THESIS

DIFFERENTIATING ASSOCIATIONS BETWEEN TASKS AND OUTCOMES IN THE HUMAN BRAIN

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In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2022

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ABSTRACT

DIFFERENTIATING ASSOCIATIONS BETWEEN TASKS AND OUTCOMES IN THE HUMAN BRAIN

In order to successfully achieve their goals in a noisy and changing environment, organisms must continually learn both Pavlovian (stimulus-outcome or S-O) and instrumental (action-outcome or A-O) associations. A wide range of brain regions are implicated in reinforcement learning and decision-making, including the basal ganglia, medial prefrontal cortex, the dorsolateral prefrontal cortex (dlPFC), and the anterior cingulate cortex (ACC). One possible explanation of disparate findings is that activation depends on the nature of the action or response under consideration. To investigate representations of task-reward associations, subjects switched between an emotional judgement task and a spatial judgement task, combined with either a high or low level of reward. A general linear model (GLM) compared activation for different combinations of task and reward. A cluster in the mid-prefrontal cortex was more active for right versus left response, whereas a cluster in the midbrain near the brainstem was more active for left responses. Performance of the spatial task was associated with activation in the ventral occipital cortex and ventral prefrontal cortex. Clusters in the posterior parietal cortex and lateral prefrontal cortex were more active during the emotion task. Receiving a large reward was accompanied by activation in primary somatosensory cortex and auditory cortex, while receiving a low reward appeared to recruit the anterior cingulate cortex. Comparing trials which yielded a reward versus trials with no reward revealed activation in the dorsal prefrontal cortex. A 2-way ANOVA examining independent contributions of response and reward found an effect of

response in cuneus and pre-cuneus, an effect of reward in anterior insula and sensorimotor cortex, and an interaction in the post-central gyrus. A 2-way ANOVA of task and reward found a main effect of task in several clusters in the medial occipital cortex, a main effect of reward in somatosensory cortex and anterior insula, and an interaction in the ventral occipital and anterior prefrontal cortex.

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INTRODUCTION

The brain is uniquely adapted to learn associations between contexts, behavioral strategies, and reward distributions. Learning these contingencies allows organisms to flexibly adapt their behavior depending upon the environment they find themselves in. Furthermore, engaging in goal-directed behavior requires cognitive control – the ability to adjust behavior in response to changing priorities. Prior research, both in animals and humans, has helped to elucidate the regions of the brain which play a role in goal-directed behavior and cognitive control. One crucial question is how stimuli, tasks, and outcomes are individually represented in the brain, as well as stimulus-outcome (S-O) and action-outcome (A-O) associations. These representations are crucial for learning and optimizing behavior.

Research from multiple fields within neuroscience has begun to shed light on the nature of both Pavlovian (S-O) and instrumental (A-O) learning. Single-unit electrophysiological recording in rats and monkeys strongly implicates the dorsal anterior cingulate cortex (dACC) in the learning of A-O associations, specifically (Amiez et al., 2006; Kennerley et al., 2011; Matsumoto et al., 2007; Seo & Lee, 2007). However, research utilizing magnetic resonance imaging (MRI) in humans has yielded more nuanced results. A-O associations have been detected in several areas in humans, including ventromedial prefrontal cortex (vmPFC), dorsolateral prefrontal cortex (dlPFC), caudate, and posterior parietal cortex (PPC) (Fitzgerald et al., 2012; Mcnamee et al., 2015; Wisniewski et al., 2015).

One potential reason for this confusion stems from the nature of the response being examined. While the response in animals is typically a simple motor behavior, fMRI studies have utilized anything from a right or left button press, to two entirely different tasks. This raises an

intriguing question as to how A-O associations might be differently encoded based on how one defines the response.

In order to better understand the encoding of relationships between tasks and outcomes, this experiment will examine where in the brain there exists differences in activation for differing combinations of tasks and rewards. Based on prior research, I expect the posterior parietal cortex to respond to differences in task-outcome associations.

Computational Models of Instrumental Learning

The simplest model to describe operant conditioning, or reinforcement learning, is the temporal difference model (O'Doherty et al., 2003). In this framework the expected value of a specific stimulus or state is calculated at each time point *t*. The reward prediction error, then, is the difference between the reward received and the learned value.

This model can then be expanded to incorporate action. In instrumental conditioning, an organism must learn not only stimulus-outcome associations, but action-outcome associations. Thus, reinforcement learning (RL) models learn expected values for each state (S) and action (A) combination (Sutton & Barto, 1998). The "agent" moves from state to state by performing actions. The aim of the model is to maximize reward. It achieves this by maximizing the summed, weighted rewards of the current state and all future states.

Perhaps the most common "flavor" of RL is known as *Q*-learning models. In this type of model, the agent learns a quantity *Q*, reflective of the quality, or associated value, of a given state-action pair, *Q* (s, a). This type of algorithm is model-free, meaning it is capable of learning through trial and error rather than from a mental model (e.g., a rule or hypothesis). It will generate optimal behavior for any finite Markov decision process (FDMP), and performs well even in the face of noisy transitions and rewards (Jakkola et al., 1994).

Strong similarities exist between RL algorithms and neuronal activity during learning. In particular, dopaminergic neurons projecting from ventral tegmental area (VTA) release dopamine into the striatum in a manner that correlates strongly with reward prediction error (RPE), or the difference between an expected outcome and an actual outcome (Cohen et al., 2012; Fields et al., 2007). One difficulty with standard RL models, however, is their slowness. That is, they do not lead to efficient reward-maximizing behavior in sufficiently few trials to mimic animal behavior.

One solution to this has been hierarchical RL models. Haruno and Kawato (2006) propose that reward prediction errors move from loops connecting prefrontal cortex (PFC) and caudate, part of a mid-brain structure known as the basal ganglia, progressively to loops in the putamen, part of the basal ganglia adjacent to caudate, and motor cortex. Activity in these loops begins as coarse representations of reward prediction errors, but the representations become progressively more refined. The authors suggest that this gradual transfer of information from executive prefrontal regions to motor cortex underlies the transition from goal-directed to habitual responding.

An altogether different way of describing decision making is to model choice as an evolving parameter of time. Whereas RL models calculate static choices that change as a function of state-action values, drift diffusion models calculate the evidence for a certain choice as it moves towards a critical decision threshold a at rate v, at which point the action is performed (Milosavljevic et al., 2010). Greater accuracy and speed both increase v, which is typically proportional to the relative values of possible choices. The decision threshold a is in turn modulated by conflict, as determined by the relative choice values (conflict is high when choice values are similar). Drift diffusion models have been demonstrated to accurately capture

such phenomena as choice proportion as well as complete response time distributions (Frank et al., 2015).

Neural Substrates of R-O learning

Basal Ganglia

Researchers learned early on that the structure of the basal ganglia was well suited for reinforcement learning. Closed corticostriatal loops span almost the entirety of the cortex, from early visual areas to prefrontal cortex, and are therefore well-suited for the integration of information across multiple modalities (Yahya et al., 2020). Furthermore, the administration of chemicals which induce dopamine release is known to be highly rewarding in rats (Phillips et al., 2003). Reinforcement learning occurs via the release of dopamine from dopaminergic neurons in midbrain structures including the substantia nigra and ventral tegmental area (Fields et al., 2007; Morales & Margolis, 2017).

The striatum lies within the basal ganglia, and is further divided into the dorsal striatum, which contains the caudate and putamen, and ventral striatum, which contains the nucleus accumbens. The caudate is strongly associated with goal-directed behavior. Experiments using gambling tasks and conditional reinforcement show the caudate to be especially active in early learning (Delgado et al., 2005). When models including action are fit to fMRI data, activation in the dorsal striatum disappears, supporting the hypothesis that the dorsal striatum is especially involved in learning which movements lead to a high reward (McClure et al., 2003).

The putamen is implicated in habitual responding. When fit to a reinforcement learning model, activity in the putamen correlates closely with stimulus-action dependent reinforcement prediction, a sensible finding given the corticostriatal loops between putamen and motor/premotor areas (Haruno & Kawato, 2006).

