

Behavioral and Neural Substrates of Decision-Making Under Perceptual and Reward Uncertainty: The Role of Task Structure

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ACADEMIC ABSTRACT

Real world decision-making requires simultaneously determining what we are observing in our environment (perceptual decision-making; PDM) and what the stimuli and actions are worth (reward-based decision-making; RDM). There is evidence of a bi-directional relationship between reward and perceptual information in guiding choice, with some studies suggesting that individuals optimally combine the two. Uncertainty in both reward expectations and perception have been shown to alter choice behavior, however few studies have manipulated both variables simultaneously. Given the distinct theoretical and computational foundations of PDM and RDM, it has also been assumed that the underlying behavioral and neural substrates of perceptual and reward-based choice are separable. However, there is evidence that task structure and subjective value/uncertainty more generally contribute to activity in large-scale networks of the brain, rather than domain specific features (perceptual salience/reward). Variability in task structures and methods of manipulating and modeling sensory and reward uncertainty, make it hard to draw definitive conclusions across these perspectives with currently available data. The current study used behavioral and fMRI techniques to investigate the neurobehavioral substrates of decision-making under simultaneous perceptual and reward uncertainty in a sample of healthy adult volunteers. The primary objectives of this project were to test: a) how simultaneous manipulations in sensory and reward uncertainty influence choice, b) whether task structure alters the influence of sensory and reward information on choice behavior, and c) whether activity in underlying neural substrates reflect domain-specific or domain-general processes. Results showed that choices were best predicted by a combined model of perceptual salience and reward, with an overall bias towards perceptual salience information. Choice percentage was not impacted by task structure, however choices were better predicted by individual features (salience and reward) when they were manipulated stably, than dynamically. Activity in the brain showed greater overlap between dynamic task conditions when compared to both salience and reward conditions. There was also greater overlap between stable task conditions when compared to reward but not salience conditions. Preliminary evidence suggests that activity in decision-relevant regions of the brain varied by uncertainty and value rather than salience and reward per se.

Behavioral and Neural Substrates of Decision-Making Under Perceptual and Reward Uncertainty: The Role of Task Structure

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GENERAL AUDIENCE ABSTRACT

Real world decision-making requires knowing what things in our environment are and knowing what they are worth. Uncertainty about what different options are, can affect the actions we take and the outcomes we expect. Uncertainty about the outcome of our choices or actions can also influence how we attend to or consider options when making choices. We also know that context can affect our behavior. For example, when our environment changes frequently, choices that might have been good in the past, may not necessarily be the best course of action in the future. This can add further confusion about what to do. Across several mental health conditions, we see that problems arise when individuals need to take actions based on incomplete, uncertain, or frequently changing information.

The first goal of this study was to better understand what healthy individuals do when they are faced with different levels of uncertainty around about what different options are (through changes in visual clarity), and what they are worth (through changes in probability of reward). A second goal was to see whether how the frequency at which choice clarity and outcomes change, effects the kinds of choices people make. Third, the study used a measure of brain activity, to determine what the brain is doing which participants make these complex decisions. Results showed that people's choices were best predicted by considering both clarity of the options and their outcome. Having certainty about the identity of the choices was more important than the value of those choices. Also, information about clarity and value of options were more likely to be considered when they were stable, versus when they were changing frequently. Decision-relevant regions of the brain seemed to respond most to overall information about uncertainty and stability of options rather than their clarity or outcome value per se. Future research should test these findings in a larger sample, further explore individual differences in how people respond to various types of uncertainty and determine how knowledge of these individual differences can inform personalized treatment for individuals with related mental health challenges.

Dedication

This dissertation is dedicated to my parents for their tireless struggle as immigrants; for the space they created so that I could have the privilege to discover, learn, and grow instead of surviving.

To Mahyar, with utmost love and admiration, for the endless support and sacrifice. You will always hold space in my heart.

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1 Introduction

1.1 Background

A decision is a choice selected from a series of alternatives (reviewed in Rangel, Camerer, & Montague, 2008). Cognitive neuroscience has traditionally approached decision-making within two separate sub-disciplines, *perceptual decision-making* (PDM), or the process of making decisions about what objects/actions are, and *reward-based decision-making* (RDM), or the process of making decisions based on what objects/actions are worth. In real-world environments, however, actions are often impacted by the association between sensory and outcome information, which can be profoundly influenced by uncertainty in either sensory or outcome domains. In the broader context of decision-making, uncertainty is defined as internal or external noise associated with the decision-process that may alter the validity/reliability of a predicted event. Validity in this context is the probability that a single predicted event (stimulus/outcome) will be correct, while reliability refers to the probability that events (stimulus/outcome) are consistent over time. For example, difficulty determining whether someone's emotional expression depicts anger or focus, a perceptual categorization, will impact subsequent predictions about their response (outcome) if approached (action). In this way, decision-relevant sensory uncertainty can indirectly impact the possible actions we take, and the validity of our expected outcomes. Another real-world example of the interaction between sensory and reward information is observed in studies on medical decision-making. For example, when faced with a noisy ultrasound image, practitioners often rely on their probabilistic knowledge of outcomes associated with other known attributes, such as age or BMI, to diagnose conditions like carotid artery stenosis (Hunink, Weinstein, Wittenberg, Drummond, Pilskin, Wong et al., 2014). This strategy, however, biases medical professionals to over-detect the condition in ultrasounds from higher-risk populations, while under-detecting in others (Hunink et al., 2014). As such, seemingly sub-optimal type I and type II errors in noisy perceptual categorizations, may be systematically influenced by prior experience and knowledge about associated outcomes. While these real-world examples suggest a bi-directional relationship between sensory and reward information in decision-making the separation of PDM and RDM has led to variability in the theoretical

frameworks, task designs, and computational approaches used to study decision-making across these two domains (reviewed in Gold & Shadlen, 2007; Rangel, Camerer, & Montague, 2008; Summerfield & Tsetsos, 2012). For example, RDM tasks typically make sensory information known and certain, varying only uncertainty associated with outcomes. PDM tasks on the other hand, manipulate sensory noise, but either offer no feedback, or make feedback fixed and certain. No known studies have manipulated sensory and reward uncertainty simultaneously under comparable task conditions. Furthermore, the few studies probing how sensory and reward information bias one another have come up with conflicting findings. For example, some studies show that higher reward associated with noisy sensory stimuli improves perceptual sensitivity (increases percent correct and reduces false alarms) by altering the tuning of neurons in sensory regions. Other findings suggest that the same conditions lead to a lowering of the decision-criterion, or an a-priori bias (higher percent correct and higher false alarms), which has been associated with pre-stimulus activity in higher-level decision-relevant regions such as the lateral intraparietal area (IPL) (Summerfield & Koechlin, 2010; Mulder et al., 2012; Whiteley & Sahani, 2008; Feng et al., 2009).

As a first step towards addressing some of the gaps in literature, the current study aimed to develop and use two versions of a combined probabilistic choice and noisy target search task to:

- a. Test whether choices are driven primarily by sensory, reward, or combined sources of information and whether task structure impacts this process
- b. Test the extent to which sensory and reward information uniquely or more generally contribute to the choice process at behavioral and neural levels
- c. To explore the utility of these tasks in potentially identifying individual differences in weighting sensory, reward, or task features.

1.2 Uncertainty in Decision Making

1.2.1 Perceptual Decision Making

In PDM tasks, speed and accuracy are used as metrics of optimal performance, and the degree of perceptual uncertainty is shown to modulate the trade-off between speed and accuracy in perceptual judgements (Summerfield & Tsetsos, 2012). In speeded PDM tasks,

higher perceptual uncertainty results in reduced accuracy (Fitts & Petersen, 1964; Harris & Wolpert, 1998). In free-response PDM tasks, higher perceptual uncertainty leads to longer reaction times, but maintains accuracy performance. This trade-off brings to light the importance of motivational context on perception. A decision-theoretic approach incorporates motivational aspects into the perceptual inference vis-à-vis a cost function that gives the distribution of costs and benefits for each outcome (e.g. speed vs. accuracy). If task demands emphasize accuracy, the overall value of speed reduces relative to the value of accuracy, leading to an expected utility (EU) that biases decisions towards longer deliberation to maximize accuracy. The opposite is true when speed is a condition for optimal performance (van Veen et al., 2008; Shadlen et al., 2006; Wenzlaff et al., 2011). Additionally, unbalanced rewards assigned to one perceptual judgment over another, can also bias perceptual judgments by assigning greater EU to the identification/discrimination of some features/categories over others (Gao et al., 2011; Rorie et al., 2009, Chen et al., 2015). For example, when foraging for food in a busy environment, animals are biased by the colors that are more frequently attributable to “ripe” fruit and can easily detect them due to their inherent caloric benefit over unripe fruits (Zhang et al., 2012). Similarly, a soccer referee unsure about whether to call an offside, may alter his/her decision based on whether the team under question is the guest team or the home team. The influence of outcomes on the perceptual process is subject to debate. Some suggest that a-priori knowledge about different reward associations is incorporated as top-down modulation of the rate at which sensory information accumulates in decision-relevant areas, modulating sensitivity and improving accuracy. Others show evidence that unbalanced rewards or different motivational contexts can alter the starting point of evidence accumulation by biasing the tuning of sensory neurons, increasing accurate detections, especially under shorter time constraints (Gao, Tortell, McClelland, 2011). A third possibility is that unbalanced rewards move the threshold at which a decision is made between options, requiring less information prior to executing choice. This can potentially lead to greater false alarms and errors (Summerfield & de Lange, 2014).

1.2.2 Reward-Based Decision Making

In RDM, sensory information is typically assumed to be known and certain, and the primary source of uncertainty is rooted in the probability of obtaining a specific

outcome given the decision made and the value of that outcome. Much like the motivational influence of perceptual costs and benefits, decision-theory assumes that individuals take actions that maximize utility (Gold and Shadlen, 2007). Uncertainty about the value or probability of an outcome is incorporated into the loss function and is assumed to be used by the brain to compare the value of certain actions over others. Much like PDM, changes to value and sources of uncertainty in RDM can be due to internal or external factors. For example, internal physiological states, such as satiety, can reduce the value of active foraging. However, unexpected changes in the external environment can also influence behavior. For example, changes to the climate that alter the probability that food will be available in the future, may increase exploration or consummatory behaviors, even when the animal is sated. Additionally, the amount of experience with a particular stimulus, or the strength of the learned/known association between a stimulus and outcome, influenced by learning and memory processes, can also alter the degree of outcome uncertainty, choice utility, and resulting action.

Unfortunately given the relatively limited literature on the interaction and integration of perceptual inferences and probabilistic reward, there are few standard methods for how reward and perceptual information should be integrated. One possibility is that all a-priori information about reward probabilities could bias prior probabilities in the form of a top-down signal to sensory or motor regions that shifts the starting point of sensory information accumulation (Ratcliff & McKoon, 2008; Mulder et al., 2012). If reward is manipulated stably and cued early in the task, it is possible that different individuals would weight this “past” information differently as time goes on, especially as other features of the environment are rapidly changing, impacting the degree to which this prior information affects newly observed information over time. Sequential sampling models of PDM (e.g. drift diffusion models), have successfully shown that especially early in the decision process (and consistent with a speeded choice context), a bias at the starting point of evidence accumulation can lead individuals to make fast but incorrect choices based on what they expected would be presented (Summerfield & de Lange, 2014).

1.2.3 Relevance of Task Structure in Decision-Making Under Uncertainty

Several forms of uncertainty have been proposed in the literature, with a large portion of the associated work addressing these forms of uncertainty in RDM (review in

Bland & Schaefer, 2012). Here, the focus will be on two general forms of uncertainty related to the instructed or known validity and reliability of stimulus-action-outcome (SAO) associations. While often used interchangeably outside of a statistical context, validity and reliability can be dissociated based on their different implications for choice behavior and underlying neural mechanisms. Validity is strictly defined here as the instructed/learned probability that an individual's prediction about a single action will be correct (Bland & Schaefer, 2012). In PDM this is manipulated by altering the signal to noise ratio of stimuli, making it hard to discriminate whether a signal is present or absent (Low validity). When there is greater noise relative to signal, the individual is more certain that the correct response is "signal absent" (high validity for hypothesis 1). On the other hand, if there is a greater percentage of signal, then the individual is more certain that the correct response is "signal present" (high validity for hypothesis 2). However, when signal and noise percentages are equal, the individual will have trouble determining whether signal is present or absent. Similarly, if there is competition between other stimuli that have similar features, then it may be difficult to quickly discriminate between them. In RDM, reward probabilities serve a similar function. High probability of obtaining a preferred reward, corresponds to high validity for the expectation that a preferred reward will be delivered. When there's a low probability of obtaining a preferred reward and therefore high probability of an undesired outcome, then there is high validity of the expectation that no reward will be delivered. When the probability of preferred and undesired outcomes are equal, then reward validity is low (i.e. risky) (Knutson & Huettel, 2015). Reliability, on the other hand, refers to the stability of the learned or instructed SAO associations, suggesting that information presented in past trials or a-priori is relevant for future events (Yu & Dayan, 2005). In PDM, across trials, this could mean that a particular stimulus category is more likely to appear, or that a target is more likely to appear in a specific location (high reliability). If behaviorally relevant sensory information changes frequently (category, location, etc.), then the location that a target was observed previously should not bias individuals to attend to that location a-priori for future trials, but might if target locations are stable. In RDM, high reliability refers to stable outcome contingencies, while low reliability refers to greater volatility (or frequent changes in stimulus-outcome associations).

Evidence for this distinction comes from several recent studies on associative learning. When the SAO associations were stable (high reliability), estimates of reward rate did not vary greatly with each new trial, such that new evidence did not heavily weight future actions (Behrens et al., 2007). On the other hand, when volatility is high, meaning that SAO associations change frequently, participants weigh new observations more heavily when guiding their future actions, leading to greater exploration of the environment (Behrens et al., 2007; Payzan-LeNestour et al., 2011). Frequent changes to reward contingencies (low reliability), leads to greater unpredictability of future outcomes and actions (Payzan-LeNestour, Dunne, Bossaerts, O'Doherty, 2013; Walton et al., 2010) and necessitates greater attention to more recent feedback in the outcome phase. When stimulus noise or available options change frequently, this same externally guided attention is crucial for appropriate behavioral response, but instead during the decision-phase of the experiment when stimuli are presented (Heekeren et al., 2008). On the other hand, greater environmental stability, stimulus or reward, may result in a higher degree of persistent decision-relevant bias, especially if the other feature is uncertain or uninformative. However, it is not entirely clear that “stability” and “validity” engage different neural systems, given that they both increase the predictability of a future event, and reduce the need to engage attentional and sensory systems. It is possible that predictability more broadly is tracked by a particular system. Likewise, it's not clear whether “low reliability/volatility” and “low validity” engage separate neural systems, or whether they more generally engage networks associated with “uncertainty/unpredictability” more broadly. This is especially true since behaviorally, both necessitate greater attentional resources and sensory processing. It is also not clear whether predictable and uncertain sensory events and reward outcomes engage similar systems or not, given that the task phases that are of interest in either case differ.

It is true that the more frequently an event is experienced, the more precise the estimate of data becomes, and the less likely new and unexpected information will impact beliefs. Stable features of the environment increase the reliability of an association, reducing uncertainty about what to expect in the future based on known information or based on observations from the past. For example, the fact that the location of traffic lights and buildings do not change, simplify navigation to and from different places. Once an

association is learned or assumed stable, the exploitation of the “best” option, reflects the perceived value of that option and our confidence in that estimate (Behrens et al., 2007; Payzan-LeNestour et al., 2011). As long as the other features of the environment (e.g. number of options, appearance of stimuli, etc.) are also stable, there is no reason to actively deliberate about which option is best before acting. Instead, individuals rely more strongly on prior beliefs about which option is best (Behrens et al., 2007). This can be further illustrated with a basic coin-tossing experiment, depicted below in Figure 2.

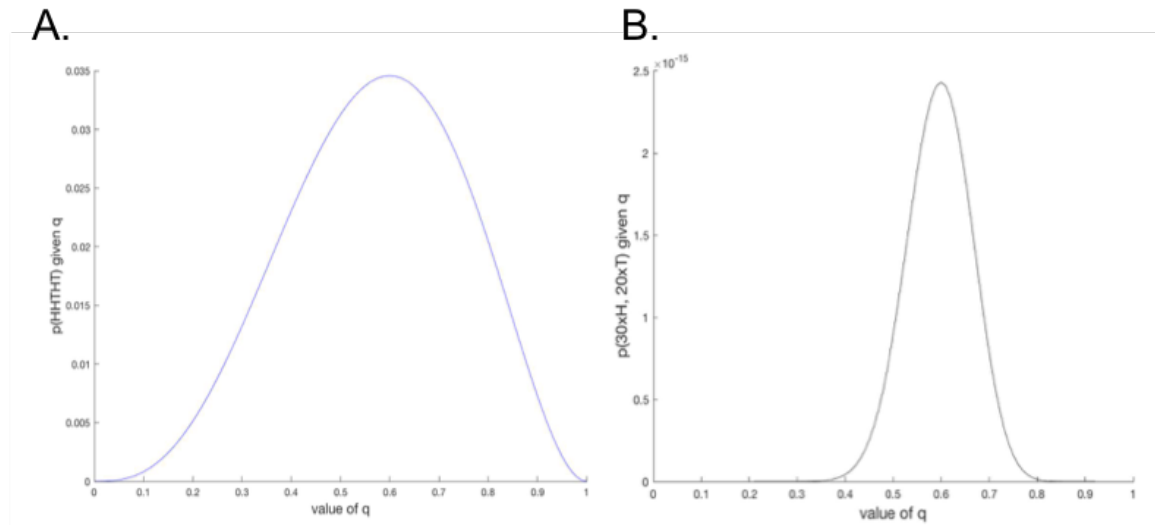


Figure 2. Graphs depicting two hypothetical coin tossing experiments with similar proportions of heads to tails, but with different number of observations.

