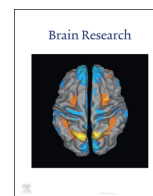




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Neural representation of stimulus-response associations during task preparation

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ABSTRACT

A partially informative cue presented before a stimulus can facilitate the production of the response. Prior information about an upcoming target can increase brain activity in both stimulus (c.f., Desimone and Duncan, 1995) and response (c.f., Leuthold et al., 1996) processing regions; however, it is unclear how the representation of the task might influence the recruitment of this network of task-relevant regions. In the current experiment, we employed an event-related fMRI design with a response cuing procedure to investigate whether S-R pairings jointly influence activity in stimulus- and response-specific processing areas during the presentation of a cue. Participants learned S-R mappings in which pictures of faces and places were paired with either left or right hand finger responses. On some trials, a cue provided partial information about the upcoming trial (e.g., that the trial would involve a face or place stimuli or a left or right hand response). Importantly, because different stimulus types were associated with each hand, any informative cue implicitly indicated both a stimulus type and response hand, allowing participants to represent the task as two distinct subtasks. Region-of-interest analyses at the cue event demonstrated a biasing of response processing regions for both stimulus- and response-related cues, as well as increased connectivity with the associated stimulus-processing regions. The results suggest that the cue results in the recruitment of just the task-relevant subnetwork on each trial.

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1. Introduction

Environmental context guides our behavior and biases our cognitive processing (Hazeltine and Schumacher, 2016; Schumacher and Hazeltine). For example, we may plan to make either a sandwich or a hamburger for dinner. If looking in the breadbox reveals that we have hamburger buns, this information allows us to select the task file for making hamburgers. In this way, the additional environmental cue (the contents of the breadbox) allows us to adjust our behavior based on knowledge of our available resources. Laboratory research supports the idea that we can use partially informative cues to modify and facilitate behavioral responses dynamically during decision making (Miller, 1982; Rosenbaum, 1983). In other words, actions can be partially planned such that some parts of a future action or action sequence are specified, but other parts are based on future stimuli. We may plan to make a burger after looking in the breadbox, but we must leave many other actions (e.g. how to flavor the beef, how to cook the patties, etc.) unspecified until we gather additional information

from the environment (e.g., what are the available spices, is the grill working, etc.).

One area of research has been identifying the locus of the cue-preparation benefit. Miller (1982) conducted a series of experiments investigating this issue. In his procedure, stimuli consisted of four crosses on the screen that were spatially mapped to four buttons on a response box that were mapped to the index and middle fingers on each hand in order from left to right (i.e., left-most cross mapped to left middle finger, second cross to left index, and so on). For each trial, the participants saw a warning signal that showed all four crosses, followed by a cue signal which consisted of all four crosses (uninformative) or a subset of two (informative). The subset of two crosses could indicate any two of the four positions; that is, any two fingers could be indicated for the upcoming response. The uninformative cue indicated all four fingers for the potential response. Participants were finally presented with a single cross in one of the four possible positions, at which point they pressed the corresponding button. Unsurprisingly, participants were faster to respond when the cues were informative than when they were uninformative. However, not all informative cues produced equal benefits; cuing two responses on the same hand produced shorter RTs than cuing two responses on the same finger (i.e., an index or a middle finger response). Miller

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proposed that information was passed in discrete quanta to the motor system as it was made available; that is, information about a response that allows for the preparation of one salient subset of responses over another is processed as it arrives, reducing the remaining processing required upon the presentation of the stimulus. To explain the difference in the benefit of different types of cues, Miller proposed that the structure of the motor system affords a hand advantage because this information can be extracted and the response subset prepared more quickly than finer-grained information (see also, Rosenbaum (1980)).

Reeve and Proctor (1984); see also de Jong et al. (1988) proposed a different explanation. They argued that the hand advantage found in Miller's (1982) results was due, not to a response preparation advantage, but to the spatial correspondence between the visual cue positions and the associated response mapping. They showed that removing this stimulus-response correspondence in turn reduced the hand advantage. Specifically, they had participants complete Miller's task, but with their hands positioned to overlap one another so that the leftmost cross corresponded to the left middle finger, the second cross to the right index finger, the third cross to the left index finger, and the fourth cross to the right middle finger. In this position, cues indicating responses on the left hand (i.e., crosses shown in the first and third positions) were no longer presented in the left side of the screen. Proctor and Reeve posited that the cuing effect takes place in response selection. They proposed that the correspondence between the stimulus and response allows participants to translate a cue into a subset of potential pairs from which the response will be selected. Removing the visual-anatomical correspondence afforded by Miller's design limits the utility of the cue.

