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Coupling Perception with Action: A Dynamic Account of the Effect of Action on Memory

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Abstract

The ability to plan, inhibit, and execute motor movements are all necessary for achieving goal-directed behavior. These processes are closely related to memory, as perceptual input and memory of that input often recruit motor movements. Unknown, however, is how the engagement of perception-action processes impact the memory of objects. One such interaction suggests that participants have worse memory recall for stimuli which elicit inhibition of a motor response than stimuli which afford the execution of a motor response (Chiu & Egner, 2015). This effect has been explained through competition for common neural resources: allocation of resources toward response inhibition reduces the amount of resources available for memory. Alternatively, this effect could be driven at the level of perception-action coupling: engaging and pairing the motor system with visual perception enhances the memory of stimuli which elicited the motor preparation or response. To test these hypotheses, we first replicated Chiu and Egner (2015). In Experiment 2, we included neutral stimuli that did not necessitate motor preparation processes. Memory was enhanced for stimuli presented in conjunction with motor engagement, providing evidence for an account of memory that is facilitated when coupled with the motor system.

Keywords: perception-action coupling; goal-directed behavior; memory; go/no-go; action-induced remembering

Introduction

Coordinating movements with perception is necessary to achieve external goals. Performing the most elementary of activities requires perception and action to interact reciprocally in real-time: perception lends to executing actions and previous motor associations impact present perceptions. The bidirectional relationship of perception and action has been well-established for decades and empirically reinforced by work such as motor control development (Corbetta et al., 2014) and the discovery of mirror neurons (Rizzolatti et al., 1996). Origins of perception-action coupling have since given way to frameworks such as embodied cognition and dynamic systems theory. These viewpoints regard cognitive processes as the softly-assembled properties of perception and action (Thelen, 1996). One obstacle faced by these and similar perspectives is that of mental representation: How do continuous variables of perception and action give rise to abstract, higher-level cognition (Lins & Schöner, 2014)? The current study attempts to further bridge this gap by investigating a possible link between systems of action, perception, and cognition.

The structural nature of how perception and action systems connect with cognition is debated. Traditional theories of action describe goal-directed behavior unfolding in a succession of steps: (1) a stimulus is identified and encoded, (2) an abstract representation is formed and compared to task goals, (3) decision making processes evaluate this relationship, deeming if a response should be called for, and (4) the motor system then executes the selected appropriate response (Sternberg, 1969). Similarly, a more recent theory, Adaptive Control of Thought-Rational (ACT-R), explains cognitive architecture as being comprised of three modules: perception, action, and a central procedural module of the frontal cortex to independently interact with the other systems (Borst & Anderson, 2015). In these contexts, motor and perceptual systems are isolated from each other; output of the motor system is based on relayed input from cognitive processes. This outlook assumes that movement grows from thought. An alternative account of goal-directed behavior describes processes of perception and action coinciding with cognitive domains in real-time feed forward and feedback loops (Clark, 1997). This view highlights a perception-action interface, of which information is ever available to cognitive domains. That is, perception-action interplay is assumed to be fundamental to cognition.

Beyond perception-action coupling, goal-directed behaviors include networks of decision making processes involved in the planning, preparation, and execution of actions. These processes are in part made possible by the cognitive and behavioral control mechanisms known as executive function (Buss & Spencer, 2015). Carrying out goal-directed actions involves multiple features of executive functioning: task switching allows for flexibility in adapting to the demands of the environment, working memory updates action planning and stores relevant task information, and response inhibition acts as a stopping mechanism when a prepared motor behavior becomes unwanted. For example, consider the processes underlying changing lanes in a vehicle. In this context, a motor movement is selected and prepared for moving the steering wheel. However, if you were to notice a car in the neighboring lane right before the execution of this movement, then it would be essential to *inhibit* that now unwanted movement, *update* the goal, and *switch tasks* to stay in the original lane. Executive functioning is therefore critical to the organization of behavior in real-world environments, and as such has been shown to be predictive of a number of positive life outcomes (Allan,

Mcminn, & Daly, 2016). For that reason, it is important to consider perception-action systems interplay with executive functions as real-time streams of environmental demands are confronted.