Panel A shows the likelihood distribution of the observing the data (3 heads and 2 tails) after 5-coin flips, while panel B shows the same but for 30 heads and 20 tails after 50-coin flips. While the maximum likelihood of observing the data is identical in both plots ($q = .6$), the width of the distribution suggests that there is much less uncertainty (greater perceived *reliability*) in this value after 50 observations, than after 5. This also means that for SAO associations that are assumed highly reliable, learning is possible. Furthermore, if the reliability of information is known a-priori, then priors can serve as valid predictors of future events. On the other extreme, if each new observation is different from the previous observation, consistent with a volatile environment (Bland & Schaefer, 2012; Behrens et al., 2007), then the true probability of any single event cannot be estimated and maintains

a uniform distribution across time. In such contexts, the individual cannot rely on past experiences, but must maintain vigilance to capture new, behaviorally relevant information (Yu & Dayan, 2005).

There is also evidence for that brain engages in a similar accumulation process but at a shorter timescale, towards the prediction of stimulus validity. Notably, as opposed to between-trial accumulation of information towards a more stable representation of associations, sequential sampling models originally used in PDM (Busmeyer & Townsend, 1993; Ratcliff et al. 1998; Forstmann, Ratcliff, & Wagenmakers, 2016) and later applied to preference-based choice in RDM (Krajbich et al., 2010; Krajbich et al., 2011; Krajbich et al., 2012), assume that longer within-trial accumulation of sensory information leads to a more reliable estimate of the stimulus category or preferred choice under conditions of uncertainty within a trial. Instead of the frequency of an event increasing its reliability, the length of time spent can also increase reliability, especially when stimuli are noisy or competing in value (Bitzer & Kiebel, 2015; Shimojo et al., 2003). This process is also assumed to engage arousal and visual attention systems (Shimojo et al., 2003; Simon & Shimojo, 2006; Krajbich et al., 2012).

The accumulation of information across these two timescales (within and between trial) hint at the involvement of two separate neural systems for accumulating and representing information when it is relevant for decisions based on currently available SAO information, versus those that are based on prior information for future action planning. This fits nicely within the well-established hierarchical models of cognitive control proposed by Koechlin and colleagues (2003; Koechlin & Summerfield, 2007). Briefly, the proposed model of cognitive control as it relates to prefrontal activity suggests that more dorsolateral/posterior PFC regions are involved in tasks where the current context is necessary for the selection of appropriate behaviors (*contextual control*), whereas more rostral lateral PFC regions are involved in the control of actions that rely on past events (*episodic control*) (Koechlin et al., 2003). Additionally, when prior information biases expectations towards a particular stimulus or category, experimental evidence shows greater activity in extrastriate and anterior temporal lobe regions. Prior expectations towards a particular stimulus category revealed greater backward connectivity from vmPFC/OFC to secondary and association visual cortices, whereas when expectations

about sensory information and observed information diverged, there was greater feedforward connectivity from visual sensory cortices to PFC regions. Finally, when prior expectations and observed sensory information converged, greater activity was observed in regions of the OFC, potentially reinforcing the continued reliability of prior expectations (Summerfield & Koechlin, 2008). On the other hand, the within trial accumulation of information in favor of particular response, has been associated with the firing of neurons in the parietal (lateral intraparietal and posterior parietal cortex) and dorsolateral PFC regions (Gold & Shadlen, 2007; Huk & Shadlen, 2005). A similar model of salience processing and executive control has also been proposed by Menon & Uddin (2010) (See Figure 3). This framework involves the same cortical regions discussed in the context of within trial and across trial accumulation or representation of information but interprets the role of these regions slightly differently. Notably, their model suggests that the anterior insula (aIns) is responsible for detecting salient sensory information (vis-à-vis sensory and limbic inputs), and shares this information with the anterior cingulate (ACC), which then flexibly controls the recruitment of an endogenously mediated network that includes the vmPFC and posterior cingulate cortex (PCC), or an exogenously mediated network that includes the dlPFC and posterior parietal cortex. How these cortical systems fit within the context of PDM and RDM will be discussed further below.

1.3 Neural Substrates Underlying PDM and RDM: Domain Specific or General?

Traditionally, neural substrates underlying PDM have been centered on activity in a fronto-parietal network that includes regions of the intraparietal lobule (IPL), frontal eye fields (FEF; especially for saccadic choice tasks), posterior parietal lobe (PPL), subthalamic nuclei (primarily ventrolateral thalamus), and superior colliculus (SC). In PDM, the accumulation of task-relevant sensory information has been associated with activity in feature or category sensory regions (for example motion-sensitive regions in a motion discrimination task, or face/house selective regions for a face/house discrimination task). Leading up to choice, it is assumed that noisy sensory information is combined into a decision-variable, or a quantitative value that reflects the most likely choice given noisy sensory evidence for each relevant option. This value can be computed in several different ways, based on what the assumed goals of system are (e.g. maximizing accuracy,

minimizing response times, etc.). Activity in dorsolateral prefrontal cortex (DLPFC) and regions of the parietal lobe (intraparietal lobule; IPL and posterior parietal lobe; PPL) is shown to correspond to a computed decision-variable. Several motor and pre-motor regions also show activity consistent with a perceptual DV. It is important to note that most PDM tasks vary sensory information on a trial by trial basis. Based on findings reported from the literature on volatility (or a high probability of a change in SAO associations) is positively associated with activity in the ACC (Behrens et al., 2007), which has been implicated in the flexible control of behavior (Jung et al., 2014). When events change dynamically from trial to trial, making either stimuli or outcomes difficult to predict based on past information, activity is consistently found in regions such as the dorsal ACC, anterior insula (aINS) (Sterzer & Kleinschmidt, 2010). It has been suggested that activity in these two regions are crucial links between salience detection and action flexibility, potentially detecting sources of desired and undesired information in our environments, and tasking the appropriate cortical systems to either evaluate external information further (to reduce uncertainty in the moment), to rely on learned/predictable information based on past experiences or to learn new associations (Menon & Uddin, 2010; Figure 3).

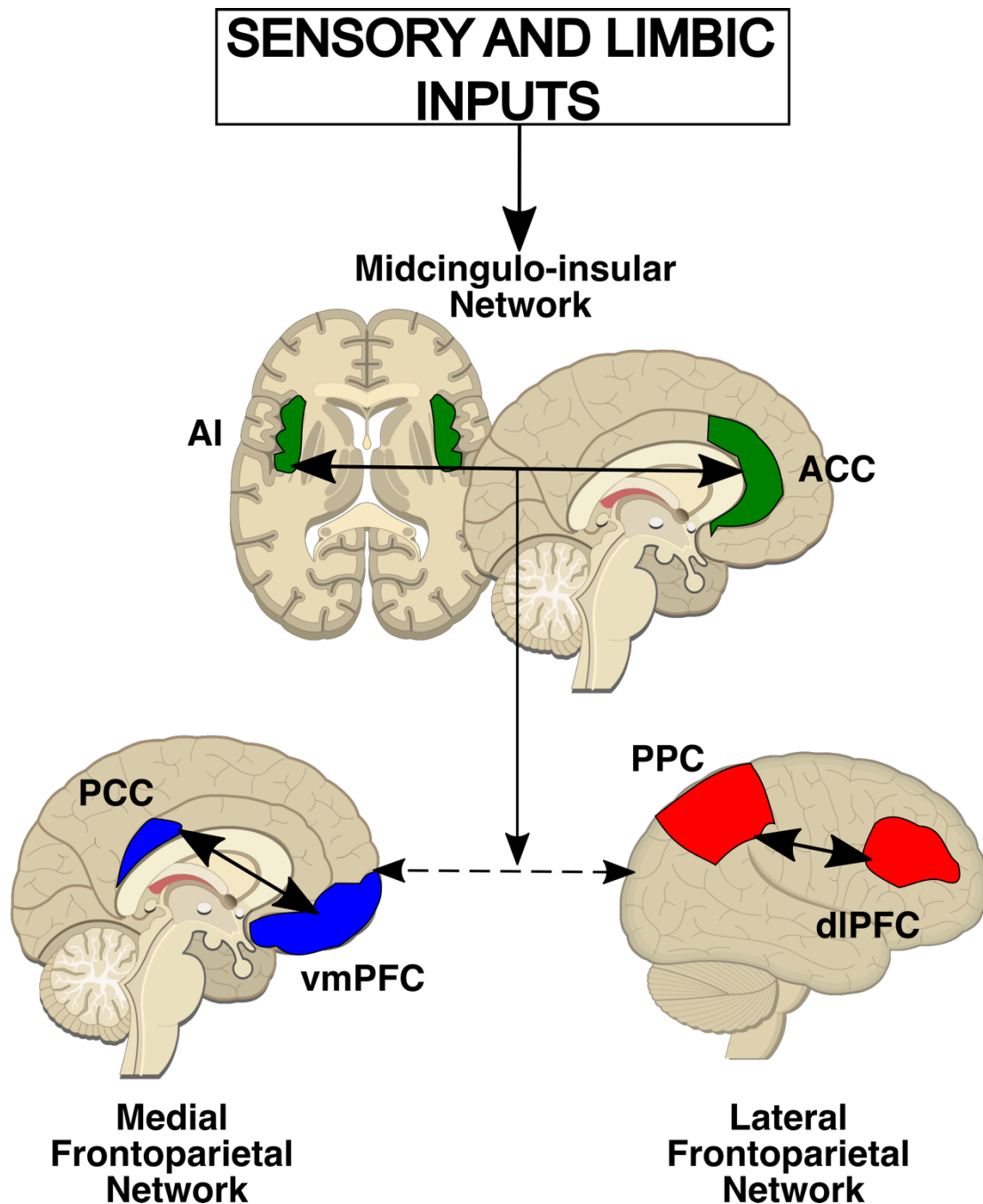


Figure 3. Original figure inspired by Menon & Uddin., 2010 and Uddin, Yeo, Spreng, 2019 depicting conceptual model of large-scale brain networks involved in control of task relevant endogenous and exogenous information. Information entering the brain through sensory and limbic regions are detected by key nodes in the midcingulo-insular network (also referred to as salience network). Based on task demands, this network then signals appropriate control signals to help dynamically switch between engagement of the medial frontoparietal network (mFPN; also referred to as default mode network) and the lateral frontoparietal network (lFPN; also referred to as the central-executive network). The mFPN is involved in processing endogenously held information (prior information, goals, beliefs, etc) while the lFPN is involved in processing exogenously observed information (new stimuli, attentionally demanding task).

In stable settings, where future stimulus or outcome events and associations are predictable, activity in these fronto-parietal regions associated with working memory (Curtis et al., 2010), PDM, and risky RDM is shown to decrease, suggesting that future predictability reduces burden on this system (Davis & Hasson, 2018). Similar patterns have been cited for sensory regions, which show a phenomenon called “repetition suppression” and forms the basis several predictive coding approaches which suggest that activity in the visual cortex and other sensory areas, reflect an estimate of the difference between expectations of sensory input, and actual input (Summerfield et al., 2008). It is currently unclear whether activity in other regions increase as a function of reduced working memory load, or reduced taxation on the fronto-parietal systems. More anterior pre-frontal regions such as the OFC and vmPFC have instead shown a seemingly opposite pattern of activity, where activity in OFC correlates with the probabilities and estimated values of all possible options (like a cognitive map), while activity in vmPFC scales with the estimated value of the chosen stimulus. These values are not specific to just explicit reward stimuli, but activity in the vmPFC seems to represent a stimulus invariant estimate of reward. From an individual differences perspective, reduced activity and connectivity in these anterior PFC regions seem to underlie increased risk-taking behavior, and reduced planning.

Most PDM studies do not look for activity that scales positively with noise or uncertainty because it is often captured in their estimate of signal to noise ratio in detection tasks. They do, instead ask subjects to report on their confidence in judgements. However much like probabilistic rewards, at both ends of the signal-noise distribution, it can be assumed that individuals are correct about their judgement (signal or no signal). Confidence in perceptual judgements, the u-shaped version of the inverse u-shaped risk function, interestingly predicts BOLD activity in value-sensitive regions of the brain including the vmPFC and striatum (Hebart et al., 2015). Alternatively, most RDM choices, which correspond to a quantitative measure of expected reward, have been associated with activity in fronto-striatal circuits, with prefrontal activity observed in more rostral and medial prefrontal regions. However, it’s important to highlight that these tasks often vary reward information stably (to encourage learning), and unlike 2 alternative forced choice tasks (2AFC) often used in PDM, RDM tasks interested in studying ambiguity and risk tend to provide individuals with risky and ambiguous options, but also provide a “safe”

option. In fact, activity associated with picking the safe/low risk option, corresponds to OFC and vmPFC regions.

This suggests that perhaps there is reason to assume that PDM and RDM are in fact distinct processes. There is also evidence that task structures and context readily impact the neural representation of action values in PDM and RDM. For example, when reward is probabilistic, or when there is risk involved (quantitatively defined as the mean-squared variance in expected outcomes), decision-relevant activity is observed in DLPFC and PPL (Huettel et al., 2005; Platt & Huettel, 2008). On the other side, in PDM, a recent study using intracranial EEG recordings and an attentional blink task in humans, showed evidence that conscious perception of a target, in the complete absence of reward, was signaled by activity in the ventral striatum (Slagter, et al., 2017), suggesting a more general role for the striatum that extends beyond its role in reward encoding, such as salience detection or the detection of behaviorally relevant information in the environment. Additionally, in PDM, increased cortico-striatal connectivity contributed to the control of speeded perceptual choices (Forstmann et al., 2008; Forstmann et al, 2010; van Maanen et al., 2016), over tasks that emphasized accuracy. Interestingly, even in the context of learning we see overlaps in the neural substrates of associative learning of stimulus-action-outcome (SAO) associations and multi-attribute perceptual category learning (independent of reward). During learning, corresponding activity has been observed in anterior PFC regions, temporal lobe regions, and pre-supplementary motor (pSMA) activity. Once associations are learned, decision-relevant activity is observed in the dorsal striatum and corresponding SMA, motor, and parietal lobe, regions commonly associated with PDM (Pesaran et al, 2008). These findings, among others, suggest that decision-relevant activity in these large-scale networks may not be unique to perceptual or reward information, but may be sensitive to domain-general changes to other task features that guide attention and motivate action. Several domain-general “dual-process” theories of decision-making and salience processing have been proposed to make sense of what drives activity in these networks, and the corresponding computational or behavioral parameters that underlie such activity (see Sanfey & Chang, 2008 for review).

1.4 Summary

Together, previous findings suggest that at the most general level, there may be two separate decision-relevant networks of the brain, that are also be involved in a wide range of crucial cognitive and affective behaviors (e.g. working memory, attention, cognitive control). While there are several forms of uncertainty proposed in the literature, it appears that increased future predictability vis-à-vis stability and momentary confidence in actions and future events corresponds to activity in anterior and medial PFC and subcortical structures like the striatum. On the other hand, when environments are rapidly changing, and current and future events are uncertain, activity scales with aINS and ACC. As such, differences in the neural substrates of PDM and RDM may not be due to the specific domain in which decisions are being made but may instead be associated with the specific task conditions and behavioral implications (future predictability based on past information versus current information and the degree of convergence between the predictions of these two systems. The current study is the first to systematically study whether activity in decision-relevant regions of the brain and especially within fronto-striatal, fronto-parietal, and moderators ACC/aINS varies as a function of sensory and reward specific information, and/or as a function of long-term (stable) and short-term (dynamic) decision-relevant processes. This is especially an interesting question given findings that sensory and reward information are integrated during choice and brings into question whether the degree of integration varies as a function of how sensory and reward information are changing.

1.5 Aims and Hypotheses

The first aim is to test the hypothesis that sensory and reward information interact and optimally integrate to drive choice behavior. Specifically, consistent with the available literature, it is predicted that choice behavior under simultaneous sensory and reward uncertainty will be best modeled using a combination of sensory and reward information rather than either alone. To test this, the study will use a repeated measures ANOVA to test whether choices vary as a function of perceptual and reward information as well as their interaction. Logistic Classification and Bayesian Model Comparison will also be used to compare three possible models of individual choice behavior. To address how task structure may additionally influence within-domain sensitivity and between-domain interactions, two versions of a combined probabilistic reward and noisy multi-target visual

search task will be used. The first version of the task is almost identical to the task used in Lou et al., 2015. In this version, sensory information is manipulated dynamically from trial to trial, while reward probabilities are manipulated stably (fixed within run, manipulated between runs). The second version of this task is novel to the literature and will manipulate sensory information stably (fixed within run, changed between runs), while varying reward probabilities on a trial-by-trial basis. It is hypothesized that task structure and uncertainty more generally will influence how sensory and reward information are respectively weighted during choice. Specifically, it is predicted that individuals will be most biased by dynamic information when the stable features of the task are uninformative (maximally uncertain), and least influenced by dynamic features when stable features are most certain. independent of the specific domain.

The second aim will be to use task-based fMRI, repeated Measures ANOVA, and conjunction analyses to test the hypothesis that the neural substrates underlying choice behavior reflect domain general processes rather than domain-specific sensory and reward information. Specifically, it is hypothesized that changes in neural activity in decision-relevant regions will correspond to changes in stimulus value (low to high) and uncertainty (low to high), independent of whether that value/uncertainty is specific to sensory or reward information. It is predicted that greater uncertainty will be associated with greater activity in DLPFC, anterior insula, anterior cingulate, and regions of the parietal lobe during decision-phase. It is also predicted that there will be greater overlap between neural representations of stable information and dynamic information compared to overlap between neural representations of sensory and reward-related information between tasks.