The ventral striatum, on the other hand, is particularly sensitive to reward. Activity in the ventral striatum and subsequent DA release in the forebrain correlates tightly with reward prediction error (Hollerman & Schultz, 1998; O'Doherty et al., 2003; Schultz et al., 1992).

Medial PFC

The medial portion of the prefrontal cortex, particularly the orbitofrontal prefrontal cortex (OFC) and the ventromedial PFC (vmPFC), receives dense dopaminergic projections from the ventral striatum (Groenewegen & Trimble, 2007). Thus, it is not surprising that this region of cortex is highly responsive to reward (Haruno & Kawato, 2006; O'Doherty el al., 2003). Medial PFC is also sensitive to monetary loss (Tom et al., 2007), and the reward signal is attenuated by factors such as delay (Kable & Glimcher, 2007). The vmPFC has been shown to encode many reward-related variables, including reward anticipation (Schoenbaum, Chiba, & Gallagher, 1998), magnitude of reward (Kim, Shimojo, & O'Doherty, 2006; O'Doherty et al., 2001), and simple stimulus-reward associations (Tremblay & Schultz, 1999). The vmPFC/OFC is also responsive to aversive as well as reinforcing signals (Tom et al., 2007). However, when value and salience are dissociated, the vmPFC and OFC have been demonstrated to encode value (Kahnt et al., 2014).

Value representations in vmPFC/OFC seem to be action-independent. For example, when subjects viewed faces, activity in the vmPFC correlated with the subject's preferences, but was unrelated to the arbitrary judgements subjects were required to make (Lebreton et al., 2009). This does not imply, however, that the vmPFC is not a necessary region for value-guided decision making. Lesions to the analogous region in monkeys impair decision making and this impairment increases as the choice values become more similar (Noonan et al., 2010).

The function of the vmPFC appears to be more complex than pure subjective valuation. A particularly interesting study by Boorman et al. (2009) demonstrated that the vmPFC represents the difference in value of a chosen option minus an unchosen option, suggesting the ability to compare and contrast alternative choices. The vmPFC has also been shown to represent abstract task variables, such as the probability of choice *A* in a given trial in a probabilistic learning task (Hampton et al., 2006). Further analysis of this task demonstrated that a structured RL model fit these data better than a standard RL model, suggesting the intriguing possibility that the vmPFC is not simply learning action-outcome associations independent of one another, but is rather learning more complex information about the overall task structure. These studies suggest a more nuanced role for the vmPFC than a simple "reward detector".

Central Executive Network

The lateral PFC, particularly dorsolateral prefrontal cortex (dlPFC) and posterior parietal cortex (PPC), comprise the central executive network (CEN), which is reliably elicited by task performance and top-down control (Petrides, 2000). Activation of this network increases as a function of increased cognitive load (Rypma & D'Esposito, 1999). Working memory and task-switching ability are severely impaired when the frontoparietal network is lesioned (Goldman et al., 1971; Dias et al., 1996).

Lateral PFC is not as directly involved in reward representations as vmPFC and OFC. However, RPE-related activity has been demonstrated occasionally in areas such as the inferior frontal sulcus and dorsal premotor cortex (Badre & Frank, 2011). When compared to OFC, the lateral PFC preferentially encodes action-value representations, a finding which mirrors both findings in the putamen and the underlying neuroanatomy (Wallis & Miller, 2003). In contrast to regions like the vmPFC, which are more active when the difference in value between choices is

large, activity in parietal regions is actually strongest when two choices are similar and therefore difficulty is high (Basten et al., 2010).

The dlPFC is involved in working memory and manipulating mental models. When comparing a simple learning task which is deterministic to the same task using probabilistic reward, the dlPFC and ACC are recruited preferentially in the probabilistic condition (Yoshida & Ishii, 2005). In working memory tasks, activity in frontoparietal regions increases as interference demands increase (Bomyea et al., 2017).

Anterior Cingulate Cortex

The dorsal anterior cingulate cortex (dACC) is active for a wide variety of cognitive domains, including emotion, pain, movement, and a range of cognitive processes relevant to decision-making (Bush et al., 2000). Because the dACC is implicated in so many different processes, a "unified theory" of dACC function has proven elusive. Indeed, the dACC receives projections to and from a large portion of cortex, including ventromedial PFC, ventrolateral PFC, premotor and motor cortex, dorsolateral PFC, and parietal cortex, midbrain structures such as the amygdala, thalamus and basal ganglia, and even the spine (Paus, 2001). Lesions of this piece of cortex lead, somewhat puzzlingly, to both apathy and impulsive behavior, suggesting that the dACC plays an important role in motivated behavior (Njomboro et al., 2012). Electrical stimulation induces the sensation of determination, or a will to persevere (Parvizi et al., 2013).

Early research focused on the role of the dACC in processing pain and unpleasant emotion. As more sophisticated techniques became available, the focus shifted to error processing. As research expanded, so too did the theories, to encompass the broader category of processes known as conflict monitoring. Finally, modern theories often stress a more

neuroeconomic view, which centers on the dACC's role in calculating value in order to guide action.

Theories of ACC function

Early theories centered on the role of the anterior cingulate cortex in error commissions. Indeed, the dACC is strongly responsive to errors (Braver, 2001), and is thought to be responsible for the error-related negativity (ERN) in EEG research (Hohnsbein et al., 1990; Gehring et al., 1993). Single-unit neuronal recording confirms a clear correlation with the ERN (Gemba et al., 1986; Ito et al., 2003). However, it was quickly realized that activation of the dACC can be elicited without errors (Aarts, Roelofs, & van Turennout, 2008; Botvinick et al., 2001). For example, activity in dACC is higher in environments where error is likely but not actually committed (Brown, 2005). Modern neuroscientists generally agree that errors are part of a broader range of stimuli to which the dACC is sensitive, including conflict, reward, and in general, a range of variables relevant to decision making (Amiez et al., 2005; Heilbronner & Hayden, 2016).

` Subsequent theories of dACC function focused on its role as a conflict monitor (Botvinick et al., 1999; Carter, 1998; Kerns et al., 2004). One of the earliest findings regarding the dACC was differential recruitment in incongruent trials in a Stroop task, suggesting its role in either detecting or resolving conflict between competing responses (Pardo et al., 1990; Swich & Jovanovic, 2002). The dACC has also been found to correlate with interference in a complex working memory task (Bomyea et al., 2017). It is a somewhat vexing problem that although conflict signals exist in multiple fMRI and EEG studies, single-unit recordings have essentially failed to find them (Nakamura et al., 2005; Amiez et al., 2006; Cai & Padoa-Schioppa, 2012).

One potential explanation for this might be that conflict signals are encoded not by single neurons, but rather by weak activity of large clusters of neurons (Nakamura, 2005).

In addition to error and conflict, the dACC represents a diverse range of reward and decision-making variables. In monkey studies using electrophysiological recording, neurons in the dACC reflect which action will be taken (Matsumoto, 2003; Shima & Tanji, 1998), prediction error (Matsumoto et al., 2007), the value of an alternative option (Hayden et al., 2009), and the average reward associated with a certain task (Amiez et al., 2006). The most common findings stress a strong correlation between dACC activity and (signed) reward prediction error (Kennerley et al., 2011; Matsumoto et al., 2007; Seo & Lee, 2007), although others have reported signals consistent with unsigned prediction error (Bryden et al., 2011; Hayden et al., 2011a). Some studies have found neurons increase firing rate with decreasing reward (Hayden et al., 2011b, Kennerley et al., 2011), while others have found exactly the opposite (Hayden et al. 2009). A particularly intriguing discovery by multiple researchers is that reward sensitivity in the dACC is context dependent (Hayden et al., 2011a; Luk & Wallis, 2009; Matsumoto et al., 2007). The manner in which neurons in dACC encode reward has been shown to change as a function of task (Luk & Wallis, 2013). When reward amount, probability, and effort are manipulated, neurons in the dACC track the integrated value with all three variables taken into consideration (Kennerly et al., 2009).