Resource-Competition and the Action-Induced Remembering Hypothesis

One context in which both motor and executive function processes can be examined is within that of the go/no-go task: participants are instructed to respond with a button press to one stimulus type (go) while inhibiting a motor response to the other type (no-go). One study employed this paradigm to test the effect of response inhibition on subsequent memory recall (Chiu & Egner, 2015). Using face stimuli, participants were instructed to respond to one sex (e.g. females) while inhibiting a response to the other sex. Participants were then administered a surprise subsequent memory recall task which included faces seen from the go/no-go task and a collection of new, unseen face stimuli. The authors found that go stimuli had better memory recall ratings than no-go stimuli. Ensuing fMRI results revealed that engaging in response inhibition processes to a higher degree resulted in fewer neural resources available for encoding no-go stimuli (Chiu & Egner, 2016). Importantly, this reported resource-competition was distinct to two systems associated with memory and response inhibition: the right ventrolateral pre-frontal cortex (rVLPFC) and right superior frontal gyrus (rSFG). In a competitive manner, more activation in the rSFG left fewer resources available for the encoding of faces in the rVLPFC and vice versa. In this way, a core component of executive function, response inhibition, is suggested to play an adverse role and impairs memory--an effect termed inhibition-induced forgetting.

Drawing conclusions from resource competition can be potentially premature when comparing conditions that share coinciding cognitive processes. The pattern of previous results could also be explained by an inverse process that facilitates memory for stimuli associated with the execution of a motor response. Specifically, in a linear fashion, the extent to which the motor system is engaged could predict the likelihood of memory formation. From the perception-action perspective of cognition, such an effect would be a natural consequence of coupling the go stimulus with the motor system. This coupling could serve to reinforce activation associated with the encoding of the stimulus. Thus, the current study proposes an alternative account that explains memory data through facilitation of memory based on the degree of motor system involvement. In turn, we hypothesize stimuli which are associated with the preparation or execution of a motor response will result in superior memory recall than stimuli presented in the context of no motor system engagement (visual input only). We term this the action-induced remembering (AIR) hypothesis. In the following sections, we review research supporting such an account, as well as highlight neuroimaging studies of attention and inhibitory demand in relation to the resource-competition hypothesis and response inhibition networks.

Attention and No-go Stimuli

The proposed mechanism of the resource-competition hypothesis is specific to a lack of attentional resources available for encoding no-go stimuli. That is, this account explains response inhibitions effect on memory is mediated through the suppression of attention. The prefrontal cortex, where response inhibition is believed to primarily function, also recruits the top-down control of attention by processing behaviorally salient stimuli (Rossi et al., 2009). The neural dissociation of response inhibition from attentional capture has been contested: the right inferior frontal gyrus (rIFG), for example, is traditionally implicated for its involvement in suppressing a motor response, while some argue it is indicative of attentional capture as it responds to the unexpectedness of no-go stimuli (Hampshire et al., 2010). Crucially, Chiu and Egner (2015) did not find rIFG activation associated with forgotten no-go stimuli. While this debate is still ongoing, it is difficult to dismiss the role of the rIFG in inhibition entirely.

Similarly, there has been growing debate regarding whether no-go stimuli prompt suppression not only at the level of a motor response, but also at the level of attention. In the current context, understanding the role attention plays in inhibition is important given how memory formation and attention interact. Whether implicit or explicit, attention is required to consolidate information into memory (Chun & Turk-Browne, 2007). Thus, if attention is not suppressed when no-go stimuli are presented, then it is difficult to tie this process to memory impairment, as the resource-competition hypothesis would suggest. Barras and Kerzel (2016) explored such an interaction using EEG and a modified spatial cueing paradigm. Participants were first cued to a location (of either a go, no-go, or neutral color), then were tasked with executing or inhibiting a response to a go or no-go target location. Results indicated that spatial locations cued with a no-go stimulus did not result in slower reaction times compared with neutral cues. Cues associated with the go stimulus, however, resulted in faster response times. Additionally, the authors found an increased N2pc response (an attentional index) to go cues but found no differences between neutral and no-go cues. These results suggest that attentional sets, in this context, may exclusively include stimuli which evoke a motor response (go stimuli). Importantly, these results provide evidence that no-go stimuli may not be suppressed at the level of attention compared to stimuli absent of motor preparation processes.