The final exploratory aim will be to describe the degree to which these tasks provide insight into individual differences in weighting of sensory/reward information or stable/dynamic task features in the context of decision-making.

2 Methods

2.1 *Participants*

Due to COVID-19-related restrictions, data collection was stopped at the pilot stage. Participants for the pilot fMRI portion of the study included 10 total subjects. Data from 4 subjects were either incomplete or unusable due to data not saving properly. The final sample that completed both fMRI sessions included 6 participants (4 Male, 2 Female), Mean Age: 30.33 years. Experimental and study procedures were approved by the Institutional Review Board of the National Institute of Mental Health. All participants provided informed consent and were recruited from the healthy participant subject pool. Inclusion criteria included right-handedness, normal/corrected to normal vision, no MRI contraindications, and no current mental health diagnoses/neurological conditions. All participants were screened and deemed eligible for participation in fMRI and behavioral experiments based on initial screening criteria specified in the IRB protocol and following physical evaluation by a licensed medical professional at the NIH. Data from this pilot dataset was used to determine full sample size needed.

2.2 *Stimuli*

Face, house and car stimuli were selected from publicly available databases (Max Planck Institute Face Database (Troje & Bühlhoff, 1996), CalTech House Database, Stanford Car Dataset (Krause, Stark, Deng, Fei-Fei, 2013)). 15 images were selected from each category, with a near even proportion of front facing, left facing, and right facing orientations. Each stimulus was separated from its original background, which was replaced with a grey background (comparable to methods used by Lou and colleagues (2015)). Images were 204 x 204 pixels in size, with 8 bits per pixel, and were matched on magnitude spectra, equated for luminance, contrast, and spatial frequency. The weighted mean phase technique (Dakin 2002) was used to manipulate phase spectra. All image pre-processing was completed using the SHINE Toolbox (Willenbockel, Sadr, Fiset, Horne, Gosselin, & Tanaka, 2010) in MATLAB (Mathworks, 64-bit mac version R2016a 9.0.0.341360). Phase spectra manipulation was coded and implemented in MATLAB. Experiments were written in MATLAB using the Psychophysics Toolbox

extensions (PTB-3.0.13; Brainard, 1997; Pelli 1997; Kleiner et al., 2007). Stimuli were presented in the MRI scanner using a projector and mirror.

2.3 Procedures

2.3.1 Task Design

Participants completed two versions of a combined perceptual discrimination and probabilistic reward task, based on similar theoretical and practical designs by Navalpakkam et al. 2010 and Lou et al. 2015. On each trial, participants viewed one house (target), one face (target) and two car images (distractor) presented randomly across four fixed locations (x eccentricity: 3.1 degrees; y eccentricity: 3.1 degrees; image width: 5.5 degrees) around a central fixation (.5 degrees). To test the effect of domain-specific task manipulations, reward uncertainty (RU) was manipulated by altering the probability of receiving either 8¢ or 2¢ for selecting face or house targets (5-levels) and perceptual uncertainty (PU) by altering the phase coherence for face and house targets (5-levels). One minus the probability of High reward (8¢) equals the probability of low reward (2¢) for each target, and high and low reward probabilities are negatively correlated between face and house (e.g. when face has a high probability of 8¢, house has a low probability at ratios $P(8¢|F)/P(8¢|H)$: $\{.25;.5;1;2;4\}$). Similarly, when face is high in phase coherence, house is low and vice versa, with phase coherence percentages (Lou et al., 2015) adding to 81% (Face coherence ($C_f \in \{32\%, 35\%, 38\%, 41\%, 44\%\}$); House coherence ($C_h \in \{49\%, 46\%, 43\%, 40\%, 37\%\}$). Within-target coherence was defined in a linear manner similar to reward probability on a scale of 1-5 (Low Coherence Face/High Coherence House to High Coherence Face/Low Coherence House). Between target uncertainty is lowest at levels 1 and 5 (certainty highest), where face and house respectively are easiest to discriminate from each other. Perceptual uncertainty is assumed highest at level 3, when face and house are of medium coherence but least distinguishable from each other during the brief viewing period. Levels 2 and 4 are medium uncertainty conditions.

In task 1 RU was fixed within run (varied across 5 levels between runs), while (PU) varied across trials. In task 2, PU was fixed within run (varied across 5 levels between runs), and RU varied across trials (Appendix A). These two task designs allow the evaluation of stable and dynamic effects of PU and RU, as well as the interaction between

them. Distractor images (cars) were always of low coherence (35%) and were associated with no reward. Participants were told to make the best choice. A behavior-only version of this task was used for piloting (not described here), and timing was adapted for use with fMRI using AFNI's "make_random_timings.py" in combination with "@stim_analyze" to determine the optimal timing and order of events.

For the fMRI task, before the scanner was triggered, each run started with a self-timed cue instructing participants which RU (task 1) or PU (task 2) run condition they were completing. Each trial began with a fixation cross (initial fixation 9.2 sec), followed by a trial cue informing participants about the PU (task 1) or RU (task 2) condition they were experiencing in the upcoming trial (cue .7 sec). Participants then viewed a stimulus display of four images (stimulus .3 sec) followed by a grey mask (mask 1.3 sec). To earn the reward associated with either target, participants were required to respond with one of the four location choices via corresponding keyboard button press before the mask disappeared (total 1.6 sec). There was a jittered ISI (ISI 2.3-6.9 sec) between decision phase ($\sum$ (cue, stimulus, response) = 2.3 sec) and outcome (Feedback .8 sec), followed by a jittered ITI (ITI 1.5-8.4 sec). Participants were informed that they receive no reward if they did not respond within allotted time and instead viewed feedback that states, "You missed!" Feedback included information about which stimulus the participant selected, and the reward won in that trial only.

In total, participants completed 20 trials x 25 conditions (5 RU x 5 PU) x 2 Tasks for a total of 500 trials per task. For each of the two scanning sessions, trials were presented in 2 mini-blocks of each run-type (5 RU levels in Task 1 and 5 RU levels in task 2), with 25 trials per block, uniformly distributed across the 5 PU (Task 1) and 5 RU (Task 2) levels.

To prevent wealth effects (Osman et al., 2008; Witt et al., 2006) and keep participants from adjusting their choice strategies to optimal, participants did not receive any cumulative feedback about their earnings. Furthermore, to motivate performance, participants received the sum of earnings from 5 randomly selected runs per task, were informed of this at the start of the study, and for this reason were encouraged to try their best in all runs. Participants completed a practice prior to being put into the scanner that included a few trials from each condition

2.3.2 *Data Collection*

Data collection was conducted across two sessions, separated by a minimum of 24 hours and a maximum of two weeks. Participants completed a battery of self-report measures described above. During the first session, participants were provided with task instructions presented in a standardized way using PsychToolbox. Each participant then completed 5 mini-practice runs of 15-trials each (3 of each trial condition per run) for each of the two tasks outside the scanner. In the scanner, participants completed 10 runs of each task (20 total) per session, and 40 runs across both sessions (maximum scanning time per participant, per session is 2.5 hours). There were 10 trials per condition in each run with a total of 20 trials per condition across both scanning sessions. The order of task presentations was counterbalanced within participants (per session) and between participants. The order of the run types for each task were randomized between subjects, while the order of trials was randomized between runs but fixed across subjects. Following each session, participants completed a debriefing questionnaire (Appendix B). Respiration and heart rate were collected when possible, to control for related confounds during fMRI data analysis.

2.3.3 *fMRI Scan Parameters*

fMRI data were collected on a Siemens 3T Prisma scanner (Software Version syngo MR D13D) with a Siemens 32-channel surface coil. A high resolution T1-weighted Magnetization Prepared Rapid Gradient Echo (MPRAGE) sequence was run at the start of each session (TE = 3.3 msec; TR = 2530 ms; flip angle = 7°; matrix size = 256 x 256; voxel size 1 mm x 1 mm x 1 mm; 176 sagittal slices). Functional images were collected using a whole brain simultaneous multi-slice, multi-echo T2-weighted echo-planar sequence (Parameters for each run: TR= 2300 ms; TE₁= 13.6 ms; TE₂= 33.8 ms; TE₃= 54.04 ms; FOV = 224 mm; flip angle = 78°, 2.8 mm isotropic; 390 oblique axial slices across all 3 echos; AP phase encoding direction; in-plane acceleration factor = 2; no multi-band accelerator factor used).

2.4 Analyses

2.4.1 Choice by Reward, Salience, and Task Conditions

The study used a 5 (Salience) x 5 (Reward) x 2 (Task) repeated measures ANOVA to test whether mean percent face choices varied as a function of the main effects and interactions of the independent variables (IVs). Percent face chosen was used as the dependent variable (DV) given that manipulations to the IVs were negatively correlated between face and house. Percent face, house and car choices were computed after eliminating all miss trials. It was hypothesized that higher reward would increase choice of low salience targets and higher salience would increase choice of low reward probability targets.

2.4.2 Behavioral Modeling

The study used Logistic classification to test whether individual subject choices, face/no-face (house or car, misses excluded), were best predicted by one of three models. Model 1 assumes that individuals make decisions based on the salience of the target stimuli, with higher likelihood of choosing the target with greater salience. Model 2 assumes that individuals make decisions based on the reward probability of the target stimuli, favoring the target that has greater probability for high reward versus low reward. Model 3 assumes that individuals make choices using both salience and reward probability of the target stimuli, favoring targets with both high salience and high reward probability most. Each of these three models were trained and tested at the individual subject level, separately for each task, using 5-fold cross validation to avoid overfitting. Given that the combined model had more parameters than the single parameter models, AIC and BIC criterion were used to penalize fit for number of parameters. To compare the combined model to alternative single parameter models, the natural log of the approximated Bayes factor $\ln(\text{BF})$ between two models (Equation 1) was computed. These differences were interpreted using Jeffreys' Scale of Evidence for Bayes Factors (Table 1; Jeffreys, 1961). The combined model was treated as model one and therefore positive values indicated greater evidence in favor of the combined model while negative values suggested greater evidence in favor of the single parameter model.

Equation 1.

$$BF_{M1-M2} = \exp \left(-\frac{1}{2} (BIC_1 - BIC_2) \right)$$

Table 1. Interpretation of Bayes Factor based on Jeffreys' Scale of Evidence

BF_{ij}	lnBF_{ij}	Interpretation
>100	>4.61	Decisive evidence for H _i
30-100	3.40-.61	Very Strong Evidence for H _i
10-30	2.30-3.40	Strong Evidence for H _i
3-10	1.10-2.30	Substantial Evidence for H _i
1-3	0-1.10	Not worth more than a bare mention
1/3-1	-1.10-0	Not worth more than a bare mention
1/10-1/3	-2.30 to -1.10	Substantial Evidence for H _j
1/30-1/10	-3.40 to -2.30	Strong Evidence for H _j
1/100-1/30	-4.61 to -3.40	Very Strong Evidence of H _j
<1/100	<-4.61	Decisive evidence for H _j

To test whether subjects had a bias towards perceptual or reward information, a $\ln(\text{BF})$ comparing salience and reward only models within task (Task 1 Salience – Reward and Task 2 Salience – Reward) was computed. Positive values were indicative of a salience feature bias, while negative values would suggest a reward feature bias. To test whether individuals were biased towards dynamic or stable information, an $\ln(\text{BF})$ was computed, comparing the fit of salience only models (Task 1 Dynamic Salience – Task 2 Stable Salience) and reward only models (Task 2 Dynamic Reward – Task 1 Stable Reward). Positive values in this case would indicate a dynamic feature bias, while negative values would be indicative of a stable feature bias.

2.4.3 fMRI**2.4.3.1 Preprocessing**

MRI data were preprocessed and analyzed using AFNI's `uber_proc.py`. Anatomical images collected at the first session were skull stripped and non-linearly warped to the standard MNI 152 atlas using the `@SSwarper` command in `afni`. Data collected from each of the two sessions were preprocessed and analyzed together. Functional images were concatenated after removing the first 4 TRs from each run. Functional data were then slice time corrected, aligned to anatomy, and anatomy was aligned to standard MNI template.

Data were then registered to the volume with the lowest motion for each run (echo 2 was used to drive registration), and masked. All echoes were then optimally combined for each run, data were blurred at 4 mm FWHM, and each voxel of each run was scaled to a mean of 100 and max of 200 (so that post-analysis results can be interpreted in terms of percent signal change from mean).

2.4.3.2 Analysis

Stimulus times for regressors of interest (cue-stimulus-choice phase for each condition) were convolved against a fixed two-parameter block function lasting the duration of the cue-stimulus-choice phase (2.3 sec with peak height of 1; Block Function = incomplete gamma function convolved with boxcar function). These regressors were included in a general linear model (GLM) for parameter estimation at the first level. Stimulus times for outcome phase were included in the GLM as a single regressor (not separated by condition) to account for associated variance. Motion parameters (demeaned and derivatives) were included as regressors of no interest for each run separately. A motion censoring threshold of .3 was applied.

At the second-level, beta estimates for the choice-phase were included in a 5x5 mixed effects repeated measures ANOVA. It is not expected, based on collected pilot data, that behavior will vary substantially for the same task between sessions. As such, data for each task type was combined between sessions and analyzed separately for each task. Of the 9 subjects who completed the behavioral pilot of the task, only 1 significantly changed their choice percentages between sessions due to self-reported change in strategy. To minimize the chance for order effects or confounds associated with effects of interest, task order was counterbalanced between sessions within and between subjects and run type orders were randomized within each task, session, and between subjects.

In addition to a baseline model with nuisance and motion parameters of no interest, first level regressors included onset times for each condition at the decision-phase of the task, convolved with a double gamma hemodynamic response function. Onset times for outcome were included as a regressor of no interest in the model. The decision phase consisted of the period beginning at trial cue and ending with response (cue, stimulus, response). Voxel-wise beta estimates were acquired for decision > baseline, controlling for outcome for all 25 conditions (5 Salience x 5 Reward) in each task.

First level beta estimates for each task were included in two separate 5x5 mixed repeated measures ANOVAs at the second level, with “subject” included as a random factor. F-maps were used to determine which regions/networks showed activity that varied as a function of the main effects of salience, reward, and their interaction. Due to small sample size, F-maps were thresholded at an uncorrected $p = .05$, with a cluster threshold of 50 voxels (nearest neighbor = faces must touch). Given that subcortical regions are generally smaller than cortical regions, the cluster size was lowered to 5 voxels. It is important to note that these methods leave considerable room for Type 1 error, however given the pilot nature of the fMRI portion, any related findings are conservatively interpreted and only serve as potential areas for future exploration. Power analyses were conducted using t-maps for linear and quadratic salience and reward contrasts of interest (NeuroPowerTools; Durnez et al., 2016). Initial threshold to determine peaks (local maxima) was set to $p = .001$ with a corrected $\alpha = .05$, and desired effect size of .80. Results indicated that a sample size of 30 participants is necessary. To better understand which regions showed activity that varied in a domain specific or domain general way, conjunction maps were computed between Task 1 and Task 2 Main effect and Interaction maps. To test whether overlap was greater between domain general or domain specific features, a difference of proportion was computed using a chi-squared test. This approach was used to compare for proportion of voxels overlapping between stable and dynamic features in both tasks to the proportion of voxels that overlap between salience and reward features in both tasks at selected threshold (Nichols et al, 2005). The conjunction maps and their interpretations are listed below:

- Conjunction of Task 1 and Task 2 Reward Main Effect: regions with reward-specific activity during the decision phase.
- Conjunction Task 1 and 2 Salience Main Effect: Regions with salience-specific activity during the decision phase.
- Conjunction of Task 1 Reward and Task 2 Salience Main Effects: Regions with domain-general activity associated with stable manipulations (not due to salience or reward specifically).

- Conjunction of Task 1 Salience and Task 2 Reward Main Effects: Regions with domain-general activity associated with dynamic manipulations (not due to salience or reward specifically).

To describe the direction and nature of decision phase activity for domain specific or domain general activity, 3 mm spherical seeds were placed at the coordinates (Center of Mass) for decision-relevant regions that overlapped between Task 1 and Task 2 in the interaction, dynamic, or stable conjunction maps. From each ROI, mean percent signal change for each subject was extracted for each condition and averaged across subjects for a group mean. Regions of interest were identified based on key nodes of several large - scale cortical brain networks covered in the introduction. These networks include the dorsal frontoparietal network, lateral frontoparietal network, midcingulo-insular network (includes ventral attention network/central executive network), and medial frontoparietal network (overlaps with the rostro-anterior cortico-basal ganglia network/default mode) (Figure 4; Uddin, Yeo, & Spreng, 2019). To ensure that stimulus specific activity scales with face and house responsive regions, fusiform and parahippocampal gyri regions were also of interest. Regions of the cortical somatosensory and motor networks were not explored.

