provide evidence against the conclusion that *all* nonspatial response selection relies on *different* neural substrates than spatial response selection. An analysis of these studies and their methodological and conceptual differences leads to a possible reconciliation of the results, which may provide insights into the nature of response selection. Perhaps response selection is not a unitary cognitive process. Perhaps different task manipulations, such as S–R compatibility and S–R numerosity, affect different aspects of response selection, which have different neural substrates. Each of the subprocesses, however, may be independent of stimulus modality and type. Additionally, it may be that to find functionally distinct processing in the brain, one must narrowly define the processes of interest and use manipulations that affect these processes selectively.

COGNITIVE INSIGHTS FROM NEURAL DATA AND FUTURE DIRECTIONS

Modern cognitive neuroscience goes beyond mere localization of functions by testing whether common or distinct neural substrates support different cognitive processes. The studies discussed here focus on the level of brain activation in each voxel to assess these similarities and differences. One study found mostly similarities in brain activation for response selection, the other found mostly differences. One result suggests that response selection is a unitary cognitive process, the other suggests otherwise. Yet, two different activation patterns based on peak voxels may share deep similarities because the voxels that did not show peak activation may carry important information (Spiridon & Kanwisher, 2002; Haxby et al., 2001). And conversely, two similar activation patterns may arise from different underlying cognitive processes (D'Esposito, Ballard, Aguirre, & Zarahn, 1998). Accordingly, the interpretation offered by each study must be tempered in light of viable alternate hypotheses. Perhaps the application of multivariate analysis techniques will provide new insights into the mechanisms of response selection and other questions in cognitive neuroscience.

What have we learned about response selection from these studies that we did not already know from the behavioral literature? Firstly, these studies directly investigate the possible neural substrates for response selection, a question unaddressed in the cognitive literature. In fact, in his review, Pashler (1994) was completely agnostic as to how the putative central response-selection bottleneck may be implemented in the brain. He wrote:

Of course, such a device need not be localized in one particular region of the brain; it could be widely distributed anatomically. Alternatively, . . . the bottleneck could result from an active process of mutual inhibition (p. 223).

The two studies published here show that indeed response selection is distributed widely anatomically, involving prefrontal, premotor, and posterior brain regions.

In addition, the results from Jiang and Kanwisher may suggest why response selection for tasks with different input and output modalities may compete for common cognitive mechanisms—task interference occurs because the same brain regions are recruited by response selection across modalities. The results from Schumacher, Elston, and D'Esposito challenge the oversimplification of response selection as a unitary process. Their spatial and nonspatial response-selection tasks, or their compatibility and numerosity manipulations, may have different underlying neural substrates and correspondingly may affect different response-selection processes.

This observation may promote additional cognitive research into the nature of response selection. Thus, guided by cognitive research, cognitive neuroscience not only provides complementary evidence about the human information processing system, but also opens new avenues for investigation.

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