There is some debate whether the primary role of the dACC is as a monitor, as in conflict monitor, or a controller, as in a direct part of the cognitive control process which promotes goal-directed behavior. The dACC is indeed sensitive to errors and conflict, as would be required for a monitor, but evidence also exists for a role as controller. Activity in this area is strong when

there is a need for control (Johnston et al., 2007; Shenhav et al., 2013). The dACC is also active when switching tasks (Rushworth et al., 2002), and when tracking progress towards a goal (Hayden et al., 2011b). Activity in dACC is higher when two choice values are similar, reflecting perhaps a detection of response conflict, or a need to recruit additional cognitive resources (Boorman et al., 2009; FitzGerald et al., 2009). Interestingly, when rewards of the same value require different levels of control, neurons in the dACC do not represent absolute reward; rather, firing rates rise slowly and to a greater threshold when there is a greater need for control (Hayden et al., 2011b). Firing rates rise in response to reward anticipation and are correlated with control as measured by accuracy (Shidara & Richmond, 2002).

It seems clear that neurons in the dACC encode reward-related variables in a nuanced and flexible, context-dependent manner. In particular, these neurons have often been found to encode specific combinations of actions and associated outcomes (Cai & Padoa- Schioppa, 2012; Luk & Wallis, 2009; Matsumoto, 2003). Furthermore, lesions to the dACC prohibit the association between actions and outcomes (Amiez et al., 2006; Hadland et al., 2003; Kennerley et al., 2006; Rudebeck et al., 2008). For these reasons, modern theories of anterior cingulate function have centered on its role in calculating the value of various actions (Haggard, 2008). Although these models vary somewhat in their particulars, they all posit a key role of the dACC in decision making which involves ascribing value to various actions.

This theory is supported by multiple studies which find that neurons in this region are especially active when contingencies between actions and outcomes change, or when switching between tasks or strategies. In an experiment in which monkeys switched between two different actions for reward, activity in dACC was greatest when the monkeys needed to switch actions to

keep receiving reward (Shima & Tanji, 1998). This ability to flexibly shift between tasks is impaired in individuals with dACC lesions (Rushworth et al., 2003; Shima & Tanji, 1998). When reward is held constant while manipulating the need for adjustment, neurons in dACC predict the amount of adjustment; when adjustment is held constant while varying the magnitude of reward, they predict the amount of reward (Hayden et al., 2009). Whether the dACC is controlling the change in actions, or whether it detects the need for a change and then relays it to other areas, is not fully understood.

The theory of dACC as controller is supported by a range of studies which find that recruitment of this region correlates with self-control. For example, dACC activity tracks restraint in inter-temporal choice tasks (Peters & Buchel, 2010;), delay tasks (Narayan & Laubach, 2006), and in response inhibition tasks (Floden & Stuss, 2006). Activation of the dACC in humans produces intense feelings of determination to persevere (Parvizi et al., 2013).

A related cognitive process that the dACC is also closely associated with is learning. This is not contradictory but rather complementary to a putative role as monitor and controller, since instrumental learning is shaped by the detection of errors, specifically reward prediction errors. When learning a task, the dACC is strongly active during the first few trials but less so over time (Alexander & Brown, 2011; Kennerly et al., 2011; Rudebeck et al., 2008), and activity in this region correlates with the learning rate of an individual (Behrens et al., 2007). This region is also more active during exploration phases versus exploitation phases in foraging style experiments (Procyk et al. 2012).

A variety of models have been created in order to best capture the behavior of the dACC. One influential model by Botvinick (2007) posits that neurons in this area monitor for conflict.

This activity would then become a teaching signal that trains downstream areas of the brain to perform correctly in order to generate optimal behavior.

Kolling et al. (2013) propose a neural network model of the dACC inspired by foraging models, whereby pools of neurons move from reflecting search value initially towards engage value during learning. The result is that neurons begin firing at the same time as difficulty increases even though no neurons actually reflect difficulty per se, reproducing the observed behavior of the dACC from single-unit recordings. Evidence supporting the model derives from an experiment in which participants were surprised occasionally by a cue in an unexpected location (Posner & Peterson, 1990). Activity in the dACC correlated with surprising cues only when these cues provided information about possible reward, suggesting that the ACC may play an important role in updating mental models of various response mappings,

In contrast, researchers at Princeton University have developed the Expected Value of Control Theory (Shenhav et al., 2016). Much as it sounds, this theory posits that neurons in the dACC weigh the costs and benefits of recruiting more cognitive control, presumably from frontoparietal regions such as the dlPFC. The theory has been recently updated to suggest that the strength of this control signal is modulated by how beneficial or costly a given action will be. This model is attractive for explaining results incongruent with a pure conflict or error explanation, and because it is arguably more generalizable than theories based on foraging.

The predicted outcome-response (PRO) model is a similar model developed by Alexander & Brown (2011). This model is a variant of standard reinforcement learning models. In contrast to standard RL models, the PRO model trains outcomes for actions in a given stimulus context, as opposed to stimulus-outcome associations. Furthermore, prediction errors

are modeled as vectors rather than scalars, allowing for multiple outcomes to be learned simultaneously. The signed prediction error is capable of modeling both unexpected non-occurrences and unexpected occurrences. Negative surprise, or ω^N, represents the probability of an expected event not occurring. The model successfully captured many biological phenomena such as the error-related negativity. Importantly, the model captures the finding of increased mPFC activation in response to prediction error, even after correct responses in congruent trials, a phenomenon which would seem to contradict theories based solely on error or response conflict.

. The debate regarding whether the dACC is fundamentally a monitor or a controller hinges on whether the signal generated in this region lies within the decision-making circuity (controller), or outside (monitor). The problem is complicated by the highly correlated variables under consideration, such as error rate, reward prediction error, and response conflict. A more fundamental problem lies in the basic nature of which parts of the brain actually constitute the decision-making network. If an area of the brain generates a signal that ultimately informs motor output, how would one test whether that signal is "inside" or "outside"? In this sense, all parts of the brain could be said to lay within the decision-making circuitry, since all parts of the brain function in concert to ultimately bring about goal-directed behavior. For this reason, the controller/monitor debate is best set aside. A better use of time is to precisely describe the parameters that influence firing in the dACC, what effect this activity has on other regions, and the nature of the representations it may encode.

Single-unit recording and lesion data of action-outcome representations

As previously mentioned, consensus is emerging that the dACC is particularly involved in the learning and representation of action-outcome associations (Rudeback et al., 2008; Procyk

et al., 2000). Unlike response conflict, which appears mostly in fMRI studies, the bulk of the evidence for action-outcome representations stems from electrophysiological research.

Matsumoto (2003) trained monkeys to either move a joystick or not in response to various stimuli (Go/No-Go task). Importantly, the relationships changed over time, such that all possible stimulus-outcome, response-outcome, and stimulus-response combination were represented. Neurons in the ACC were found to be responsive to reward and to movement preparation, but more strikingly, many of the neurons were found to predict the specific action-outcome combination reflected in that trial.

A similar experiment by Hayden & Platt (2010) examined the coding of neurons the anterior cingulate cortex of two rhesus monkeys. The monkeys were trained to perform a task in which they made a saccade to one of eight visual cues. The color of the cues signaled the amount of reward associated with a saccade to the cue. A high percentage of neurons contained information about both action and reward. Moreover, 60 percent of neurons encoded information about both reward and action.

Lesions of the ACC selectively impair the learning of action-outcome associations. Hadland (2003) directly compared reward-guided selection, in which delivery of a juice reward provided information about which action to perform in order to receive a second juice delivery, to stimulus-guided selection, in which a visual cue instructed which action to perform. Lesions to the anterior cingulate disrupted reward-guided but not stimulus-guided selection, suggesting that the anterior cingulate is specifically necessary for the learning of outcome-action, but not stimulus-outcome, relationships.