Large Scale Functional Networks

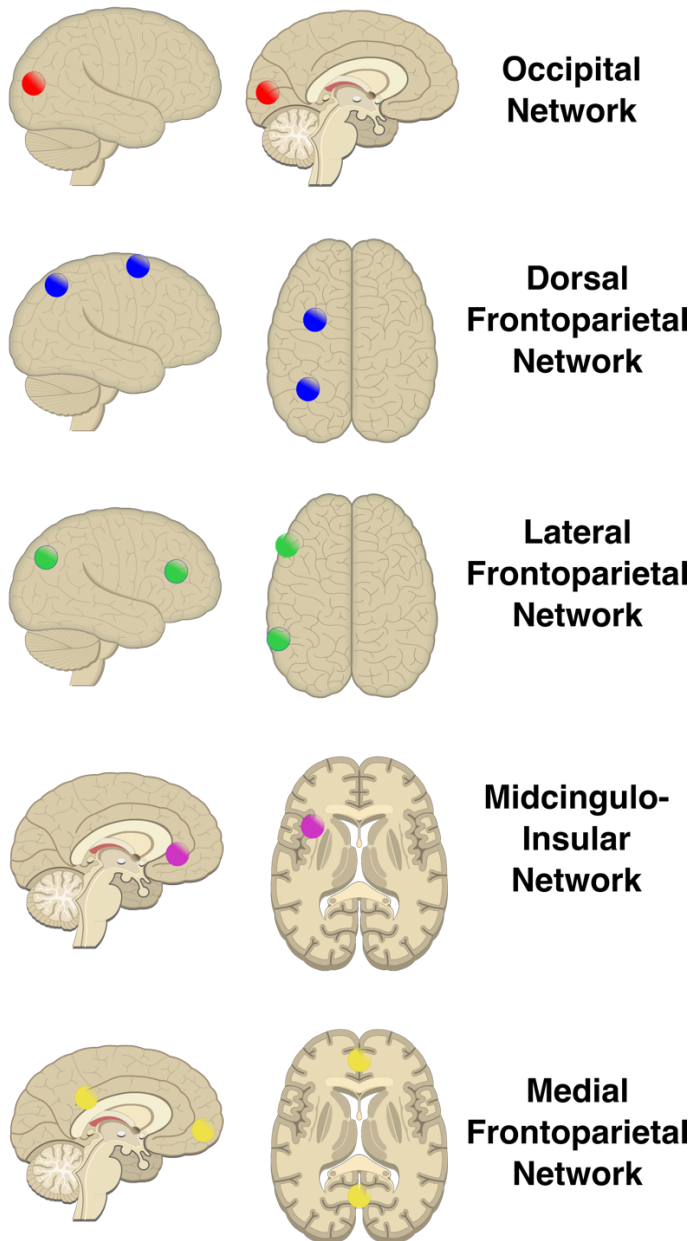


Figure 4. (Original figure based on paper by Uddin et al., 2019) This figure shows key nodes from several large-scale brain networks often cited as relevant to the decision-process.

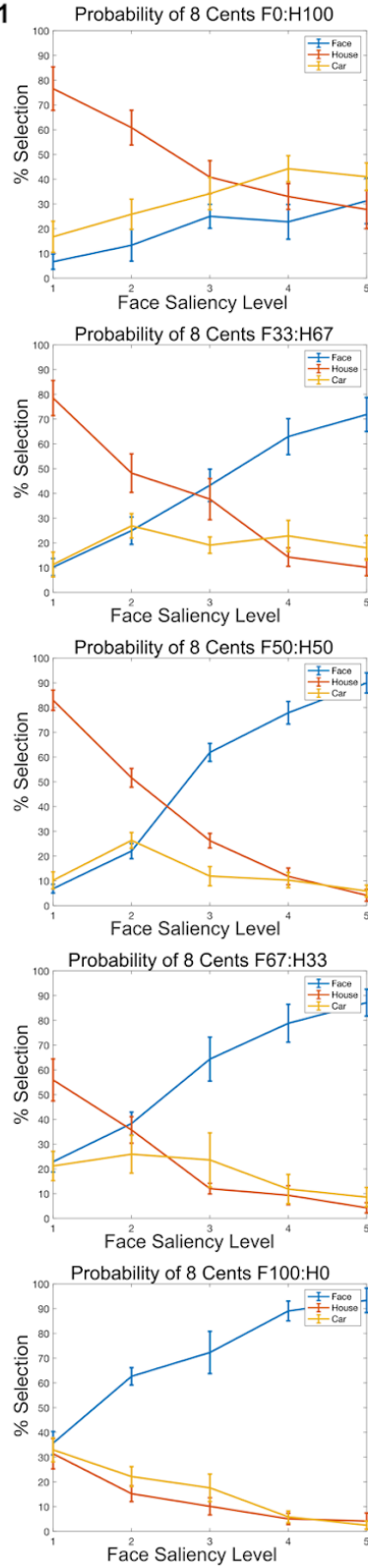
3 Results

3.1 Behavioral Results

3.1.1 Basic Descriptives

Participants were able to complete the task as expected and responded to 98.5% of the trials on average. As expected, overall percent face and house choices were highly and negatively correlated in both tasks (Task 1 Pearson $r = -.871$, $p < .001$; Task 2 Pearson $r = -.862$, $p < .001$). Car choices were relatively higher when reward probability for 8 cents was high for a particular target (face or house) and salience for that target was low (Figure 5). Car choices provided no reward and served as distractors. As such, this finding is likely attributed to participants mistakenly selecting car (due to low target salience) while attempting to select the most rewarding target. This condition is also a high conflict condition, such that reward and salience features are incongruent. This finding is consistent with findings reported by previous studies of combined perceptual and reward-based decision-making (Lou et al, 2015; Navalpakkam et al., 2010; Chen et al., 2013). In both tasks, participants showed a slight perceptual bias towards face such that when reward was equal and salience was high, on average the difference in face-house choices was 15.4% in Task 1 ($t = -2.36$, $p = .065$) and 6.9% in Task 2 ($t = -2.49$, $p = .055$).

Task 1



Task 2

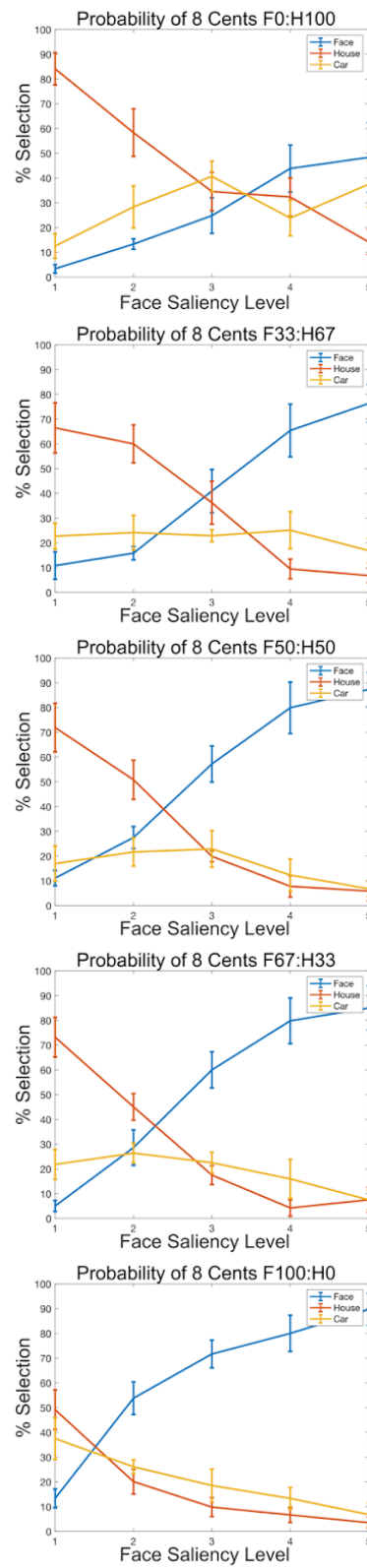


Figure 5. Average percent selection of targets (face and house) and distractor (car) across participants for task 1 (left column) and task 2 (right column). Error bars are standard error.

3.1.2 Repeated Measures ANOVA

Assumptions of sphericity were violated (Epsilon values $< .75$) for all factors and interactions except for the effect of Task. As such, Greenhouse-Geisser corrected tests are reported. There was a significant within-subject main effect of reward level ($F(1.42, 7.120) = 16.025$, $p = .003$, $\eta_p^2 = .762$) and salience level ($F(1.68, 8.42) = 97.96$, $p < .001$, $\eta_p^2 = .951$) on face choice. Percent face chosen increased as a function of increasing face reward and increasing face salience respectively. There was also a reward by salience interaction ($F(2.56, 12.8) = 5.20$, $p = .017$, $\eta_p^2 = .510$) on choice. Face choices increased when salience for face was higher than house and probability of high reward for face $\leq$ house. However, when high reward probability for face $>$ house, percent choice increased significantly only when face salience was lower than house salience. This suggests that high reward target choice increases at low levels of salience and low/uncertain reward targets are chosen more frequently when salience is high. These findings suggest both an integration but also a potential tradeoff between salience and reward features in choice (Figure 6). There was no significant task, reward by task, salience by task, or 3-way reward, salience, task effects (all p s $> .05$).

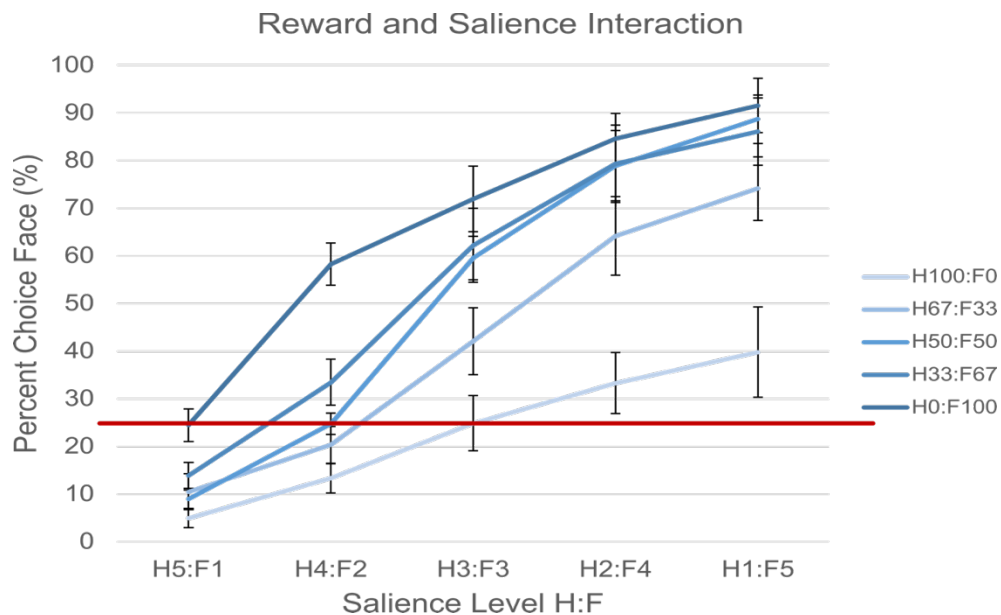


Figure 6. Interaction between salience and reward on percent face choice from ANOVA averaged across both tasks. Lines depict different reward levels and x-axis labels refer to different salience levels.

3.2 Modeling Individual Subject Choice

3.2.1 Comparison of Combined Model to Individual Models

In all subjects, all models were able to classify face/no-face choices greater than chance accuracy (Figure 7). At the group level, using mean BIC values, there was decisive evidence (Jeffreys, 1961) in favor of the combined model over the salience or reward only models for Task 1 ($\ln(\text{BF}_{\text{cs}}) = 43.28$; $\ln(\text{BF}_{\text{cr}}) = 56.31$) and Task 2 ($\ln(\text{BF}_{\text{cs}}) = 25.92$; $\ln(\text{BF}_{\text{cr}}) = 85.52$). This suggests that choices are on average better predicted using a combination of salience and reward information, rather than either alone. At the individual level, for 5/6 subjects, there was decisive evidence in favor of the combined model (Jeffreys, 1961) compared to either individual model for Task 1 ($\ln(\text{BF}_i) > 4.61$). For subject 3, there was substantial evidence in favor of the salience model over the combined model ($\ln(\text{BF}_{\text{cs}}) = -1.64$). For Task 2, there was decisive evidence in favor of the combined model for 4/6 subjects. As in Task 1, for subject 3 showed strong evidence in favor of the salience model over the combined model ($\ln(\text{BF}_{\text{cs}}) = -2.77$) for Task 2. Subject 2 showed similar evidence in favor of the salience and combined models ($\ln(\text{BF}_{\text{cs}}) = -.215$) in Task 2.

3.2.2 Domain Specific Effects: Salience versus Reward Bias

At the group level, there is decisive evidence in favor of the salience only model compared to the reward only model for Task 1 ($\mu \ln(\text{BF}_{\text{SR}}) = 13.03$) and Task 2 ($\mu \ln(\text{BF}_{\text{SR}}) = 59.60$), suggesting a bias towards salience information over reward information in driving choice behavior. This was largely consistent at the individual-level as well (all $\ln(\text{BF}_{\text{SR}}) > 4.61$). However, subject 4 had decisive evidence in favor of the reward-only model in Task 1 relative to the salience only model.

3.2.3 Domain General Effects: Dynamic versus Stable Feature Bias

At the group level, there is decisive evidence of a bias for stable versus dynamic information in choice behavior. Both salience and reward only models were better fit when those features were manipulated stably versus dynamically (Salience ($\mu \ln(\text{BF}_{\text{SDynamicVSStable}}) = -32.50$) and Task 2 ($\mu \ln(\text{BF}_{\text{RDynamicVSStable}}) = -12.95$). This was consistent for 5/6 of the subjects at the individual level. There was similar evidence for

stable and dynamic salience models and decisive evidence in favor of the dynamic versus stable reward model for subject 3.

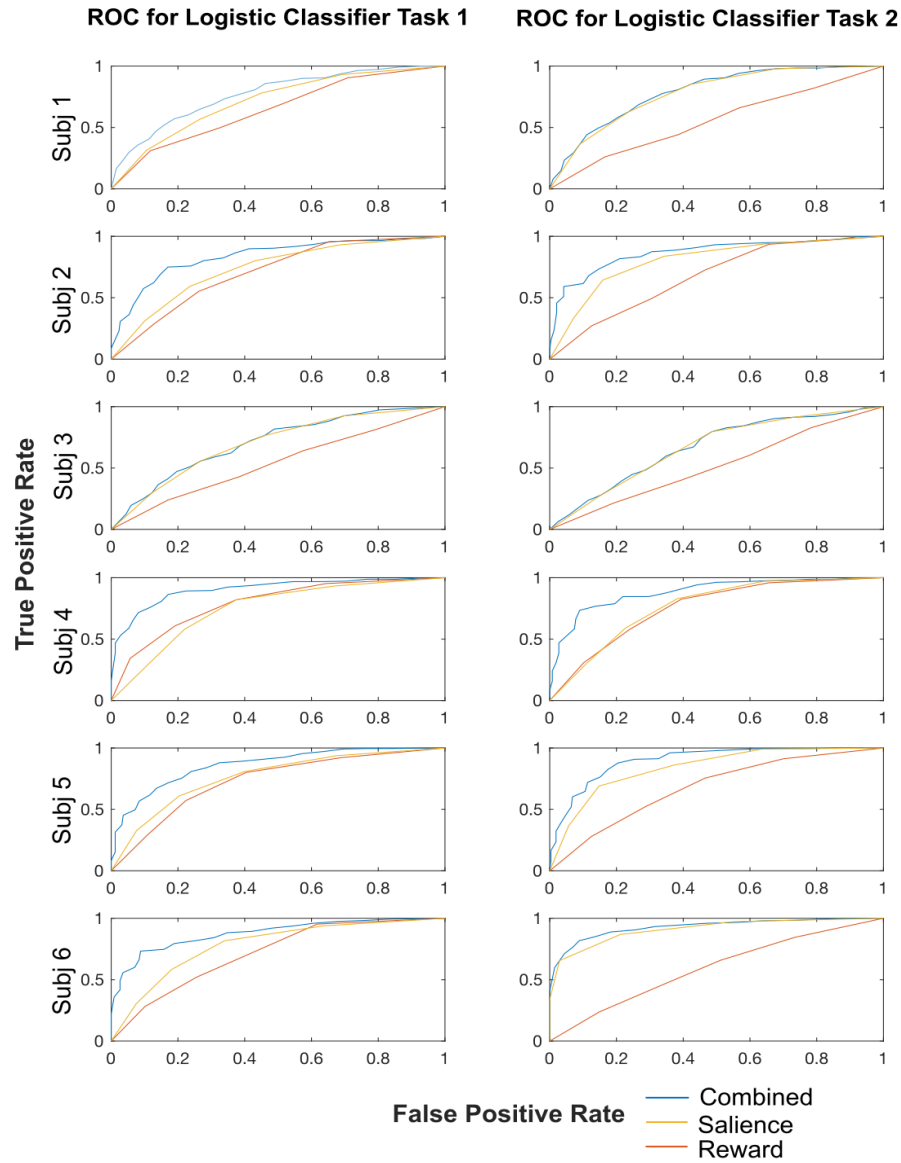


Figure 7. ROC curves per subject depicting classification accuracy of combined, salience, and reward models. Chance would be a straight line from the (0,0) to (1,1) position. All models performed above chance for 5/6 subjects. The reward only model performed at chance for participant # 3. See results for further description.