Inhibitory Demand and Motor Preparation

A common aspect of go and no-go trials is motor preparation. That is, for response inhibition to occur, the planning and preparation of a motor movement must come first. Therefore, the degree of preparation directly contributes to the demands of inhibiting a response. Taking this perspective, an index of motor engagement via preparatory processes may instead account for differences between subsequent memory of go and no-go stimuli. Go/no-go tasks can vary inhibitory demand by disproportionately

distributing go and no-go trials, such that 75% go trials and 25% no-go trials would indicate a need for high inhibition, whereas the vice versa would return low inhibitory demands. Behaviorally, this manipulation can be observed in the error rates and reaction times of go and no-go trials: a high probability of go trials tend to result in faster reaction times than low go trial probability, and more errors of responses are made during a low probability of no-go trials compared to high no-go trials (Meffert et al., 2016).

Recent research supports the idea that a neural system involved in motor preparation and execution can facilitate memory. In a direct comparison of activation between low and high no-go trial frequency, Kolodny et al. (2017) showed high inhibitory demand was localized in the posterior parietal cortex (PPC): a region also found to be important in attention and memory formation. Specifically, the intra-parietal sulci had greater activation during high inhibition, or high motor preparation trials. These results demonstrate the importance of the parietal cortex in action processes, while raising questions about the traditional perspective of the frontal cortex's role in inhibition. One possible explanation could be that frontal regions act as the stopping mechanism, while parietal regions contribute to resolving the inhibitory demands associated with motor preparation. While more research is needed to investigate a possible fronto-parietal network of response inhibition, these findings suggest that response inhibition, and critically inhibitory demand processes, reach beyond the rSFG.

When performing goal-directed actions, motor preparation has been shown to enhance visual processing for spatially relevant items (Mason, Linnell, Davis, & Velzen, 2015) as well as distributing visual attention to spatial locations which are task relevant (Baldauf & Deubel, 2010). The functional role of motor preparation resides primarily in the pre-supplementary motor area (pre-SMA) and premotor areas. The pre-SMA is believed to be involved in motor planning and motor imagery, in addition to the preparatory periods of initiating a motor response (Cunnington, Windischberger, Robinson, & Moser, 2006). Research has also shown that activation in the pre-SMA comes prior to that of the rIFC, implicating its involvement in response preparation as well as inhibition (Swann et al., 2012). Considering the dynamic function of the pre-SMA in action, the following section will review the pre-SMA in the specific context of motor engagement, where we suggest its involvement in memory formation via an attentional network of the PPC.

The Dorsal Attention Network

The PPC has traditionally been regarded as a sensory-motor hub, involved in motor planning, control, and visually guided motor behavior (Buneo & Andersen, 2006). Additionally, recent research has shed light on the involvement of the PPC in the allocation of top-down attention and in turn, memory formation. In particular, the dorsal portion of the PPC, termed the dorsal attention network (DAN), is responsible for top-down control of perceptual attention (Sestieri, Shulman, & Corbetta, 2017).

The DAN also has mutual connections with hippocampal memory regions of the medial temporal lobe (Cabeza, Ciaramelli, Olson, & Moscovitch, 2009). Beyond that, research using fMRI and memory recall paradigms have illustrated a greater hemodynamic response at the time of encoding and retrieval in the dorsal PPC for remembered versus forgotten items (Uncapher & Wagner, 2010).

Moreover, the pre-SMA, involved in the preparation and execution of movements, has reciprocal connections with the DAN. Importantly, the pre-SMA has been shown to have sustained neural activation from the preparation phase to the execution of a movement in response to a stimulus (Cunnington, Windischberger, Robinson, & Moser, 2006). Taken together, we hypothesize, given the involvement of the PPC in perception-action coupling, that a network involving motor areas and the PPC may interact with and facilitate memory encoding for objects paired with action. Our study is aimed at identifying behavioral signatures of such an interaction.

Experiment 1

The main purpose of Experiment 1 was to investigate subsequent memory ratings for go and no-go stimuli. Here, we attempted to replicate the pattern of results found by Chiu and Egner (2015), such that go stimuli should result in better memory recall than no-go stimuli.