However, some studies have seemed to contradict this. A single-unit recording study by Luk and Wallis (2013) examined activation during action-outcome (A-O) trials and stimulus-

outcome (S-O) trials. Although they did not find A-O encoding in the ACC, neurons in the ACC were more responsive to action during A-O trials, whereas neurons in the orbitofrontal cortex (OFC) were more responsive to action during S-O trials.

There is evidence that the ACC is capable of calculating the summed value of an action when there are both negative and positive outcomes (Salamon et al., 1994). When rats are given a choice between an arm of a maze with a small reward, and an arm with a larger reward but also an obstacle which they must climb, healthy rats learn to choose the arm with the larger reward. Lesions to the ACC, however, cause rats to revert to choosing the arm with the smaller reward.

Multivoxel Pattern Analysis

For decades, researchers analyzing fMRI data have traditionally used a univariate approach. This technique tests each voxel in the brain independently, asking whether there is a significant difference in activation between two conditions, such as performing a working memory task compared to rest (Friston et al., 1994a).

There is much to be said for this traditional analytic approach. Its relatively simple nature renders it more difficult to misuse, and the plethora of studies using this technique promotes comparability and replicability. Univariate analysis performs well assuming the effect in question is relatively large and unidirectional across a reasonably large region, and proper corrections for multiple comparisons are implemented (Friston et al., 1994b). However, univariate analysis may fail to detect effects that are weak, coded sparsely, or widely distributed across the brain.

An increasingly popular approach to ameliorate these problems is multivariate analysis, or multi-voxel pattern analysis (MVPA). This approach has the advantage of including multiple voxels in a model to probe their joint contributions to a pattern. Thus, MVPA is capable of

detecting widely distributed, fine-grained representations that would be missed by the univariate approach. MVPA, then, is powerful, but lacks specificity (Haynes and Rees 2006, Norman et al., 2006).

While univariate analysis is based upon the classical statistics, MVPA is derived from information theory (Hebart & Baker, 2018). Because MVPA is uniquely designed to detect information of interest, it is well poised to answer questions about the nature of representations in the brain.

FMRI studies of reward and decision-making

Encoding of reward

A number of machine learning analyses have now been performed to address how the brain encodes various reward-related and decision-related parameters. One particularly notable result by Vickery et al. (2011) suggests that reward (win versus loss in a simple game) is decodable from nearly every cortical and subcortical region. The question then becomes not where reward signals are present, but rather, what distinguishes the types of signals found across different regions.

It is not always apparent in standard RL tasks whether a reward-associated signal reflects value directly, or rather a sensory signal which has become associated with value through learning. Kahnt et al. (2010) dissociated sensory information from value information by attaching separate combinations of sensory attributes to the same value. It then becomes possible to decode reward using one stimulus set to train the classifier, and then testing the classifier on an independent set. This experiment revealed sensory-independent reward information in the OFC and vmPFC. When comparing patterns of activity across anticipation and reward receipt, the patterns were found to be similar.

One method to address integration of multiple value signals is to have subjects perform a task in which various stimulus features such as color, shape, etc., all contain value information which then must be integrated to form an overall value signal. Kahnt et al. (2011) used this approach and found that the combined value could be decoded from the vmPFC, whereas the variability of the different stimulus attributes was decodable from dlPFC activation.

Clithero et al. (2009) examined coding of reward information across an intertemporal delay task and a probabilistic RL task. The pattern of activation in posterior superior parietal lobule contained information about which type of task was being performed. They propose that the posterior parietal cortex is an early part of a layered process in the computation of value.

A fundamental question in the neuroscience of decision making is whether there exists a domain-independent value signal, or so-called "common currency". Although this issue remains unresolved, there is preliminary evidence in support. One way to assess the common currency hypothesis is to train a classifier to distinguish between high and low value items in one domain, such as food, and then test its ability to classify high versus low value items from another domain. This feat was successfully accomplished by McNamee et al (2013) and has been successfully replicated by other researchers (Chikazoe et al., 2014; Gross et al., 2014). Reward is decodable from vmPFC/OFC even when reward level is varied within-stimulus and tested across stimulus identity (Howard et al., 2015).

In contrast to the medial portion of the ventral PFC, the lateral PFC may encode specific reward identities (Howard et al., 2015; Howard et al., 2017; McNamee et al., 2013). When reward outcomes were predicted by specific stimuli, the lateral PFC encoded specific stimulus-outcome combinations (Klein-Flugge et al., 2013).

Encoding of decision-making

The OFC and vmPFC are evidently crucial for Pavlovian conditioning and the conversion of specific outcomes to a common value currency. But where might instrumental learning, e.g., specific action-outcome associations, take place? Electrophysiological experiments clearly demonstrate the ability of neurons in the anterior cingulate cortex to represent such action-outcome associations. FMRI studies, however, have been less conclusive.

Mcnamee et al. (2015) examined the encoding of various decision-making variables while subjects underwent a binary decision task. Information about outcome was available in a wide range of areas, including vmPFC, OFC, dlPFC, and the caudate. Only the dlPFC was found to encode information about action and outcome at time of stimulus presentation, consistent with its hypothesized role in goal-directed behavior. The lateral putamen and supplementary motor cortex contained information only about action and not outcome, affirming a role in habitual (outcome-independent) behavior. Intriguingly, integrated stimulus-action representations were found in the caudate nucleus and hippocampus, suggesting a possible function interplay between these two disparate memory systems.

A somewhat different approach was taken by Fitzgerald et al. (2012), who used Multivariate Bayes Analysis to probe action-specific value signals. Subjects underwent a binary decision task, where they made a right or left button press in response to stimuli that each had independent reward probabilities associated with each response. Action-specific value, then, was defined as the difference in values of the two responses: $AV = Q_R - Q_L$. The ventromedial prefrontal cortex and putamen contained action-specific value representations, as well as the thalamus and hippocampus. This finding is in partial agreement with McNamee et al. (2015).

While prior studies focused on relatively simple action-outcome associations, Wisniewski et al. (2015) used MVPA to decode associations between different cognitive tasks and outcomes.

In the experiment, subjects switched between a magnitude and parity judgement (A) and received either a small or large reward as outcome (O). While task-specific (A) activation was found in inferior parietal cortex and premotor cortex, specific task-reward (A-O) associations were found only in inferior parietal cortex.

How can we make sense of these conflicting findings? One important distinction to make is that electrophysiology can detect signals from individual neurons, where fMRI cannot. Even the smallest level of spatial resolution, the voxel, contains the summed activity of millions of neurons. If the coding of action-outcome representations is sparse, or heterogenous, it will not be detectable with fMRI. Another important distinction is the differences across experimental paradigms, which varyingly compare relatively simple actions or complex tasks. Mcnamee et al. (2015) compared two distinctly separate actions, a trackball roll versus a double button press, whereas Fitzgerald et al. (2012) compared a right and left button press, and Wisniewski et al. (2015) compared two completely different numerical judgement tasks that utilized the same responses. We can infer, then, that the parietal cortex may preferentially distinguish anticipation of a task, whereas the dlPFC may be more directly involved in learning about outcomes of specific motor behaviors. It seems likely that neurons in the dACC do contain information about A-O associations; but it may be the case that the number of neurons containing this information is so few as to be indetectable with fMRI.

The current study sought to compare and contrast how the brain encodes associations between motor responses and rewards, and higher-level tasks and rewards, using combinations of tasks, motor responses, and rewards. Findings from fMRI suggest that action-outcome associations may be encoded in different regions depending on the nature of the action or task. Previous electrophysiological findings suggest that task-outcome associations may be reflected

by activation in posterior parietal cortex. The dorsolateral prefrontal cortex, in contrast, may encode associations between reward or outcomes and simple motor responses.

METHODS

FMRI data was collected from subjects undergoing random combinations of two tasks (emotional judgement and spatial judgement) and two levels of outcome (high reward and low reward). Each trial included two abstract symbols informing subjects as to which task would pay out a large reward or a small reward, followed by a delay. Following this delay, subjects were presented with a picture of a human and judged the picture as either happy or sad (emotional task) or as having long or short hair (spatial task) using either a right or left button press.