Table 2. Task 1 and 2 Individual subject AIC, BIC, and Log-likelihood values for three models

Subj	Value	Saliency T1	Saliency T2	Reward T1	Reward T2	Combined T1	Combined T2
1	AIC	596.59	530.20	630.99	646.16	553.72	526.46
	BIC	604.95	538.57	639.35	654.53	566.26	539.00
	Log- Likelihood	-296.29	-263.10	-313.50	-321.08	-273.86	-260.23
2	AIC	587.21	523.61	605.11	624.94	499.43	449.74
	BIC	595.58	531.98	613.49	633.31	511.99	462.30
	Log- Likelihood	-291.60	-259.80	-300.56	-310.47	-246.71	-221.87
3	AIC	622.89	621.16	683.50	662.45	621.97	622.48
	BIC	631.30	629.58	691.91	670.87	634.58	635.11
	Log- Likelihood	-309.45	-308.58	-339.75	-329.22	-307.98	-308.24
4	AIC	588.20	575.09	546.51	585.01	397.51	429.87
	BIC	596.61	583.51	554.92	593.42	410.13	442.49
	Log- Likelihood	-292.10	-285.54	-271.25	-290.50	-195.75	-211.9
5	AIC	567.49	484.79	602.31	634.28	460.50	399.26
	BIC	575.88	493.19	610.70	642.68	473.09	411.86
	Log- Likelihood	-281.75	-240.40	-299.15	-315.14	-227.25	-196.63
6	AIC	558.89	365.99	609.19	664.94	443.63	338.54
	BIC	567.31	374.41	617.62	673.37	456.28	351.18
	Log- Likelihood	-277.44	-277.44	-302.59	-330.47	-218.82	-166.27
	Mean AIC	586.88	516.81	612.94	636.30	496.13	461.06
	Mean BIC	595.27	525.49	621.33	644.70	508.72	473.66
	Mean Log- Likelihood	-291.44	-272.48	-304.47	-316.15	-245.06	-227.53

3.2.4 Behavioral Summary

Overall, behavioral results support the hypothesis that sensory and reward information together best predict choice. Results also partially support the hypothesis that

task structure and uncertainty will influence the weighting of sensory and reward information in choice in a domain-general, rather than domain specific way. Specifically, subjective choice behavior was driven by *both* domain specific and domain general features. The influence of domain specific features is such that behavior is biased by salience information, relative to reward. At the same time, a single feature (salience or reward) seemed to influence choice most when the value of the other feature was comparatively low (i.e. higher uncertainty between targets or high conflict between target features (reward high/salience low and vice versa)), suggesting a domain general role of feature value/uncertainty on behavior. At the same time, bias towards salience and reward information increases in a domain general way; specifically, stable manipulations of either feature improved choice classifications based on that feature.

It's important to note that there were some individual differences in the degree participants chose to rely on one or both features, however due to small sample size, this should be interpreted with caution and is an area of further exploration. While the sample size here is small and therefore not powered enough to study these individual differences in more depth, similar results were observed in the sample of 9 pilot behavior-only subjects that was collected.

3.3 *fMRI Results*

3.3.1 *Domain Specific Conjunction: Main Effect of Reward and Salience*

In task 1 the main effect of reward was observed in the occipital and portions of the midcingulo-insular networks (Figure 8; Appendix C). The main effect of reward in task 2 was observed in the lateral and medial fronto-parietal networks, as well as portions of the midcingulo-insular network (Figure 8; Appendix D).

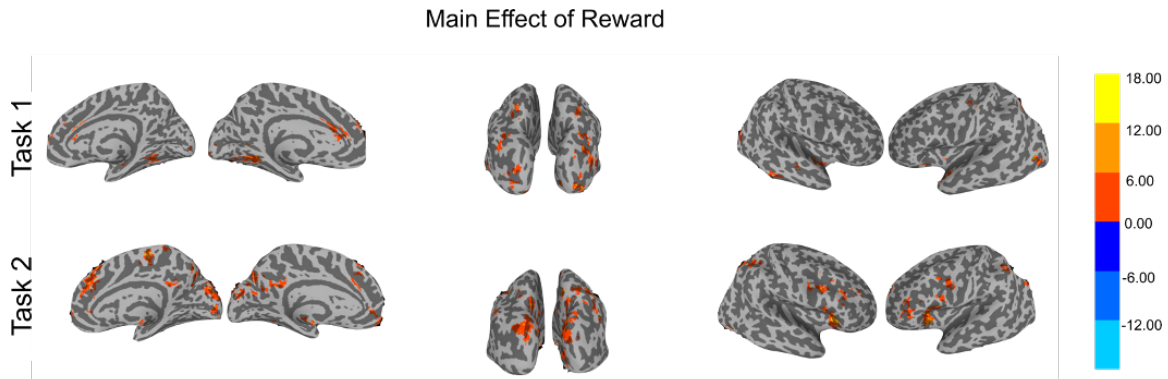


Figure 8. Top: Main effect of reward from task 1 (reward stable), threshold at an uncorrected $p = .05$, cluster threshold = 50 voxels (nearest neighbor = faces touching). Bottom: Main effect of reward from task 2 (reward dynamic), same threshold as top.

There was minimal overlap between stable and dynamic main effects of reward (47 total voxels; .85% of all total voxels between two maps; Figure 9). Areas of overlaps included key regions within the visual and dorsal fronto-parietal network, as well as the anterior cingulate (part of cingulo-opercular network). The most notable differences were observed in the vmPFC/OFC, lateral PFC, medial PFC, bilateral middle insula, precuneus, and IPL, which were active above threshold only when reward was dynamically manipulated (task 2). Additionally, in task 1, activity in the posterior half of the brain, including extrastriate regions appears more laterally, while in task 2, these regions are activated more medially. This supports the basic hypothesis that the frequency at which reward is manipulated considerably changes where in the brain reward-related variance is observed. Given that there was no behavioral reward by task interactions, this effect cannot be primarily attributed to differences in task difficulty.

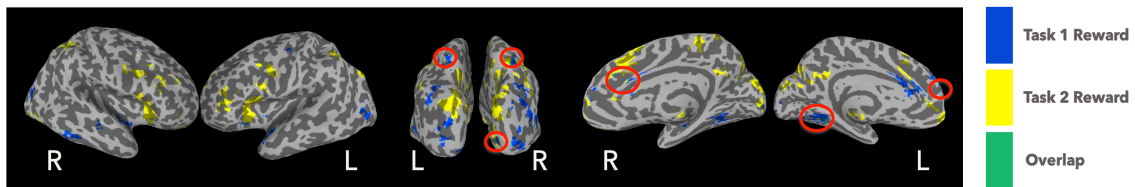


Figure 9. Conjunction between reward main effect in task one and two. Overlap was observed in the ACC, visual regions, and parietal regions from the dorsal fronto-parietal network.

In task 1 the main effect of salience was observed in lateral, medial, and dorsal fronto-parietal networks (803 voxels, 5.18% of total voxels between across both maps; Figure 10; Appendix E). The main effect of salience in task 2 was observed primarily in the lateral frontal parietal network (Figure 10; Appendix F). When salience was varied

dynamically (task 1) we see greater engagement of anterior frontal and anterior temporal regions, primary and secondary visual regions, and more medial activation of visual cortices.



Figure 10. Top: Main effect of saliency task one (saliency dynamic), uncorrected threshold $p = .05$, cluster threshold 50 voxels (nearest neighbor = faces touch). Bottom: Main effect of saliency task two (saliency stable), threshold same as above.

There were several key regions of overlap between dynamic and stable manipulations of perceptual information (Figure 11). Overlap between tasks was observed in portions of the occipital, lateral fronto-parietal, dorsal fronto-parietal, and midcingulo-opercular networks. Dynamic manipulation of saliency engaged posterior and mid-cingulate cortex, portions of the OFC and medial PFC regions, and precuneus above threshold, while stable saliency did not. There was also more diffuse above threshold activity in ventro-lateral temporal cortex and medial portions of the occipital network under dynamic saliency conditions. Stable manipulation of saliency engaged somatosensory association (Brodmann area 5) and bilateral FEF regions (Part of dorsal fronto-parietal network), while dynamic saliency conditions did not. Like the results reported for reward, regions showing saliency associated activity varied as a function of stable and dynamic manipulations of this feature.

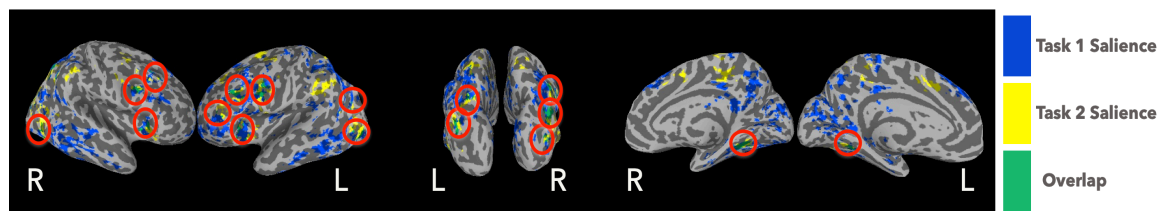


Figure 11. Conjunction of thresholded main effect maps of saliency from task one and task two. Overlap was observed in visual regions including MT+, parts of the inferior frontal gyrus and , inferior parietal lobule (IPL), precentral gyrus, ventral and

3.3.2 *Domain Specific Summary*

Overall, for domain specific maps, there was consistent overlap between occipital and lateral fronto-parietal networks, as well as portions of the midcingulo-opercular network. However, there were also some important differences between dynamic and stable manipulations of salience and reward. Specifically, dynamic salience and reward seemed to uniquely engage more anterior and rostro-medial prefrontal regions, precuneus, as well as posterior cingulate regions. These regions have been associated with endogenous control of attention (Uddin et al., 2019). This may be because dynamic features have a potential for altering any prior choice participants made based on the stable feature cue, requiring subjects to inhibit quick responses, especially when dynamic information conflicts with expectations based on the stable cue.

Greater prefrontal activation when one feature is manipulated dynamically and the other is stable, potentially reflects the conflict between prior expectation of a choice based on stable information, and the need to inhibit response until dynamic feature is observed. Decision to stay or switch choice therefore depends on congruency of stable and dynamic features, rather than the domain specificity of this feature; with greater inhibitory control needed when these features maximally conflict.

3.3.3 *Salience and Reward Interaction*

In task 1, activity in portions of the midcingulo-opercular, medial, and lateral fronto-parietal networks varied as a function of the reward-salience interaction (Figure 12). In task two, this effect was observed in the dorsal fronto-parietal, medial fronto-parietal, portions of the midcingulo-opercular, and lateral fronto-parietal networks (Figure 12). Overlapping activity was observed in regions of the midcingulo-opercular, medial, and lateral fronto-parietal networks.

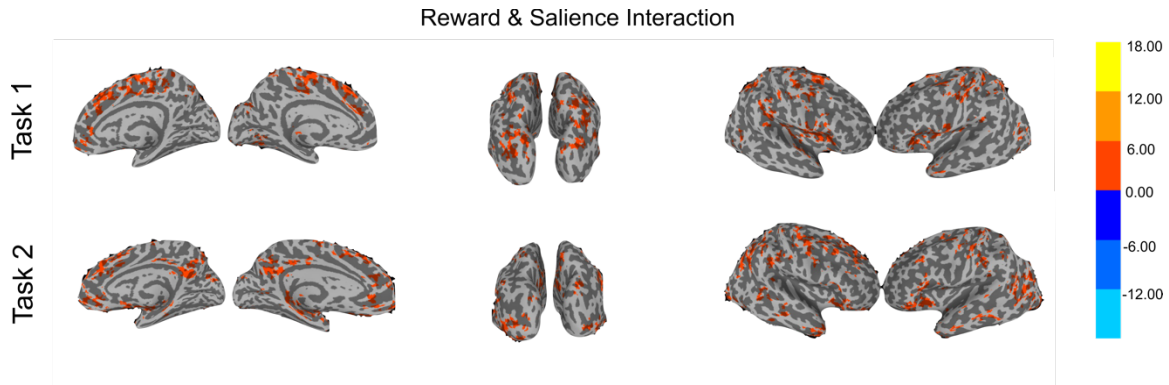


Figure 12. Top: Interaction for saliency and reward in task 1 (reward stable, saliency dynamic). Uncorrected threshold $p = .05$, cluster threshold 50 voxels (nearest neighbor = faces touch). Bottom: Interaction between saliency and reward in task 2 (saliency stable, reward dynamic), threshold same as above.

3.3.4 Domain General Conjunction: Dynamic and Stable Saliency and Reward

When decision-relevant features were manipulated dynamically, overlap was observed in regions of the occipital, medial frontoparietal, dorsal frontoparietal, midcingulo-opercular, and lateral frontoparietal networks (1,221 voxels, 8.46% of total voxels; Figure 13). There was significantly greater overlap between dynamic feature maps than domain specific maps across the two tasks (Dynamic > Saliency $\chi^2 = 126.536$, $p < .0001$; Dynamic > Reward $\chi^2 = 386.91$, $p < .0001$).

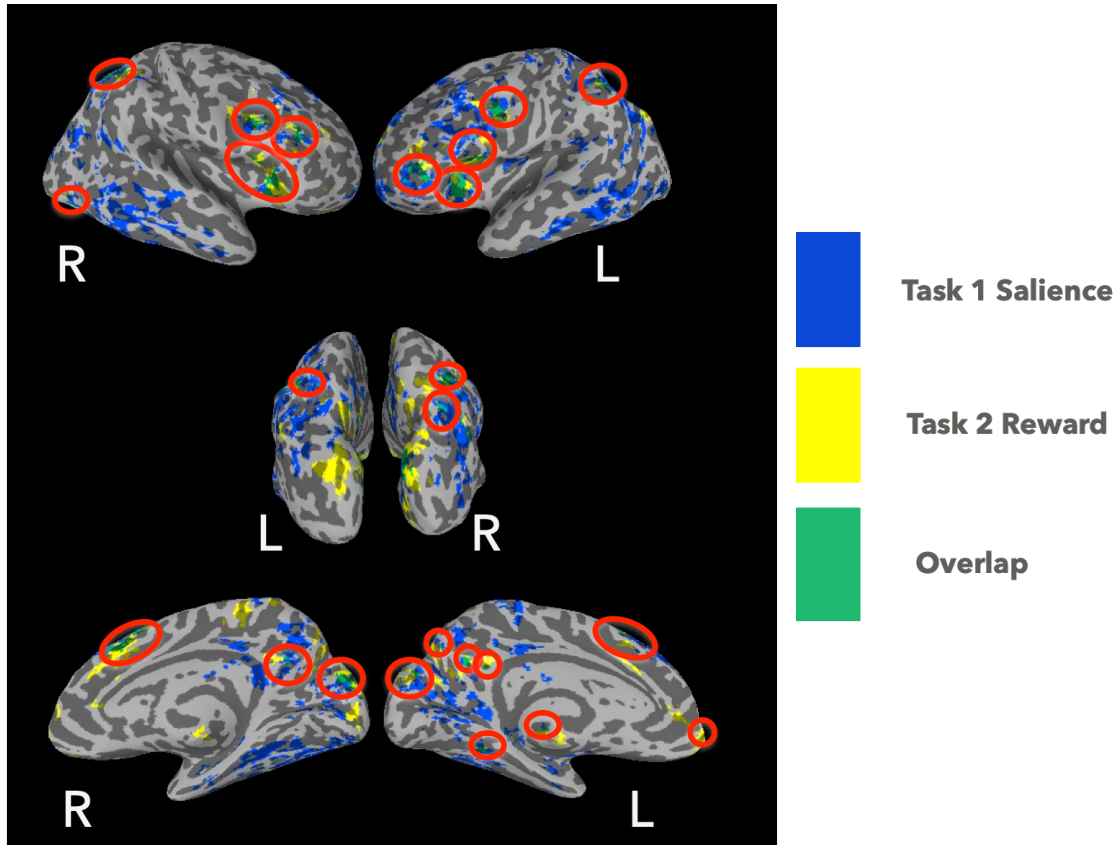


Figure 13. Conjunction of thresholded main effect maps of salience from task one and reward from task two (dynamic features). Overlap was observed in regions of the lateral frontoparietal network (IPL, Intraparietal, ITG, dlPFC, vlPFC), the midcingulo-opercular network (insula), medial fronto-parietal network (vmPFC, PCC, dmPFC, SFG, Precuneus), and occipital network (V1-V4 (medial), FFA, PPA).

When decision-relevant features were manipulated stably, overlap was observed in regions of the occipital and dorsal frontoparietal networks (Figure 14). There was significantly greater overlap between stable feature maps than reward specific maps ($\text{Stable} > \text{Reward } \chi^2 = 126.82, p < .0001$) and significantly less overlap than salience specific maps ($\text{Stable} < \text{Salience } \chi^2 = 8.40, p < .0038$).

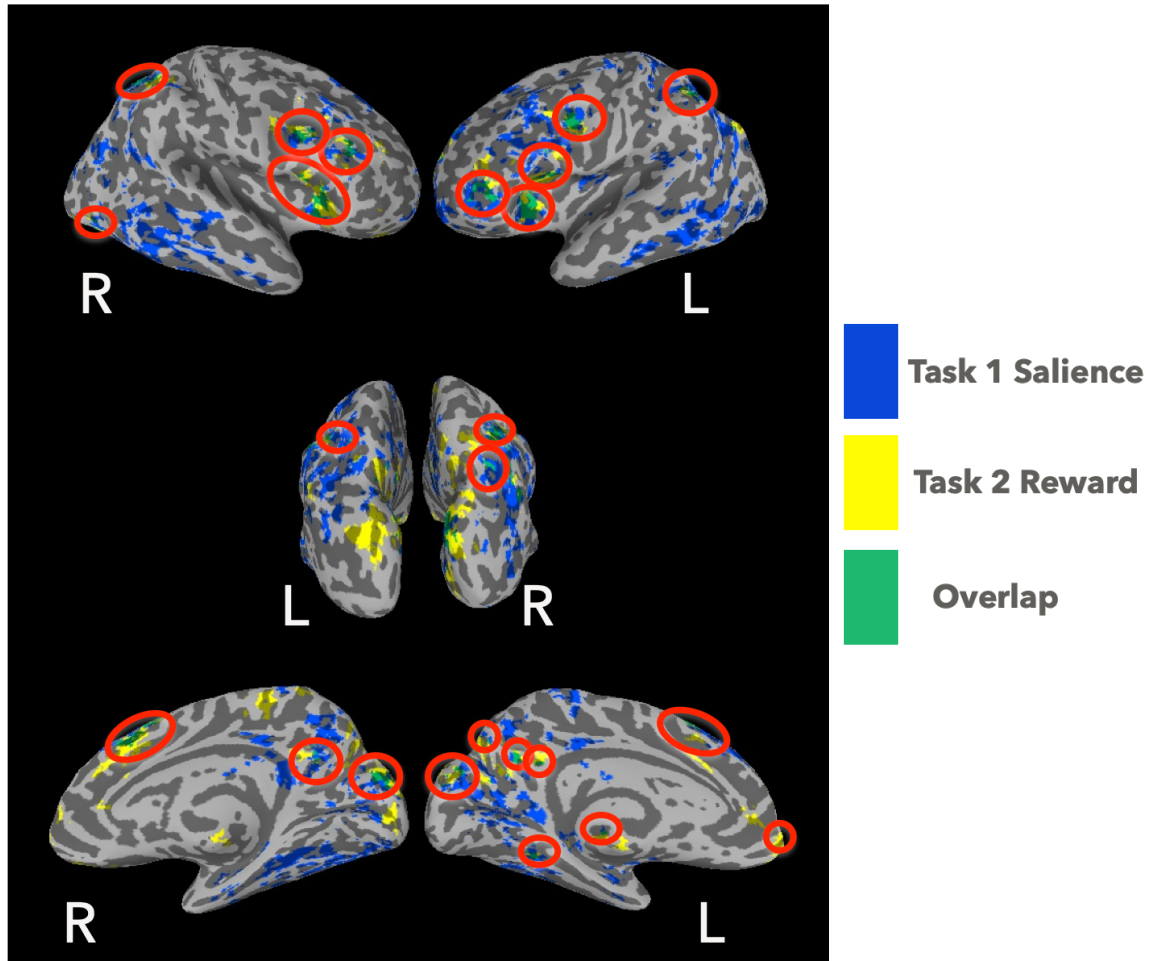


Figure 14. Conjunction of thresholded main effect maps of reward from task one and salience from task two (stable features). Overlap was observed in regions of the dorsal frontoparietal network (intraparietal sulcus/intraparietal, inferior frontal junction), and the occipital network (PPA, lateral occipital gyrus).