Participants

Twenty-eight undergraduate students (mean +/- SD age, 20.1 +/- 1.8; 16 females, 12 males) of the University of Tennessee-Knoxville participated. Participants were recruited via SONA, the University of Tennessee's research participation system. Participants were compensated class credit upon completion. Participants completed an informed consent and demographics form upon arrival, approved by the Institutional Review Board. Two participants were dropped due to poor behavioral performance.

Stimuli

240 face stimuli (half male/female) were used. All stimuli were affectively neutral and grayscale. 120 of the stimuli were used during both the go/no-go task and subsequent memory task, while the other 120 only appeared during the memory task. Presentation of stimulus sets were balanced across participants, such that each stimulus appeared in the go/no-go task (as an "old" go or no-go stimulus) or only in the memory task (as a "new" stimulus) an equal set of times. The filler task included 78 grayscale stimuli (39 house/apartment stimuli). This stimulus set size was chosen to fulfill a 5-minute encoding-retrieval delay before the subsequent memory task.

Design and Procedure

Go/no-go Task: Participants were first instructed to respond to one gender of face stimuli using the spacebar while withholding a response to the other. Half of the

participants responded to male stimuli, while the other half responded to female stimuli. Each trial began with a fixation cross (250ms), followed by the presentation of a face stimulus (800ms). During the presentation of the stimulus, participants had until stimulus offset to execute a response if it was a go trial. After stimulus offset, a feedback display appeared (1s), stating either "Correct!" or "Incorrect!" dependent on their performance; feedback marked the end of a trial. Inter-trial intervals were distributed equally across trials and were jittered from 2.5s-4.5s (step sizes of 250ms). Four blocks were administered during the go/no-go task, with each face stimulus appearing once per block, thus creating 480 total trials.

Filler Task: Participants then performed a filler task, which acted solely as an encoding-retrieval delay (5-min) prior to the subsequent memory task. Participants were presented with house and apartment stimuli and were tasked to categorize them using the "z" and "m" keys. Timings were the same as those utilized in the go/no-go task, except for the inter-trial intervals, which were set at 2s.

Surprise Subsequent Memory Task: Participants incidental memory was then tested for the face stimuli presented from the go/no-go task. To do this, we included the 120 face stimuli from the go/no-go task, and added an additional 120 new face stimuli, creating 240 total trials. Presentation of new and old stimuli was randomized. At the start of each trial, participants were shown a face stimulus (2s), then immediately after a 6-point scale which ranged from "definitely new" to "definitely remember". The scale remained on the screen until a response was made, however only responses made within 2s were considered in the memory data. Additionally, go and no-go stimuli which were responded to incorrectly during the go/no-go task were excluded from memory data analyses. Inter-trial intervals were distributed equally across trials and were jittered from 2.5s-4.5s (step sizes of 250ms).

Results and Discussion

During the go/no-go task, participants overall accuracy was high as was expected (mean +/- SEM, 98.1% +/- 2). Additionally, no-go false alarm rates were low across blocks (mean +/- SEM, 1.46% +/- 1.06). Moreover, a pairwise comparison revealed a decrease in reaction time to go trials between the first (*M*=467.8 ms) and last (*M*=456.8 ms) block (t(27)=2.01, p=.05) of the go/no-go task (see figure 1).

We now shift to our primary area of interest in that of the subsequent memory task. To review, we excluded trials in which reaction times were longer than 2s, and stimuli which were responded to incorrectly (for any of the 4 repetitions) during the go/no-go task. The latter portion was done to exclusively test memory ratings of inhibitory and response execution processes. For the analyses, we collapsed "definitely new"- "maybe new" and "definitely remember"- "maybe remember" responses simply into "new" and "remember" responses. We then calculated d' (z (hit rate) – z (false-alarm rate)) across participants to serve as an index of memory scores for both go and no-go cues. Hit rates for go
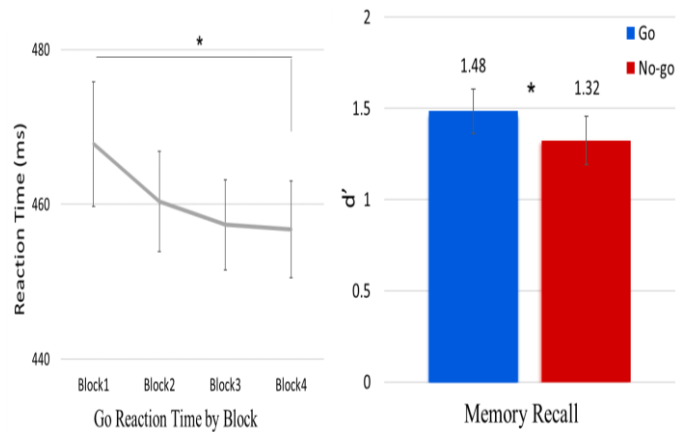