Previous literature suggests that reward should be associated with activation in a wide range of regions, including ventral striatum, vmPFC/OFC, and dACC. Response, or which finger is pressed, should activate regions including the caudate, dlPFC, and motor and premotor cortex. Activation during the spatial task should include more parietal activation compared to the emotion task.

I expected to find the combination of task and reward to be associated with different patterns of activation in the parietal cortex. This would have interesting implications for the nature of information processing and potentially suggest that the parietal cortex maintains a stable higher order task set which is then conveyed to the dlPFC to generate motor output.

Participants

Ten subjects took part in the experiment. Exclusion criteria included any psychiatric or neurological illness, as well as vision deficits. I obtained written consent from all subjects in accordance with the Colorado State University and South China Normal University Institutional

Review Board. Participants were compensated 100 RMB (approximately $15) for their time as well as additional money they earned from correct task performance.

Experimental paradigm

The task was created using Psychopy (Peirce, 2007). Stimuli were presented on a grey background using an Asus monitor.

During each trial, subjects saw a picture of a person and judged the picture as either happy or sad, or as having long or short hair using the left and right arrow keys (or buttons while inside the scanner). Stimuli consisted of forty stock photos of humans taken from the Park Aging Mind Lab database (Minear & Park, 2004). Abstract symbols presented at the beginning of the trial informed subjects as to which task would give them a high level of reward (30 RMB bonus) or a low level of reward (5 RMB bonus). Subjects received instructions to try and learn the meanings of the abstract symbols. To encourage accurate performance, subjects were informed that one trial would be randomly selected at the end of the experiment and paid out in real cash.

Each trial began with two abstract symbols (mapping symbols) presented above and below the center of the screen for 3 seconds (Figure 1). Each symbol indicated a specific task-reward mapping; one symbol indicated which level of reward task one (happy/sad judgement) was associated with, while the other symbol indicated which level of reward task two (long/short hair judgement) was associated with, with one task being associated with a high level of reward and the other being associated with a low level of reward. Two redundant sets of visual cues were used for the abstract symbols which represented exactly the same mappings. In twenty percent of trials the mapping symbols indicated that both tasks would give the same level of reward, or that only one task would give a reward. These trials were not included in the analysis. This technique has been used previously in order to encourage participants to learn and attend to

the individual mappings of each symbol (Wisniewski et al., 2015). The position of the two symbols (top or bottom) was counter-balanced across trials. Other variables, including task, mapping, cue set, picture, and the correct response (left or right arrow key) were fully randomized. Following presentation of these cues was a delay of 4 seconds (Delay 1) during which a fixation cross was presented. The four second delay ensured that subjects could not prepare for a specific task during the first portion of the trial. The portion of the trial beginning at the start of the trial until the end of Delay 1 will be referred to as the "encoding portion" hereafter.

Following the encoding portion of the trial, a message appeared for 1 second indicating which task the subject was to perform. After a second delay (Delay 2) of 500 milliseconds, the stimulus was presented, and subjects performed the specified task (happy/sad or long/short hair). Subjects had 1.4 seconds to respond. The portion of the trial beginning when the task message was displayed and lasting until the subject's response will be referred to as the "task portion" of the trial. Following a delay of 2 seconds (Delay 3), a feedback/reward screen was displayed for 500 milliseconds. If the correct response was made, the screen displayed a message informing them they were correct, as well as the amount of money earned (in green font for high reward and yellow font for low reward). If an incorrect response was made, the screen displayed "Wrong…" in red font. If no response was made, the screen displayed "Time's up!" in magenta font. The feedback screen was followed by a jittered intertrial interval (ITI) of between 1 and 5 seconds. The four-second delay between cue and task, as well the extensive intertrial interval, ensured adequate spacing and separation of BOLD activation at different points in the trial (Zeithamova et al., 2017). Subjects performed eight blocks in the scanner with 30 trials per block.

Pre-training

Prior to scanning, subjects performed pre-training to familiarize themselves with the tasks and symbols. Pre-training began with ten trials in which only the task was performed, without the symbol encoding or delay phases. The symbols were then shown to the subject along with their meanings (emotional task will give high reward, etc.). Subjects were tested on the meaning of each symbol until they reached 90 percent accuracy. Subjects then performed the complete task with symbols, delays, emotional or spatial judgement, and feedback, ten times. This whole routine, beginning after the presentation of the symbols, was repeated three times.

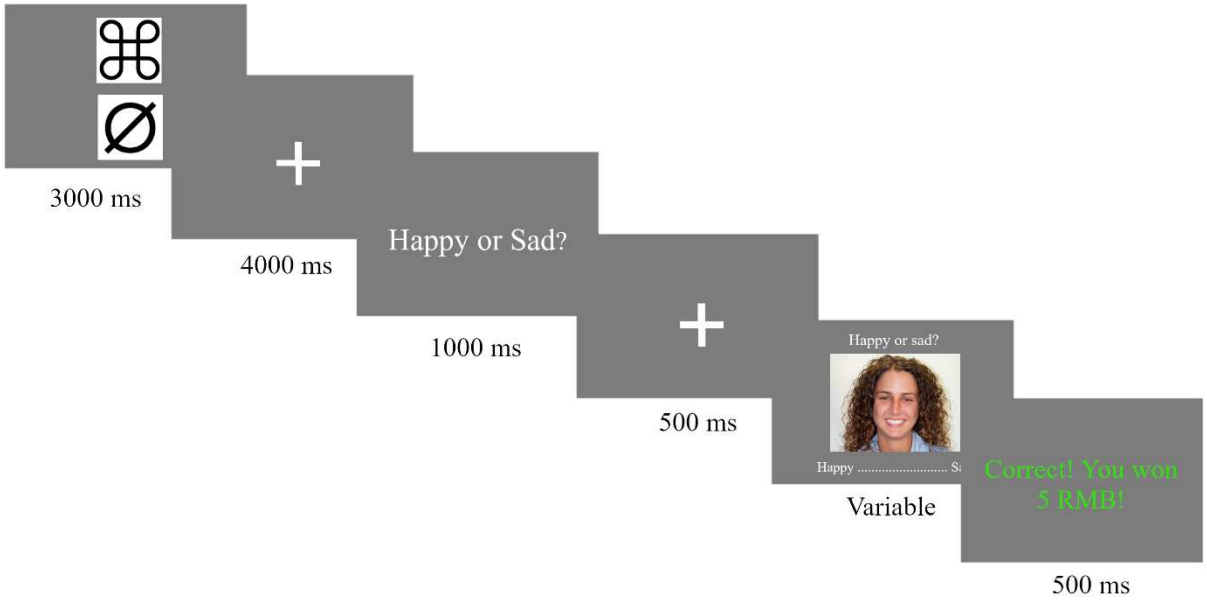

Figure 1. Order of events in a given trial. Subjects were presented with two symbols for 3 seconds, each one indicating the amount of reward to be earned for one of two tasks. After a delay of 4 seconds, a message indicating which task was to be performed appeared for 1 second. After a second delay of 500 ms, subjects were shown a photo and had 1.4 seconds to respond. After a final delay of 2 seconds, subjects received feedback for 500 ms.

Data was collected at the Brain Imaging Center at South China Normal University using a 3.0 Tesla MRI scanner (Siemens) with a 12-channel head coil. A T_1-weighted magnetization-prepared rapid gradient echo sequence was used to collect high-resolution anatomical images for

spatial normalization and localization (TR = 2530 ms; TE = 2.27 ms; flip angle = 7°; FOV = 256mm x 256mm; slice thickness = 1.0 mm; voxel size = 1.0 mm x 1.0 mm x 1.0 mm). A T_2*-weighted two-dimensional echoplanar sequence was used to record functional images (time repetition, TR = 1500 ms; echo time, TE = 30 ms; flip angle = 90°; 42 slices; field of view [FOV] = 192 mm x 192 mm; slice thickness = 3 mm; voxel size = 3.0 x 3.0 x 3.0 mm^3). For each participant, eight functional runs were performed. Each run lasted approximately six minutes and resulted in approximately 200 whole-brain volumes. The first three volumes were discarded from all functional runs.