In parallel with this debate about the information processing locus of the cuing benefit, measures of brain activity have been used to investigate the neural correlates of cue-preparation benefits. At the response level, event-related potentials (ERPs) during cue preparation and have demonstrated preparatory activity in motor regions (Leuthold et al., 1996). Leuthold and colleagues used the lateralized readiness potential (LRP), a measure of the difference in activity between electrodes above both the left and right motor cortex. They found that the LRP increased to a cue indicating which hand would be required to produce the upcoming response, suggesting that motor regions may begin to prepare a response even when the actual digit necessary for the response remains unknown. There is also a wealth of data showing that sensory regions respond to cues, especially from investigations of selective attention. For example, many studies show that a cue indicating a relevant upcoming stimulus dimension increases activity in sensory regions that process the cued location or dimension. This increase in activity is associated with a corresponding facilitation in stimulus processing (for reviews see Desimone and Duncan, 1995 and Kastner and Ungerleider, 2000).

Thus, research shows both an early (stimulus) and late (response) effect on processing of a cue in the regions that process those types of information. However, the interaction between these effects has received less investigation. Here, the cognitive literature may lead to predictions about the relationship between stimulus- and response-level influences in the brain. Returning to the response cuing literature, Miller (1982) posited that locus of the cuing effect is in response preparation. If this is the case, motor preparatory activity during cue presentation should be independent of stimulus-related activity – that is, information contained in a cue should result in activity differences only in the region that processes the information directly indicated by the cue. For example, a cue for stimulus color should result in modulation only in V4. On the other hand, Reeve and Proctor (1984) posited that the cuing effect occurred in response selection – where responses are associated with stimuli. If this is the case,

then one might expect not only that a cue will influence the regions that process that information, but also that there may be activity across both the stimulus- and response-related regions related to executing the indicated task.

A more recent cognitive theory that is consistent with the interaction between stimulus and response processing in cue preparation is the *grouping model* (Adam et al., 2003b; Adam et al., 2005). According to this account, the presentation of a cue initiates grouping processes that act on both stimulus and response representations. For example, in Miller's (1982) design, stimuli could occur in one of four spatial locations, which were mapped to the first two fingers of each hand in spatial order. The grouping model posits that participants group the stimuli into left and right hemifields, and group responses anatomically by hand. Cuing for either the left two or right two stimuli indicates salient groups at both the stimulus and response levels, resulting in a behavioral benefit. In this way, the model holds that cue information allows for the preparation of a salient set of stimulus-response pairs.

The grouping process described by Adam and colleagues (Adam et al., 2003a) results in the formation of a task file (Schumacher and Hazeltine), in which the scope of the possible stimulus and response features for a given task are bound together into associated pairs along with motivational and other contextual information that allow participants to perform the task. When preparing to perform a task, the relevant task file is activated, and actions are coordinated according to the associations within the active task file.

These task files may provide a cognitive mechanism for the complex pattern of behaviors observed in response cuing. Specifically, participants may use the grouping process to link salient subsets of the task into separate task files, with additional bound context (i.e., the relevant cue) for when to select each subset. Then, when participants are given one of the relevant cues on a given trial, they prepare the task file indicated by that cue, and execute the task according to the associations represented within that task file.

In the brain, cue-related activity may represent the preparation of these task files in anticipation of the task. Adam et al. (2003a) used fMRI to investigate this process. This study used Miller's (1982) design with consistent or inconsistent S-R mappings and compared blocks of cued activity to uncued activity, which allowed them to separate activity due to informative versus uninformative cues. They found activation in a number of regions relating to cued activity, including prefrontal cortex (PFC, including middle frontal gyrus, MFG; dorsal and lateral premotor cortex, DPMC/LPMC; supplementary motor area, SMA), parietal cortex (intra-parietal sulcus, IPS; superior parietal cortex, SPC; inferior parietal cortex, IPC) and basal ganglia. These regions, then, are specifically related to the processing and implementation of the information contained within a cue. Notably, a number of these regions are specifically related to stimulus and response processing (e.g., parietal cortex processes spatial information of stimuli).

The pattern of brain activity to the cue found by Adam et al. (2003a) closely corresponds to regions associated with response selection processes. Schumacher et al. (2003) used two choice-reaction tasks to investigate the neural correlates of spatial and non-spatial response selection. For each task, the authors varied the number of possible stimulus-response pairs on a given trial using a precue that indicated some subset of the available options. fMRI data recorded during the performance of each task showed distinct regions of activation in parietal, temporal, and frontal cortices for spatial versus non-spatial tasks. The frontal activity corresponded with premotor regions, which are involved in motor response preparation. The parietal and temporal activity, on the other hand, corresponded to regions involved in stimulus processing. Moreover, the activity in parietal cortex was more dorsal

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