3.3.5 Region Specific Response Patterns

As expected, activity in stimulus responsive regions (FFA and PPA) increased linearly as a function of increasing salience for face and house respectively (Figures 15 and 16). Activity in these regions increased at lower salience levels when reward probability for 8 cents was greater than 50% for the specific target.

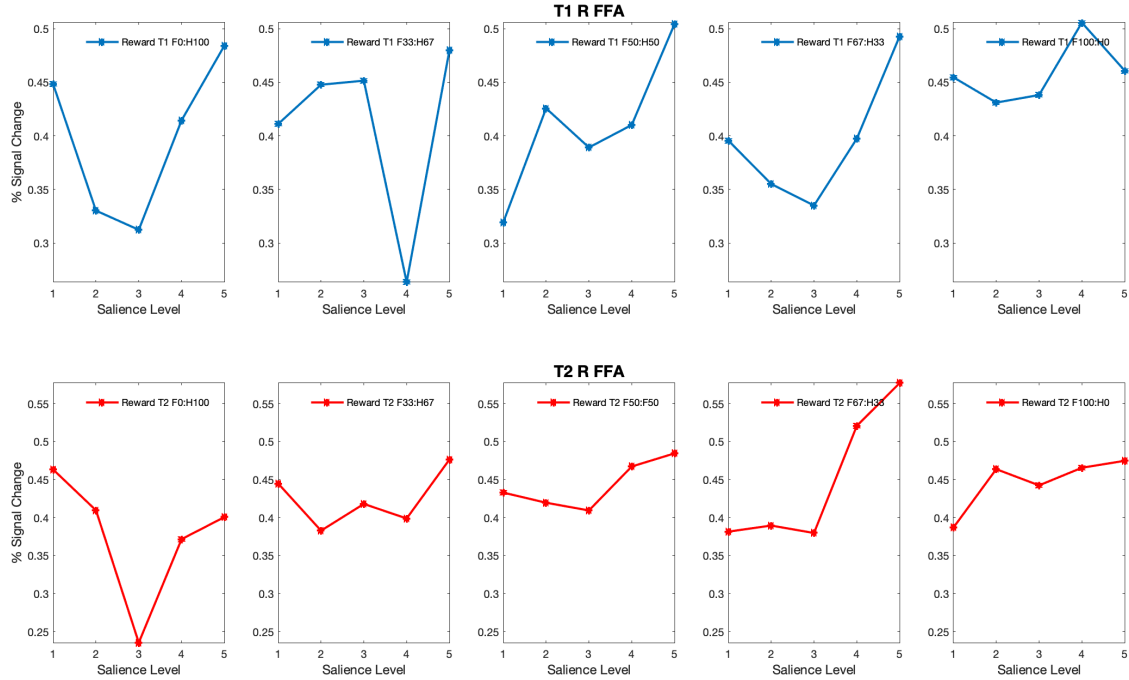


Figure 15. Top: Task 1 mean percent signal change from dynamic feature overlap FFA cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

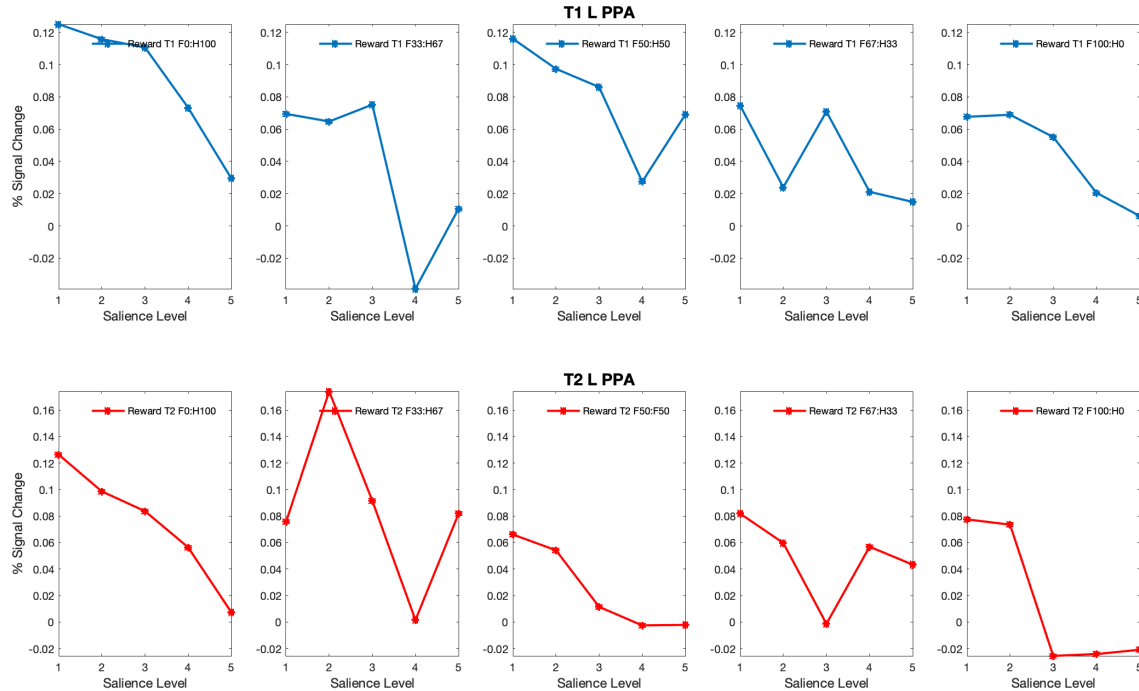


Figure 16. Top: Task 1 mean percent signal change from dynamic feature overlap PPA cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

Clusters of overlap between dynamic features in the ACC and insula (Figures 17 and 18) showed the greatest activity when conflict between salience and reward features was high. This effect was more pronounced when at least one feature was certain and less

apparent when there was uncertainty in both features. Activity in the dmPFC and dlPFC followed a similar response pattern (Figures 19 and 20).

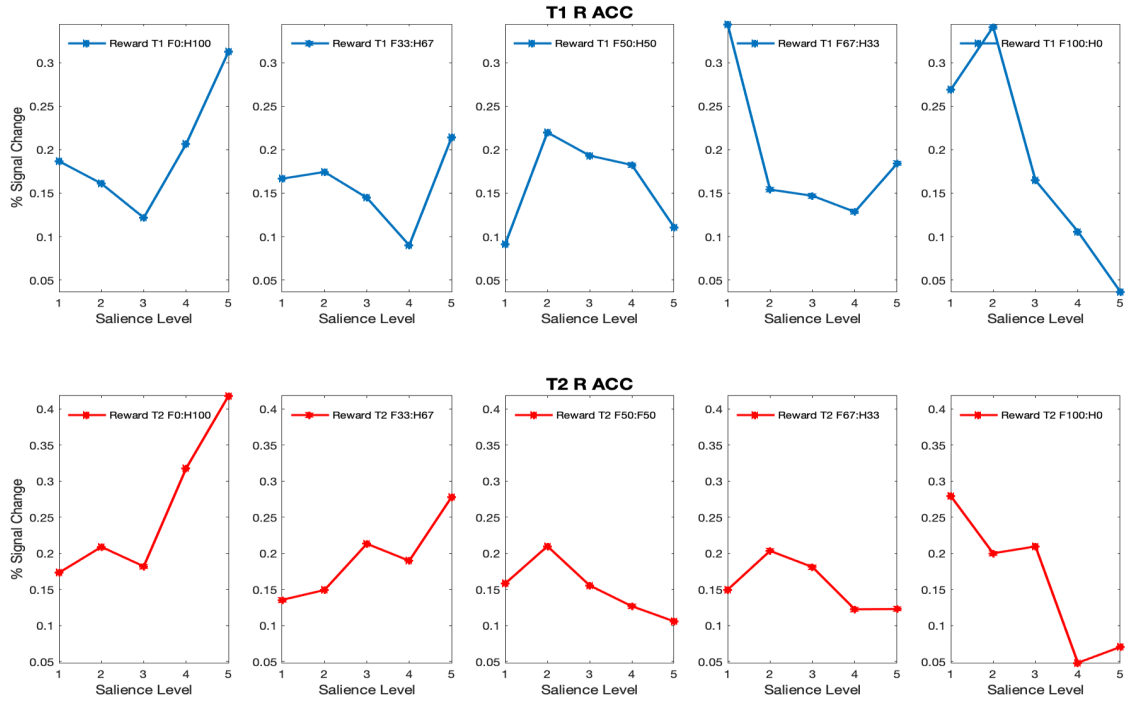


Figure 17. Top: Task 1 mean percent signal change from dynamic feature overlap ACC cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

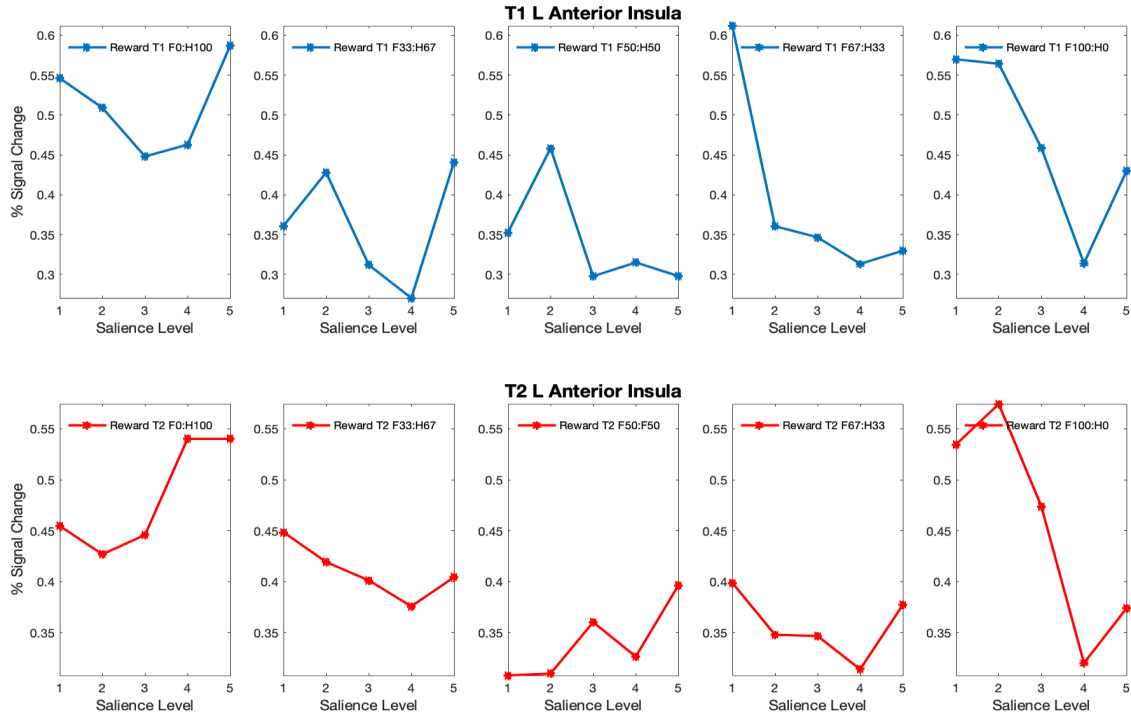


Figure 18. Top: Task 1 mean percent signal change from dynamic feature overlap anterior insula cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

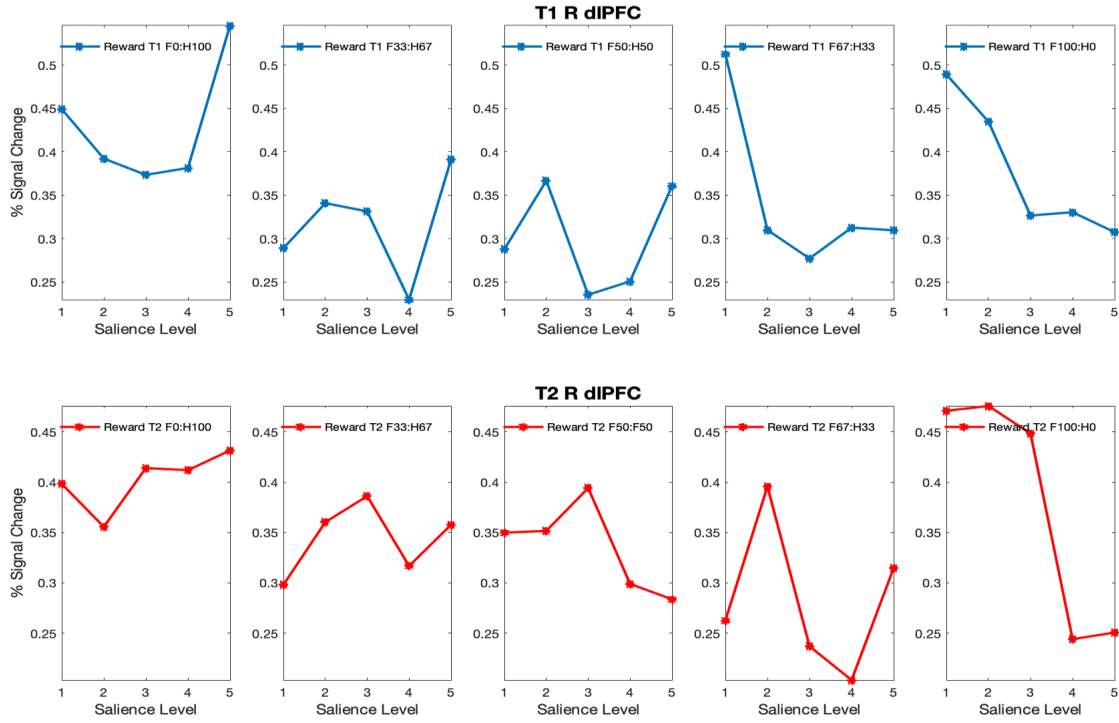


Figure 19. Top: Task 1 mean percent signal change from dynamic feature overlap dIPFC cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

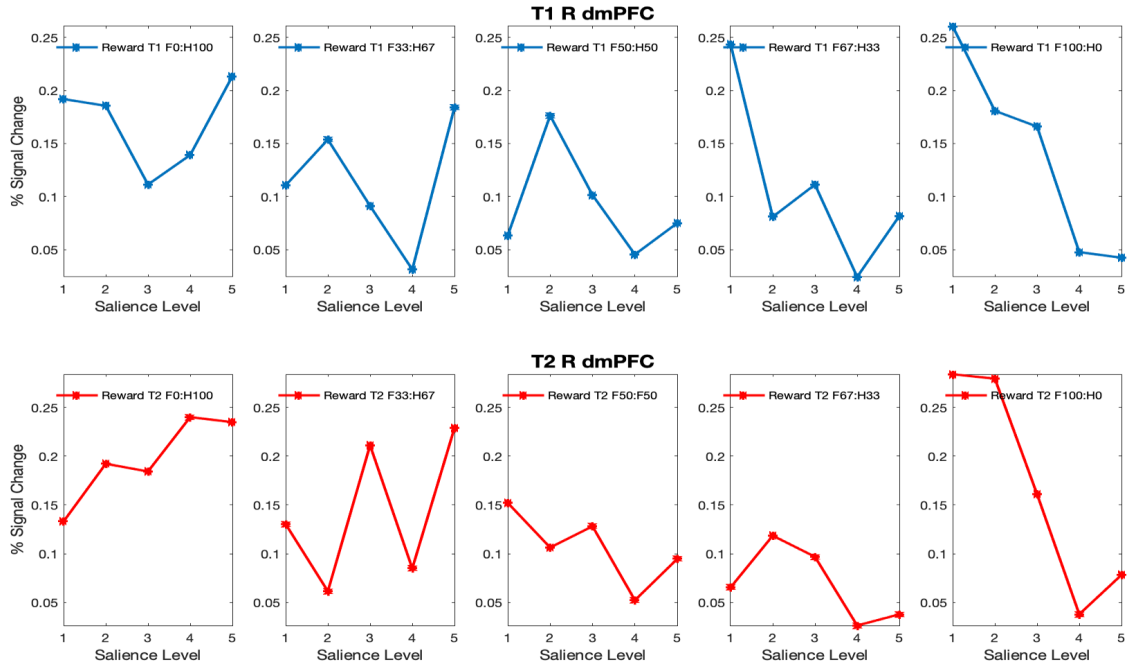


Figure 20. Top: Task 1 mean percent signal change from dynamic feature overlap dmPFC cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

Activity in parietal regions such as the IPL and Intraparietal sulcus (Figures 21 & 22) appear to signal discriminability between features when at least one feature is certain. While this may appear similar to activity observed in the ACC and insula, it differs in that its behavior seems to categorically favor the certain condition, which varies along dynamic feature, but shows lower and more noisy behavior across uncertain and risky choice conditions. The shift in activity in the ACC, insula, dmPFC, and dlPFC appeared to shift more continuously along both salience and reward features, while they appear to shift more categorically between certain and uncertain conditions in the IPL and intraparietal areas.