Analysis

Preprocessing

All fMRI data was pre-processed using the Statistical Parametric Mapping toolbox in Matlab. Functional data was re-aligned to the first volume, slice-time corrected, co-registered to the anatomical image, smoothed, and un-warped using field maps. Low-frequency components (128 s) were removed, and the data was corrected for serial auto-correlations. The first three volumes of each run were discarded.

General Linear Model

Each subject's pre-processed functional MRI data was entered into a GLM using a canonical hemodynamic response (HRF) function. Regressors included the following: Response (Right or Left), a 500-ms regressor specifying right or left hand button press that began at the time of response, Task (Happy/Sad or Long/Short), a 500-ms regressor beginning at the task onset specifying which task was performed (long/short hair judgement or happy/sad judgement), Reward (High versus Low), a 500-ms regressor beginning at presentation of reward specifying

whether a high or low reward was received, and Reward (Reward versus no Reward), a 500-ms regressor beginning at presentation of reward specifying whether or not a reward was received.

These regressors were modeled at the single-subject level before being passed on to the group level, resulting in the following contrasts: Response (Left versus Right), Response (Right versus Left), Task (Happy/Sad versus Long/Short), Task (Long/Short versus Happy/Sad), Reward (High versus Low), Reward (Low versus High), Reward (Reward versus No Reward), and Reward (No Reward versus Reward). Results are presented at a threshold of $p < 0.001$, uncorrected.

ANOVA

Two two-way ANOVAs were performed. The first ANOVA examined the independent effects and interaction between Response and Reward, at the time of receipt of reward. The second ANOVA examined the independent effects and interaction between Task and Reward, also at the time of reward.

RESULTS

Behavioral Results

Subjects achieved a high level of performance. Overall accuracy was 0.82; the proportion of misses was 0.12 and the proportion of incorrect trials was 0.07. The average reaction time was 1.09 ± 0.13 seconds. T-tests of reaction time and accuracy revealed no significant differences across tasks.

FMRI results

General Linear Model (GLM)

The following T-contrasts were created: Response (left versus right and right versus left, modelled at time of response for 500 ms), Task (emotion task versus spatial task and spatial task versus emotion task, modelled at task onset for 1 second), Reward (High versus low and low versus high, modelled at time of reward for 500 ms), and Reward (Any reward versus no reward and no reward versus any reward, modelled at time of reward for 500 ms). Due to the low sample size and preliminary nature of the results, all findings are reported at a threshold of $p < .001$, uncorrected.

A small cluster of activation in the midbrain was found when comparing left-handed to right-handed responses (Fig. 2). Right-handed compared to left-handed responses, by contrast, were associated with activation in the mid-prefrontal cortex.

A contrast of performance of the spatial task versus the emotion task yielded several clusters in the ventral occipital cortex and in the mid-prefrontal cortex (Fig. 3). The reverse contrast, emotion task versus spatial task, resulted in a cluster of activation in posterior parietal cortex and lateral prefrontal cortex.

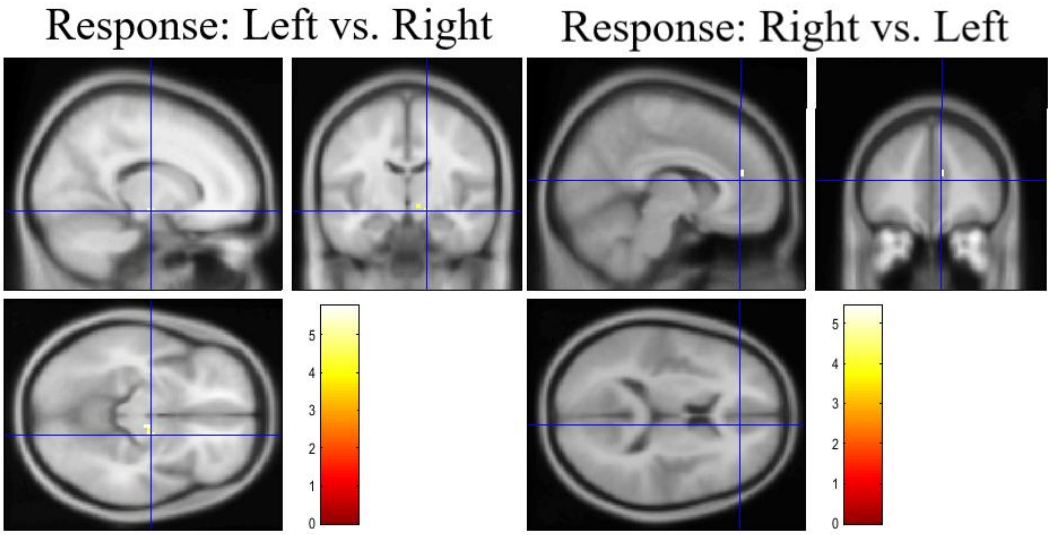

Figure 2: Comparison of trials in which subjects responded with left hand versus right hand (left), and right hand versus left hand (right), at time of response. P < .001, uncorrected

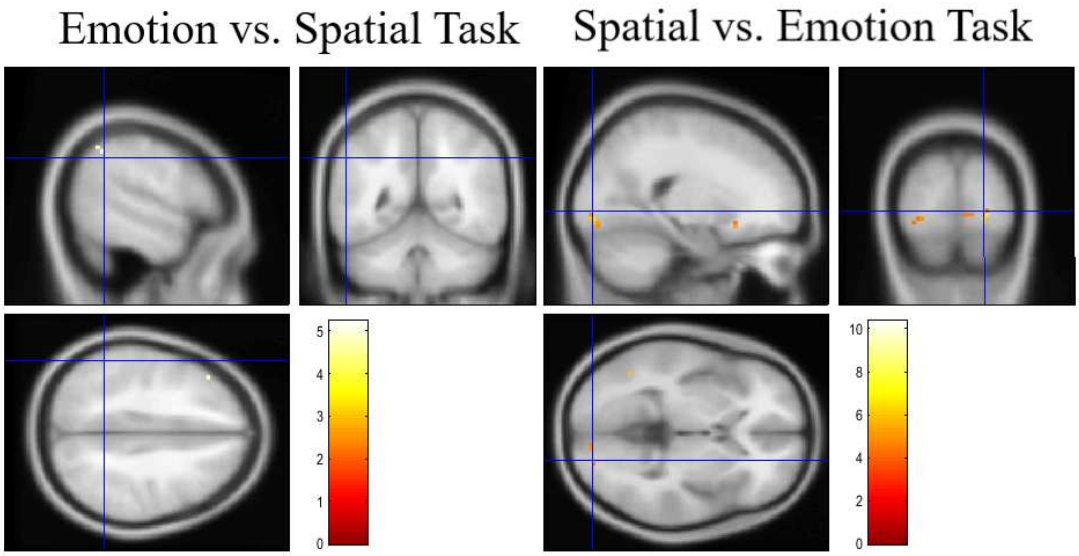

Figure 3: Activation for emotion task versus spatial task (left) and spatial task versus emotion task (right) at time of task performance. P < .001, uncorrected.

Receiving a large reward compared to a small reward was associated with activation in the auditory cortex and primary somatosensory cortex (Fig. 4). A low reward, on the other hand, was accompanied by activation in the anterior cingulate cortex.