Figure 1: Illustrated are reaction times for go trials during the go/no-go task across blocks (left) and memory ratings (d') for go and no-go conditions in the subsequent memory task (right).

(*M*=74%) and no-go stimuli (*M*=69%) were significantly above chance levels. Replicating that of Chiu and Egner (2015), we found that go stimuli were recalled significantly better than no-go stimuli (t (27) =2.39, p=.02) (see figure 1).

Experiment 2

Having replicated prior differences found between go/no-go stimuli memory, such that memory for go stimuli was superior to that of no-go, we moved to address our primary hypothesis. Experiment 2 specifically examined the influence of perception-action coupling for both go and no-go stimuli on subsequent memory recall. To do this, we modified the original go/no-go task to implement three conditions: neutral (absent of motor processes), go, and no-go. We aimed to incorporate neutral stimuli in the go/no-go task such that they remained task relevant with the exception being they did not call for motor preparatory processes. We predicted that both go and no-go stimuli would be recalled significantly better from memory than neutral stimuli, such that this difference would be specific to the underlying attentional processes arising from perception-action coupling.

Participants

Twenty-four undergraduate students (mean +/- SD age, 20.32+/- 1.4; 13 females, 11 males) were recruited for participation. Participants completed an informed consent and demographics form upon arrival, approved by the Institutional Review Board. Four participants were dropped due to poor behavioral performance.

Stimuli

Face stimuli and presentation timing across stimuli were identical to those of Experiment 1. Face stimulus sets included 4 groups of 30 (60 male, 60 female), and sets were equally tested in each of the experimental conditions. In addition to the face stimuli, we also included a grayscale image of a streetlight which was used in the go/no-go task. This stimulus acted independently as a "cue" for participants:

stimuli appearing before the cue did not require a motor response, and the stimulus following the cue would either require a motor response or the inhibition of one (see design and procedure for more details). There were 30 face stimuli in the go condition and no-go condition, with 60 cue stimuli preceding them. Before cue onset, a total of 60 neutral stimuli (30 male, 30 female) were included.

Design and Procedure

Modified Go/no-go Task: We utilized a one factor, within-subjects design with three levels: neutral, go, and no-go. Consistent with Experiment 1, participants were instructed to respond using the space bar to one gender (go) while withholding a response to the other (no-go). However, this rule was dependent on the appearance of a cue stimulus: before the cue appeared, participants were instructed to visually attend to the screen in anticipation of the cue, and after cue onset, to initiate in the original go/no-go instructions for the single face stimulus following the cue. After participants made or suppressed a response, they were instructed to visually attend and wait for the next cue. Timings and stimulus presentations were identical to that of Experiment 1, except for the text "Wait for the cue!" (1s), which appeared after feedback for the go/no-go trial type. The filler task and subsequent memory task was also identical to that of Experiment 1.