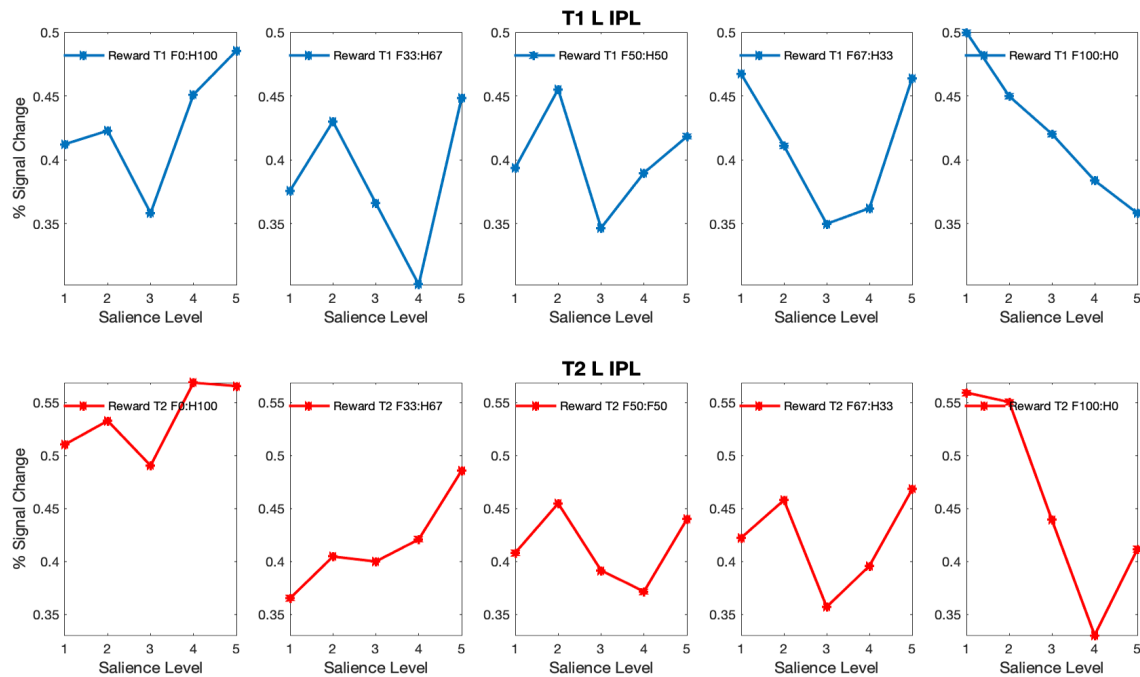


Figure 21. Top: Task 1 mean percent signal change from dynamic feature overlap IPL cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

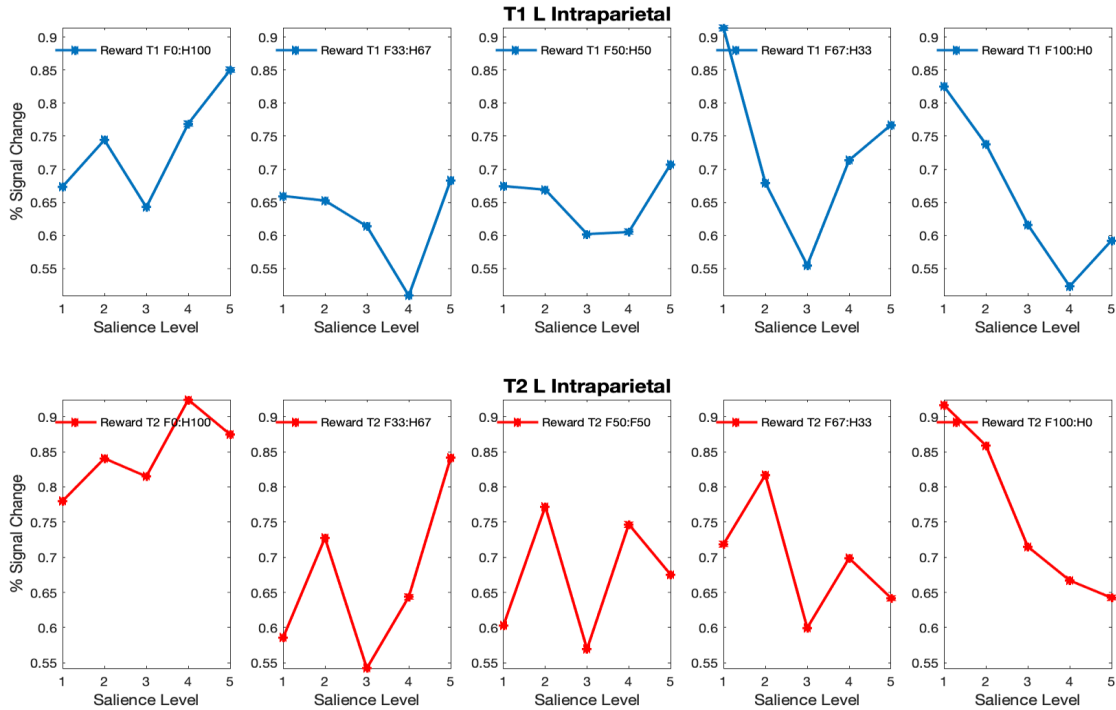


Figure 22. Top: Task 1 mean percent signal change from dynamic feature overlap intraparietal lobule cluster grouped by reward level with saliency level on the x-axis. Bottom: Same as above but for Task 2.

Activity in the vIPFC was similar between task 1 and 2 dynamic features for the certainty condition, with overall increasing activity when saliency or reward was certain and the other feature (reward and saliency respectively) increasingly conflicted (Figure 23). Activity across uncertain reward conditions in task 1 seems to increase in a u-shaped fashion while in task 2 it appears to move in an inverse u-shaped fashion, suggesting very preliminary evidence for task-related changes in uncertain reward-related activity in this region.

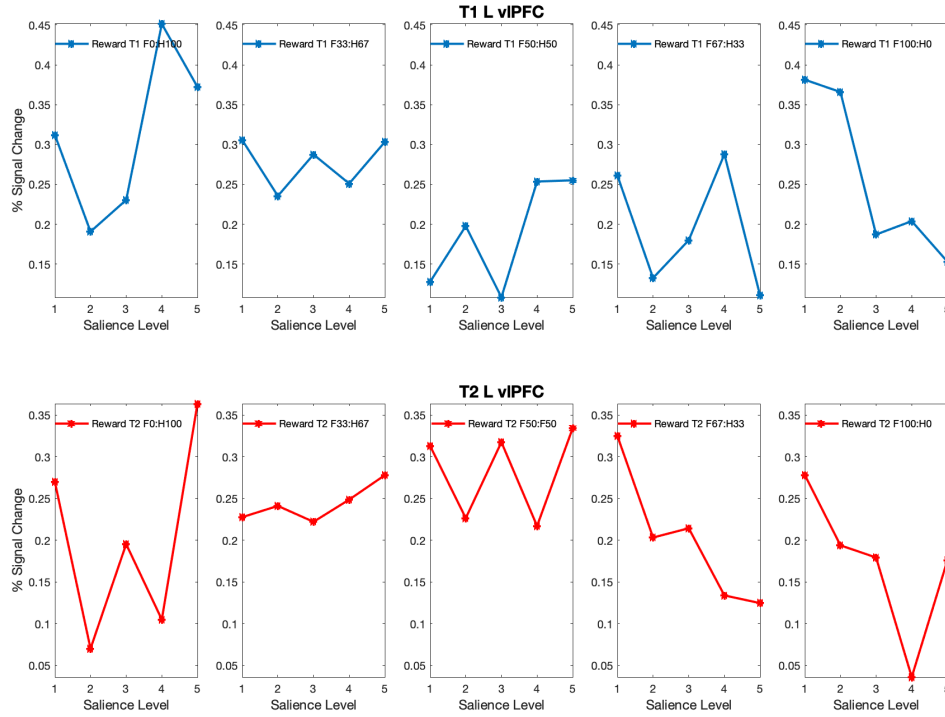


Figure 23. Top: Task 1 mean percent signal change from dynamic feature overlap vIPFC cluster grouped by reward level with saliency level on the x-axis. Bottom: Same as above but for Task 2.

There is no clearly interpretable pattern of activity in the overlapping vmPFC cluster (Figure 24). It's important to note that the mid-orbital/vmPFC clusters observed in both dynamic feature maps were largely spatially distinct and as such the small overlapping cluster may not have been the most ideal to capture associated activity. Additionally, vmPFC/OFC activity often becomes clearer when contrasting choice and outcome phase. Looking at the main effect of the dynamic conditions (saliency task 1 and reward task 2), activity in vmPFC is less negative when saliency is certain and more negative when saliency is uncertain. On the other hand, activity in this region is more negative when reward is certain and less negative when reward is uncertain (Figure 25). This result is consistent with the dynamic main effect observed in another overlapping medial PFC cluster (Figure 26). Activity in the PCC appeared to vary in a u-shaped fashion across saliency conditions in task 1 and in an inverse u-shaped fashion along saliency conditions in task 2, except when reward was certain (Figure 27). Reward-related activity varied in an inverse u-shaped fashion in both tasks and was highest when

both salience and reward were uncertain. vmPFC and PCC activity patterns suggest a possible domain specific (reward/salience) by domain general (certainty/uncertainty level) interaction, however further research with a larger sample is required to test this more explicitly.

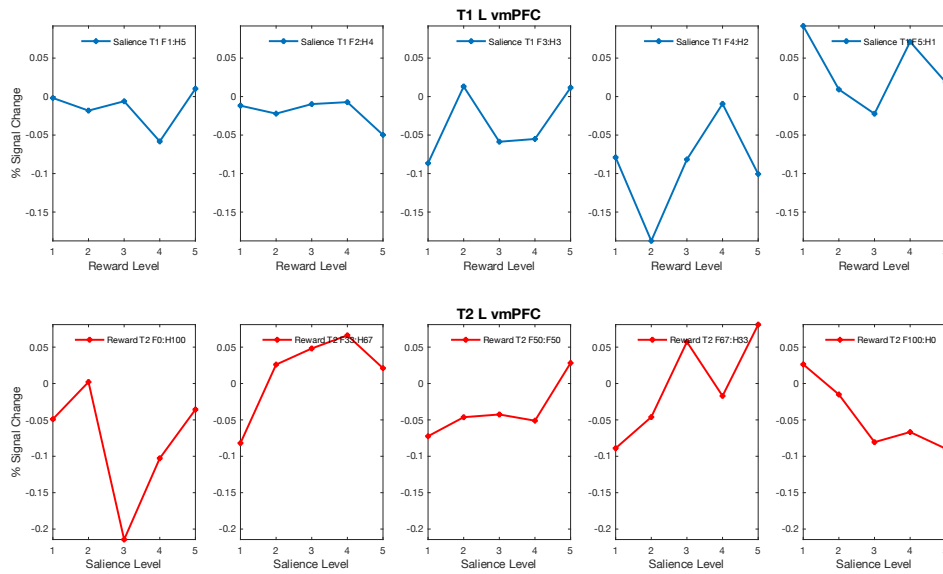


Figure 24. Top: Task 1 mean percent signal change from dynamic feature overlap vmPFC cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

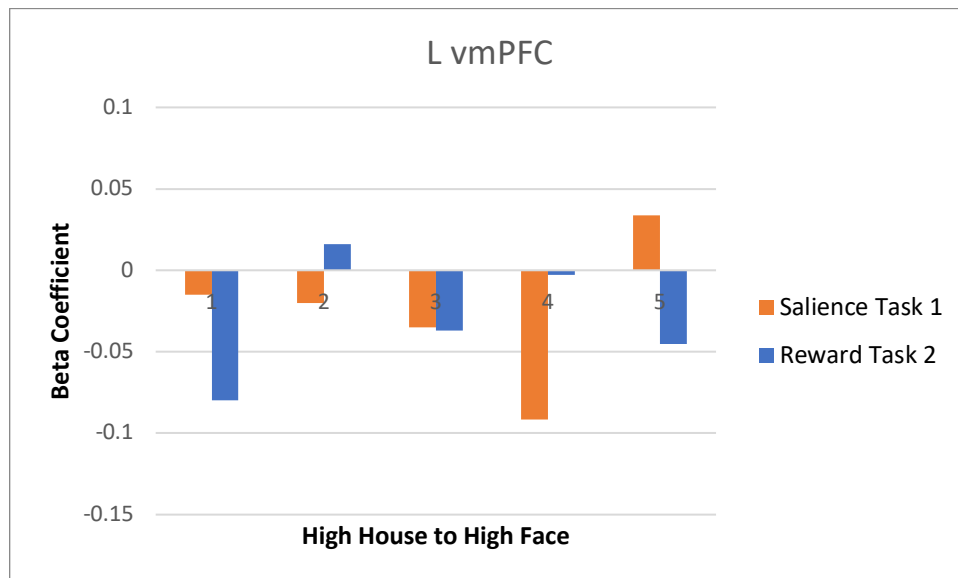


Figure 25. Main effect of salience from task 1 and reward from task 2 in the vmPFC cluster taken from the dynamic feature overlap.

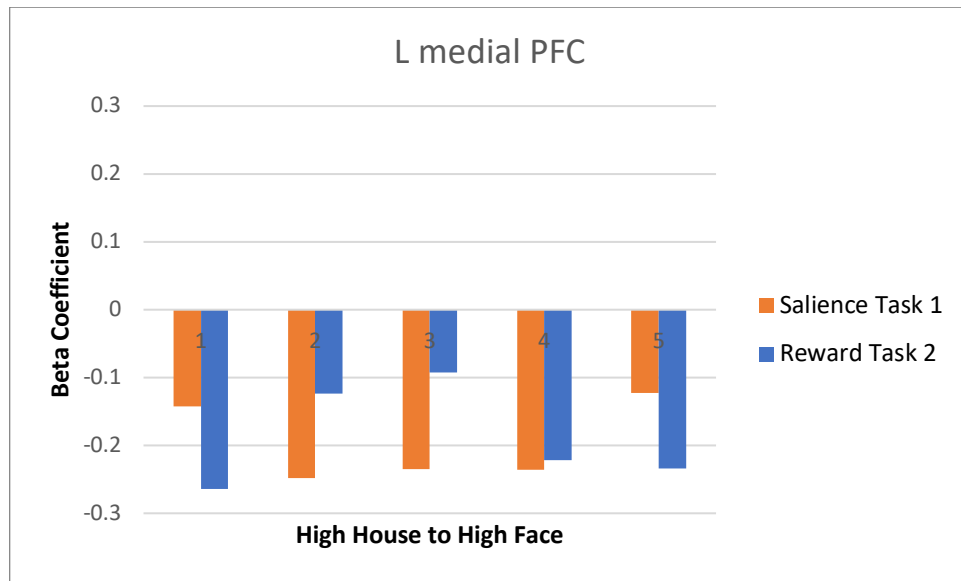


Figure 26. Main effect of salience from task 1 and reward from task 2 in another medial PFC cluster taken from the dynamic feature overlap. Activity observed here follows a similar pattern to vmPFC but is more pronounced and remains negative across all conditions.

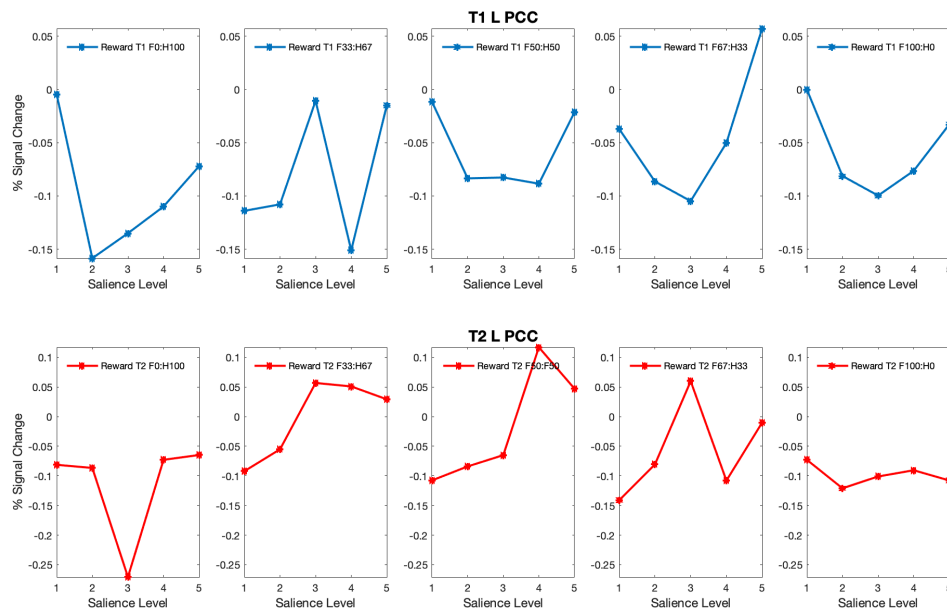


Figure 27. Top: Task 1 mean percent signal change from dynamic feature overlap PCC cluster grouped by reward level with salience level on the x-axis. Bottom: Same as above but for Task 2.