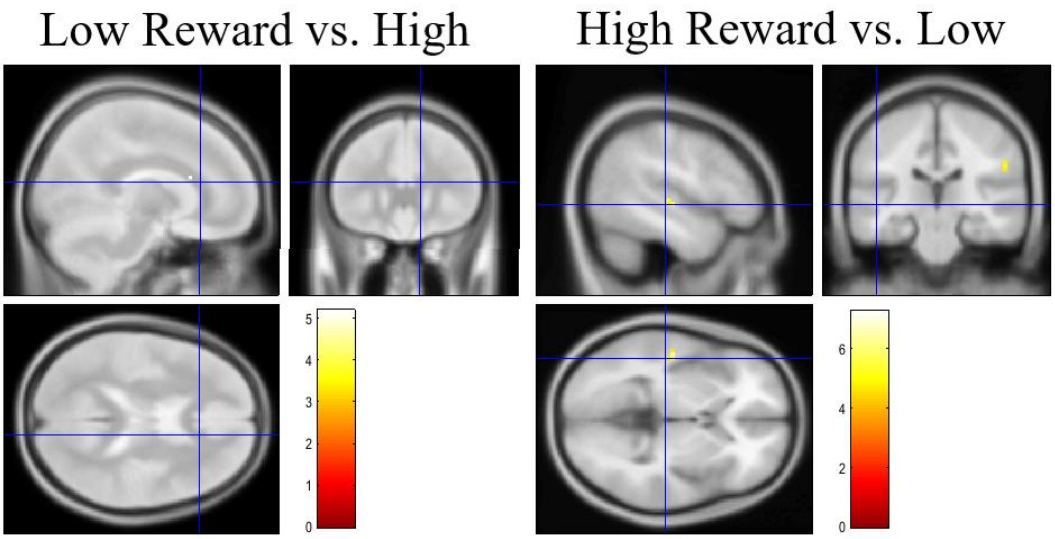

Figure 4: Comparison of high reward and low reward trials, made at time of feedback. P < .001,

A comparison of trials for which any reward was received versus trials in which no reward was received revealed a cluster in the dorsal prefrontal cortex (Figure 5).

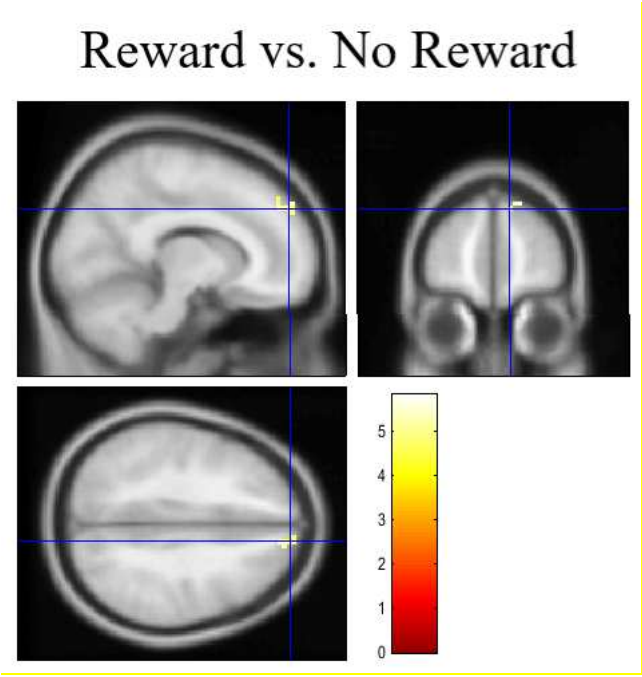

Figure 5: Comparison of trials in which subjects received reward versus trials in which subjects received no reward, made at time of feedback. P < .001, uncorrected.

Analysis of Variance (ANOVA)

Two separate ANOVAs were performed to examine the interactions between Response and Reward and Task and Reward, respectively. ANOVAs were modeled at the time of reward, and used response and reward and task and reward, respectively.

The first ANOVA revealed a main effect of response in the precuneus, cuneus, cerebellum, and other clusters along the medial wall of the occipital and parietal lobes (Figure 6). Neurons near the somatosensory cortex and also within the insula appeared sensitive to the main effect of reward. The interaction between response and reward was associated with differences in activation in the post-central gyrus.

For the second ANOVA, several clusters along the medial surface of the occipital lobe showed a main effect of task (Figure 7). Neurons near the somatosensory cortex and also within the insula appeared sensitive to the main effect of reward. The interaction between task and reward was associated with differences in activation in the ventral occipital cortex and anterior prefrontal cortex.

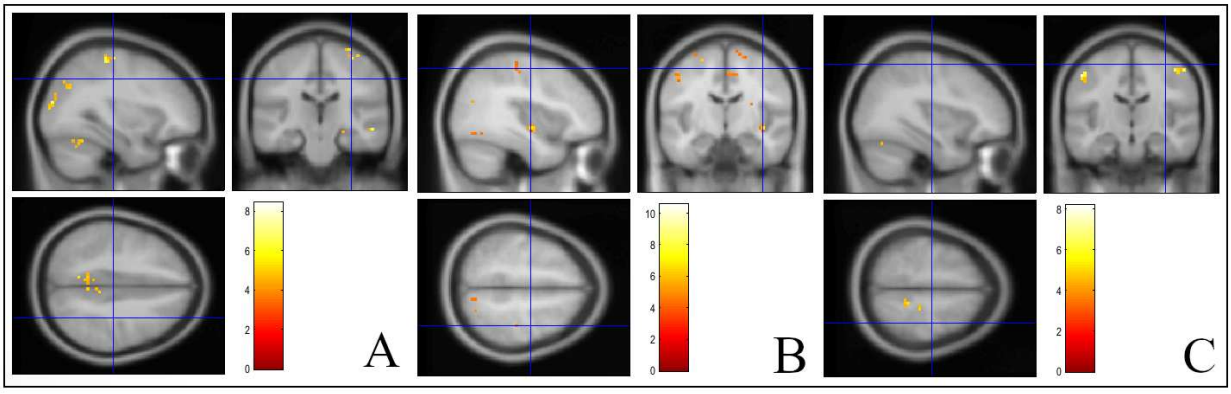

Figure 6: ANOVA of response (right or left) and reward (high or low) at time of reward. Main effect of response (A), reward (B), and interaction (

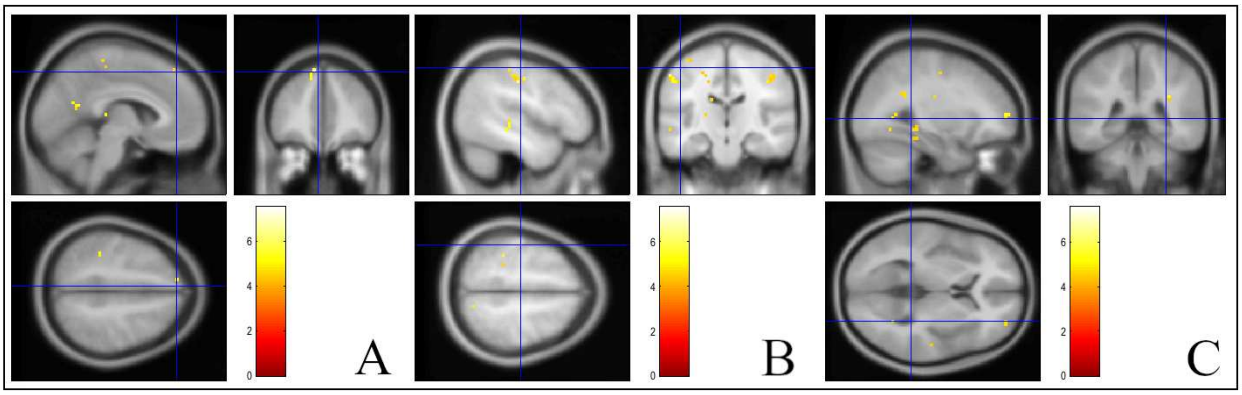

Figure 7: ANOVA of task (emotional or spatial task) and reward (high or low) at time of reward. Main effect of task (A), reward (B), and interaction (C).

DISCUSSION

The aim of this study was to examine how the brain learns associations, both between simple motor responses and outcomes, and more complicated, higher order goals and outcomes. My a priori hypothesis suggested that the dorsolateral prefrontal cortex may encode associations between simple motor responses and outcomes, whereas the posterior parietal cortex plays a larger role in learning associations between higher order information (the task being performed) and outcomes/rewards.