Results and Discussion

Accuracy in the go/no-go task portion remained high (*M*=97%) despite modifications made to the rule structure. Additionally, low false alarm rates were committed to neutral stimuli (0.05%). Replicating Experiment 1, participants showed enhanced reaction times to go stimuli from the first (*M*=476.211) to last block (*M*=441.12) (t(23)=3.18, p=.02). Together, these results suggest that the inclusion of the cue and neutral stimuli did not interfere with go/no-go performance.
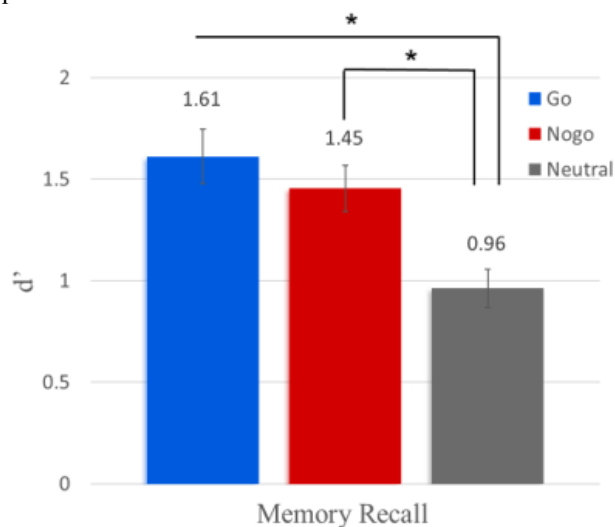

Figure 2: Depicted are memory ratings (d') across conditions of go, no-go, and neutral stimuli.

For the memory analyses, we performed the same exclusion criteria as Experiment 1. Replicating Experiment 1, hit rates for go (80%), no-go (75%) and neutral (61%) stimuli were all above chance level. A one factor repeated measures ANOVA revealed a main effect for stimulus type (F(2,23)=28.627, p<.01) (see figure 2). Pairwise comparisons using the Bonferroni correction revealed that go stimuli had better memory recall than neutral stimuli (t(23)=6.830, p<.01). In addition, no-go stimuli showed superior memory when compared to neutral stimuli (t(23)=4.94, p<.01). However, we did not find the original memory effect between go and no-go stimuli (t(23)=1.288, p=.211).

The primary aim of the present experiment was to test differences in memory recall between stimuli paired with motor engagement (go and no-go) and those absent of motor processes (neutral). We found that stimuli coupled with the motor system, either preparatory (no-go) or an executed act (go), resulted in greater recall than stimuli only presented visually without motor demands (neutral). An alternative explanation for this finding could be that neutral stimuli induce less attentional processing because they are not relevant enough to the current task set. Since stimuli only appear for 800ms, this explanation is unlikely given the necessity to detect the cue to fulfill the task goals. However, it is also possible that neutral stimuli may not demand processing at the level of sex discrimination in the same way as go and no-go stimuli.

Interestingly, we did not replicate Chiu & Egner (2015) or Experiment 1 in that we found no difference between go and no-go recall. A possible explanation could be that for this modified design, our sample size was too small to see an effect. Another account could be that this design is tapping into more controlled inhibition than automatic inhibition, altering motor preparation processes (Littman & Takács, 2017). This could be due to the single go/no-go trial occurrence after the cue, instead of continuous go/no-go task engagement.

General Discussion

The present study examined the influence of action and inhibition processes on memory formation. We first replicated previous research, finding that stimuli paired with a response (go) resulted in better memory than stimuli prompting the inhibition of a response (no-go) (Experiment 1). We then asked if these go and no-go memory variations could instead result from the degree of motor system engagement such that no-go stimuli prompt only the preparation of a response while go stimuli elicit response execution. To test this, in Experiment 2 we included neutral stimuli that did not engage the motor system but were still task relevant. Results showed that stimuli which took part in either aspect of motor engagement (preparation or execution) had significantly better memory than stimuli uncoupled with action processes. That is, no-go stimuli were not associated with poorer recall than baseline, arguing against a direct adverse role of response inhibition on memory as the resource-competition hypothesis suggests. Rather, these findings provide evidence that incorporating action processes

facilitates memory formation. Neuroimaging work could further elucidate the systems unfolding in the present study. Specifically, we hypothesize regions of the DAN, the pre-SMA, and premotor areas may mediate the influence of responses on subsequent memory recall. That is, memory recall should be associated with the magnitude of activation in these regions.

Understanding the perception-action processes which underlie goal-directed behavior, via successful executive functioning, could in turn inform future intervention efforts aimed at human cognitive development and quality of life outcomes. In this way, the proposed study offers an account of memory unique to the field, and outlines perception-action coupling as crucial to the subsequent expression of goal-directed behavior.

Acknowledgments

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