2-way ANOVAS revealed that the interaction between a simple motor response and an outcome was reflected by activity in primary somatosensory cortex. When considering the interaction between a higher order goal (which task is being performed) and an outcome, however, this was reflected by activity in the frontopolar cortex. Although these findings are not in line with the proposed hypothesis, that the posterior parietal cortex plays a key role in learning about higher order variables like the task being performed, they do make sense with what is known about these regions, in particular the frontopolar cortex.

A region in the midbrain was more active for left-handed than right-handed responses. The midbrain is known to contain strong projections to and from motor cortex (Parent & Hazrati, 1995). It is not immediately apparent why a left-handed versus a right-handed response would be associated with stronger activation. If the majority of participants were right-handed, however, it is possible that responding with the non-dominant hand required greater recruitment of neural resources. Prior research has demonstrated that when subjects prepare to respond with their non-dominant hand, activity in the dominant hemisphere is downregulated and activity in the non-

dominant hemisphere is increased (Poole et al., 2018). It is possible that the observed differences function to compensate for shifting to a less-preferred way of responding.

Performance of the spatial task appeared to recruit the occipital cortex. The occipital cortex is well known to play a primary role in visual processing (Brewer et al., 2005; Clarke & Miklossy, 1990). The nature of both tasks was heavily visual since both tasks involved making judgements about photographs. Thus, this finding is sensible given that a spatial judgement would require visual resources. These results could also point to a potential role of the occipital lobe in spatial processing.

Performing an emotional judgement, in contrast, was associated with activation in the posterior parietal cortex. Prior research has implicated the parietal cortex in emotion judgements, with one study using computer-generated faces finding increased recruitment of the inferior parietal lobule for an emotion task versus gender judgement (Sarkheil et al., 2012). In another study, when performing an emotional delayed match-to-sample task, trans-cranial magnetic stimulation (TMS) of the inferior parietal lobule (IPL) specifically improved processing of fearful stimuli (Engelen et al., 2015). Another study which had participants rate their emotions while watching a video of a dance found a correlation between and emotional rating and posterior parietal activation (Grosbras et al., 2012). One potential avenue for future research would be comparing and contrasting activation elicited by different emotions.

Receipt of a small reward versus a larger one was associated with activation in the anterior cingulate cortex. This finding is intriguing given the well-established role of the anterior cingulate cortex in situations requiring cognitive control (Botvinick et al., 2001; Bush et al., 2000). It may be that, because receipt of a smaller reward signals a need to improve performance, the cingulate cortex is either detecting the need to recruit additional resources to

improve performance or is more directly involved in exerting the increased effort. Carefully designed studies are needed that are able to tease apart these differing explanations of anterior cingulate cortex function.

Both the auditory cortex and primary somatosensory cortex appeared to be more active during receipt of a large reward. This finding is somewhat unexpected since other regions such as the basal ganglia and ventromedial prefrontal cortex are more commonly associated with representing reward-related information (Delgado et al., 2005; McClure et al., 2003). Some research has connected reward with somatosensory cortex, however. In a task where subjects discriminated sensory stimuli on index fingers, the corresponding somatosensory cortex was found to "reactivate" at the time of reward delivery in a manner that corresponded with the magnitude of reward (Pleger et al., 2008). This suggests the intriguing possibility that, rather than directly representing reward, somatosensory cortex is encoding salient task features such as motor response, which is then re-activated at time of reward to "link" it with the experienced outcome. Future research should test the replicability of this finding, potentially with different tasks or rewards, to see if these findings persist. If the activation of somatosensory cortex encodes the response being made, it should vary in a predictable manner based on whether the response is, for example, a button-press or a verbal response.

The first ANOVA showed a main effect of response in the precuneus and cuneus. The cuneus and surrounding regions play an important role in visual processing, but also support many higher order cognitive functions such as language and memory (Palejwala et al., 2021). Indeed the precuneus and cuneus seem to form an important part of a general sensorimotor network connecting visual processing with appropriate motor output (Karmonik et al., 2016). Although this is a less common finding, these regions have been shown in the past to be sensitive

to motion (Malouin et al., 2003). Differences in activation have been reported in the cuneus for obese versus healthy-weight individuals during performance of a stop-signal task (Hendrick et al., 2012). The cuneus has also been found to be recruited as part of a sensorimotor network during a 1-back matching task using letters (James & Gauthier, 2006).

The second ANOVA demonstrated a main effect of task in similar regions as the main effect of response in the first ANOVA, namely the medial wall of the occipital lobe including the precuneus and cuneus. This is sensible given that these regions are part of a general sensorimotor network as previously stated. The regions also support linguistic processing, which the judgements of happy or sad or long or short probably recruit to some degree (Palejwala et al., 2021). It would be worthwhile to compare these tasks to tasks that require less linguistic processing to test whether they also recruit these regions.

Interestingly, both ANOVAs showed a main effect of reward in much the same location. Prior research suggests that the main effect of reward should impact activity primarily in midbrain structures such as the basal ganglia and the medial prefrontal cortex (Fields et al., 2007; McClure et al., 2003; Morales & Margolis, 2017). Both ANOVAs in the present study, however, demonstrated a main effect of reward in somatosensory cortex. It is worth noting that this is the same area that was found to be more active for receipt of a large reward versus a small reward (Fig. 4). Some prior research has shown an effect of reward on somatosensory decision making (Pleger et al., 2008; Pleger et al., 2009; Stice, Burger, & Yokum, 2013).

As previously mentioned, one way to explain these findings is that the correct response is being “reactivated” in order to link it with reward. Another possible explanation is that higher rewards provide increased saliency and the resultant increase in attention increases processing in

somatosensory regions. One possible future direction for research could be to test these opposing theories.

The interaction between response and reward affected activation in the post-central gyrus. The post-central gyrus is known to contain somatic representations of the entire body, with cortical excisions in this region interfering with sensation in the corresponding body part (Corkin, 1970). Neuroimaging research confirms the involvement of the postcentral gyrus in the representations of the body (Nelson & Chen, 2008). Thus, it is not surprising that this region would show differences in activation for different motor responses. What is surprising is that this region would be sensitive to the interaction between motor response and reward.

Interestingly, the interaction between task and reward was associated with differences in activation in frontopolar cortex. Although this finding is not congruent with my initial hypothesis, that the parietal cortex is especially involved in the learning of associations between higher order tasks and outcomes, it does make sense in light of the importance of frontopolar cortex to organizing behavior and maintaining higher-order task sets. Indeed, managing competing goals has been postulated to be a critical function of the frontopolar cortex (Mansouri et al., 2017). Damage to the frontopolar cortex impairs multi-tasking (Dreger et al., 2008). The current study provides support for the importance of the frontopolar cortex in managing multiple, competing goals.

There are several important ways in which the current study might be improved. The primary limitation is sample size. The study contained only ten subjects, which is commonly considered insufficient even for simple general linear models. Flaws in several runs for many of the subjects further reduced statistical power. It is entirely possible that different findings would occur given a larger sample size.

Future research could expand on the current findings in a variety of ways. Different tasks could be used to examine the correspondence of action-outcome encoding across tasks, in addition to different motor responses. Similarly, differing rewards, such as food, could be incorporated.

The current study only examined encoding of reward at the time of receipt of reward. An important question is how representations of actions and outcomes change across time, such as during anticipation of reward rather than at the time of delivery of reward. New research should examine encoding of reward, and action-reward associations, not just at the time of reward delivery but at other time points.

A possible avenue for future research might be to have subjects learn symbols which inform them ahead of time which task and which reward they will experience. This would eliminate covariates related directly to motor response or task performance and isolate the key variables of interest.

Another intriguing possibility would be to utilize multivariate methods such as multivoxel pattern analysis. Such methods are inherently suited to the question of action-outcome encoding since this is a question of the relationship between two variables. Future research could utilize models such as support vector machines to examine encoding of tasks, motor responses, and outcomes at any point during the trials.

The present study sought to examine how and where the brain encodes associations between actions and outcomes. The results suggest that the frontopolar cortex may become especially involved when learning to associate higher order goals such as tasks with outcomes. More research is needed to verify this and to elucidate exactly how the frontopolar cortex is involved in learning associations.

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