3.3.6 *fMRI Summary*

While very preliminary, overall fMRI results support the hypothesis that there is greater overlap between domain general features (dynamic/stable) than domain specific features (salience/reward). The only exception is for stable compared to salience main effect conjunctions, where overlap between salience maps was greater. Results also show preliminary evidence suggesting that activity in decision relevant regions varies by level of uncertainty and feature conflict more generally rather than more specifically by reward or salience. There are some regions, such as the PCC, vmPFC, and precuneus (not described here) that seemed to show interactions between domain general and domain specific features (not tested directly by the ANOVA interaction term), however further research with larger sample sizes are necessary to probe this effect further. Of note, these regions showed above threshold activity only in the dynamic conditions (reward and salience), but not stable conditions. There is also a distinct domain general pattern observed for lateral and medial occipital network regions. There was evidence of greater overlap between stable feature maps in lateral occipital regions, and between dynamic feature maps in medial occipital regions.

4 Discussion

4.1 Behavioral Results

Overall, there was evidence that choice behavior in both tasks was better predicted using a combination of perceptual and reward salience information than either alone. This finding is consistent with several studies that have modeled simultaneous reward and salience information in the context of multi-alternative choice (Lou et al, 2015; Navalpakkam et al., 2010). Novel to the current study, this effect seemed to hold independent of whether reward was manipulated stably by run, with salience varying by trial (as has been the case in most of the studies above), or dynamically, with salience fixed by run. It is possible that more data is necessary to detect task-related differences in behavior, however previous behavioral pilots conducted with more trials and more participants showed the same result.

Consistent with prior literature, there was evidence that individuals are overall more biased by salience information than reward. This may be due to an intrinsic value that individuals may have previously associated with complex stimuli such as faces and houses. However, a similar salience bias was reported by Navalpakkam et al., 2010 despite having used basic visual features such as orientation and brightness as reward associated targets. While there was no significant difference in overall percent choice with task, or statistically significant interaction between task and salience or reward, findings suggest that choices are better classified by individual salience and reward models when each feature was manipulated stably rather than dynamically. While outside the scope of the current study, there may be several reasons for this shift. For example, individuals may rely less on the dynamic feature overall or more so in specific conditions (e.g. under uncertainty or conflict), thereby amplifying the influence of the stable feature. They may also increase reliance on the stable feature overall or in specific conditions, without altering reliance on the dynamic feature. Alternatively, there may be a combined effect on stable and dynamic features via a tradeoff, such that increased reliance on the stable feature, decreases reliance on the dynamic feature. From the perceptual decision-making literature, Diederich (2008) used a drift diffusion model to predict how perceptual choices were biased by varying reward magnitude and decision time (greater time = more sensory evidence accumulation and less error). Like the current study, they

also compared behavior across a version of the task that varied reward payoffs between blocks and time-limit manipulations by trial, and vice versa, however outcomes were always known and certain. Their findings showed that the task structure influenced the choice process, altered which hypothesized model fit data best, and the degree to which known and certain reward biased perceptual choices. Additionally, they found that reward had more influence on choice when time limits were short (less sensory evidence).

Like the study discussed above, results of the salience and reward interaction suggest that the degree of salience and reward bias/integration may depend in part on the specific condition and potential conflict between salience and reward features. Notably, there was a more pronounced increase in face choices when face salience was high, and reward probability was lower and uncertain (H67:F33) or equal between targets (H50:F50). A similar effect was observed when reward was high and face salience was lower than house (H1:F5) or uncertain (H4:F2). These findings support the hypothesis that the nature and extent of salience and reward integration varies as a function of domain general uncertainty between stimuli, or as a function of higher conflict between features (both capturing choice uncertainty). These findings replicate some of the work that has been done in the reward-based decision-making literature. Namely, studies report preferential biases towards lower valued but more certain/safe choices when participants are faced with decisions between safe and risky/ambiguous reward alternatives (Christopoulos et al., 2009). The current study extends these findings to show that preference towards safe/certain options is not limited to certainty in reward probability but also stimulus salience. Similarly, increases in risk/uncertainty isn't limited to reward-related risk (equal outcomes), but can be achieved by increasing stimulus ambiguity (low coherence of high valued target and high conflict with distractors) and salience between potential alternatives (greater sensory conflict between targets).

Despite differences in stimulus type, task demands, and methods for the studies reviewed above, there is robust support from both reward and perceptual decision-making literatures that supports the findings of the current study. At the same time, one to one comparison cannot be made, and further investigation is necessary to determine whether

parameters such as risk preference corresponds to behavioral estimates of error rate at high reward/low salience, or increased bias towards high salience/low reward options.

As part of an exploratory aim, there was some evidence of individual differences in biases towards domain specific features (salience and reward), domain general features (stable and dynamic), and how equally participants combined sensory and reward features in choice (versus relying primarily on a single feature). For example, in both the behavioral pilot conducted outside of the scanner (not reported here) and the fMRI version of the task, a small percentage of individuals (22% & 16% respectively) showed better prediction of choice from the reward only model relative to the salience only model, while another small portion showed no meaningful difference between the salience only model and the combined model, especially when salience was manipulated stably. It is important to note that the same participant was not different from others in all these domains. While very preliminary, this finding is worth exploring further in a much larger behavioral sample given that there may be multiple reasons for these individual differences. First, individual differences in salience and reward bias, the strength of this bias and degree of integration between the two, could be due to variability in sensory sensitivity, risk/ambiguity preference, or differences in how individuals weigh new information (trial condition or feedback) and use each to inform future behavior. Second, these individual differences may in part be due to the speeded nature of the task and may not be observed under free response time conditions. Notably studies have shown that individuals will increase response times to maintain/improve accuracy under noisy perceptual decision contexts (Gold & Shadlen, 2007). In combined perceptual and reward literatures, there are consistent reports of individual differences in choice behavior. For example, in testing how reward biases the perceptual decision process, Diederich and Busemeyer (2006) reported that some participants varied choices based on time limit (higher time limit = greater accumulation of sensory information, less error) and reward payoff, while others varied choices based on time limit alone. Given that time limit is a proxy for greater sensory evidence accumulation, it is possible that we are observing similar individual difference patterns by altering the magnitude and salience of sensory information (also see Diederich, 2008). At the same time, further research is

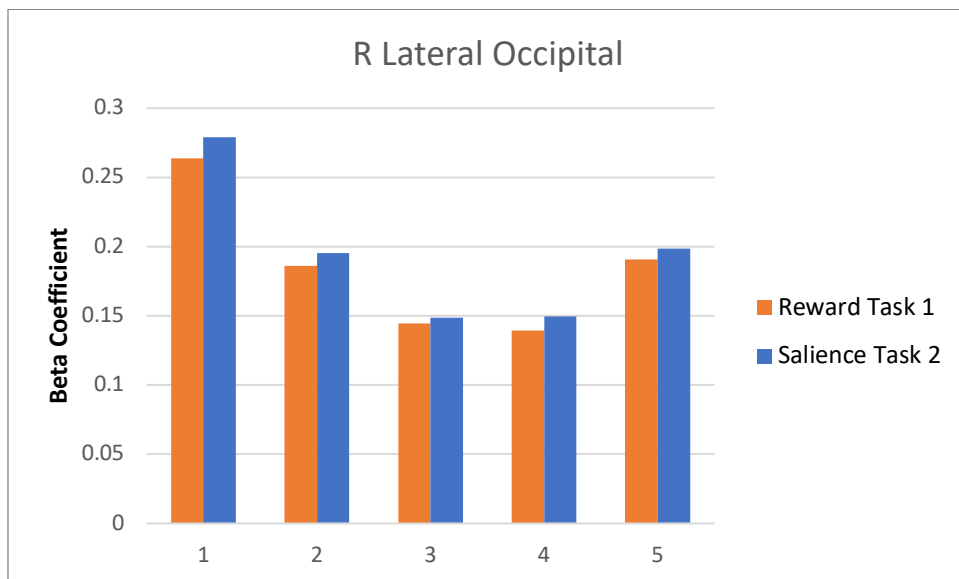
required to determine whether the individual differences observed in this study are meaningful and useful in clinical contexts.

4.2 *fMRI Results*

While preliminary and underpowered due to pandemic restrictions, results from the fMRI task show activation in decision-relevant regions reported in both perceptual and reward-based decision tasks. The study showed expected stimulus specific activity in commonly associated visual regions including the FFA (for face) and PPA for house. Activity in one or both regions were observed across both stable and dynamic salience and reward. The results, while interpreted with caution, support the general hypothesis that activity in decision-relevant regions vary as a function of how target features are manipulated (value/uncertainty of salience and reward) and domain general task manipulations (stable vs dynamic) in higher-level decision relevant areas.

Results showed greater overlap between dynamic salience and reward feature maps when compared to overlaps between both domain specific maps. There was also greater overlap between stable reward and salience feature maps and reward specific maps, but not salience specific maps. This could be due in part to the overall bias that subjects had towards salience stimulus features relative to reward. At the same time, this does not explain why the overlap between dynamic manipulations of salience and reward was greater. It is possible that modeling reward during outcome phase separately by condition, rather than estimating reward-related activity during decision-phase would have altered where and how reward related activity was observed. However, this analysis was outside of the scope of the current study and of course further limited by the small sample size. Portions of the vmPFC, PCC and precuneus were uniquely observed in the dynamic feature overlap, which may suggest a potentially crucial role in updating (or maintaining) behavior as a function of detected changes in the environment. This is consistent with findings reported by Summerfield and colleagues (2011), who found that that under volatile conditions, perceptual decision-related activity was observed in vmPFC and PCC regions. In the current study, there was also a distinction between lateral versus medial engagement of visual regions for stable and dynamic maps respectively. This effect was observed for both salience and reward and suggest a possible difference in the visual pathways that are engaged when greater external versus

internal features are relevant for choice. Resting state functional connectivity-based network parcellation studies show evidence for two visual networks that correspond to the medial and lateral distinction observed here (Yeo et al., 2011; Gordon et al., 2017). These findings may also indicate that a priori salience and reward cues (stable cue) increase engagement of more lateral and extrastriate visual regions to represent initial choice biases. Summerfield and Koechlin, 2008 reported that prior perceptual expectations, or trials that were biased in favor of a single alternative showed greater extrastriate and anterior temporal lobe activity, consistent with findings reported here. While it remains to be tested using model-based approaches, it is plausible that subjects represent bias towards the more rewarding or more salient stimulus at the start of each run in these higher-level visual regions based on the stable cue. Subjects may then update this representation as a function of the congruence of the dynamic cue that follows on a trial-by-trial basis, which is represented in lower-level medial visual regions. If this was true, we would expect a decrease in activity for stable feature in lateral visual regions as perceptual or reward uncertainty increased. Looking at the main effect of stable salience and reward in the lateral occipital gyrus overlap revealed this exact effect, providing further support of this interpretation.



Hansen, Hillenbrand, and Ungerleider (2012) reported that prior knowledge during uncertain categorical and perceptual decisions led to greater activity in lateral occipital

cortex and areas of middle frontal gyrus. There is evidence that comparisons between expected and observed stimuli result in differential activation in areas of the medial and posterior cingulate cortex. It is expected that activity in these regions would be higher when there is a corresponding mismatch between the prior expectation based on the stable cue and the observed dynamic cue. While there is distinct activation of vmPFC and PCC in dynamic stimulus conditions for the current study, to test this specific hypothesis would require separating trials by stable cue-congruent and incongruent conditions. While outside of the current scope, this analysis is a natural next step with a fully powered sample. While the studies reported above have been done primarily in perceptual decision-making tasks, the results of this study reveal a domain general role for both high- and low-level visual areas, as well as various fronto-parietal and cingulo-opercular network regions. The lack of observed activity in the OFC/vmPFC in the stable conditions is not unique to our study. Kobayashi and colleagues (2010) showed cortical adaptation in OFC neurons to stable stimuli. They observed that when reward changes were less frequent, adaptations were even stronger. This may explain why there was also no discriminable pattern in the vmPFC cluster along both stable and dynamic dimensions, but that effects were more strongly observed along the main effect of the dynamic feature. The study also showed that activity in parietal regions seemed to vary more categorically along both features, while it varied more continuously in prefrontal regions.

4.3 Limitations and Future Directions

Major limitations in this study include smaller sample size, especially for the fMRI portion, which limited proper statistical testing and corrections for multiple comparisons. As such, data should be interpreted with caution and serve only as a preliminary investigation. At the same time, results showed activity in regions of the brain that were consistent with prior literature on decision-making under uncertainty. Furthermore, activity in several of these regions followed an expected pattern both in terms of direction of response and modulation by condition. In the current study, data included in analyses all trials including those with missed and car choices. While trials were not separated by choice behavior, future iterations of associated analyses should include car and miss trials (no response in allotted time), as part of the original regression model to reduce noise in effects of interest. However, given that car choices varied systematically by condition due

to conflict with the lower salience target, it may be important to model it separately by condition. Additionally, estimating trial-wise behavioral parameters of interest based on behavior, and using them as trial-wise parametric regressors in the fMRI analysis, rather than averaging data across all trials in a condition can potentially maximize power. Additionally including behavioral parametric regressors or separating trials by behavior may help improve and clarify interpretation of activity in regions of interest.

Another limitation of this study is that participants were asked to come in for two separate scanning sessions. While it is possible that behavior might have changed between sessions, or that participants were subject to possible practice effects, pilot studies comparing session 1 and session 2 behavior found this not to be case. The study also controls for any task x session variability by a) including both task versions in each session and b) counterbalancing the order of task presentation between sessions and between participants. Additionally for the behavioral modeling, use of 10-fold cross validation minimizes overfitting and the risk that effects observed are due to systematic differences in behavior between sessions.

The current study only looked at decision-phase activity as a function of perceptual salience and reward. There is evidence that perceptual salience and reward also impact feedback-related activity (Lou et al., 2015), and as such there may be interactions associated with domain-general (stable/dynamic) and domain-specific (salience and reward) features that occur by decision versus outcome phase.

Understanding how individuals make decisions under simultaneous manipulations of sensory and reward-information, and the longer-term goal of formalizing this process through comparable methods has potential for moving the basic science literature forward. Understanding the domain-specific and domain-general impact of perceptual and reward features on behavior and their respective contributions to activity in decision-relevant regions of the brain will help simplify or build upon currently available frameworks. Just as an example, if sensory and reward value and uncertainty parameters similarly impact behavior but engage different neural substrates, then there is value to supplementing behavioral data with neural data to assess individuals more sensitively in a clinical context and may allow for the early personalization of treatment approaches. On the other hand, if sensory and reward parameters uniquely contribute to behavior, but correspond to activity

in overlapping neural substrates, then more fine-grained tools may be necessary to tease apart factors such as heterogeneity in neuronal population activity, neurochemical, or timing-related processes that may lead to unique behavioral outcomes. From a more clinical perspective, an understanding of individual differences in this process can help identify more targeted assessment and treatment approaches for individuals facing challenges in one or both domains. Examples of clinical conditions that may be impacted by impaired PDM and RDM processes include Autism Spectrum Disorders (ASD), Psychosis Spectrum Conditions, Post Traumatic Stress Disorder (PTSD), and Social Anxiety. Predictive theories of perception and cognition have been used to link clinical taxonomies across affective, motivational, and perceptual domains. Future studies should use model-based estimates of behavior to further understand the combined perceptual and reward-based integration process and underlying neural substrates.

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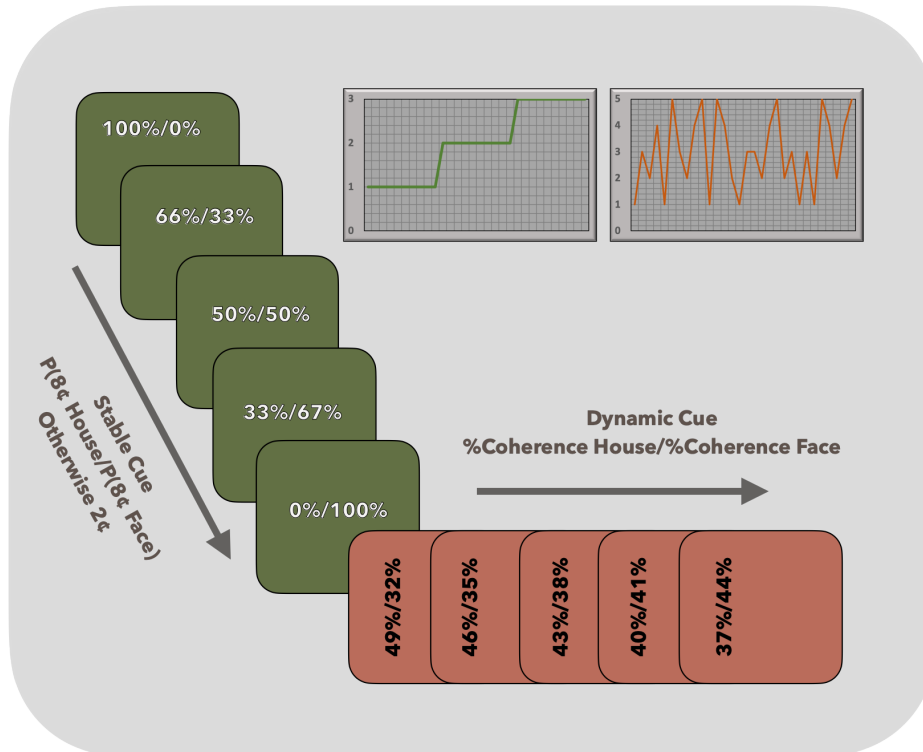
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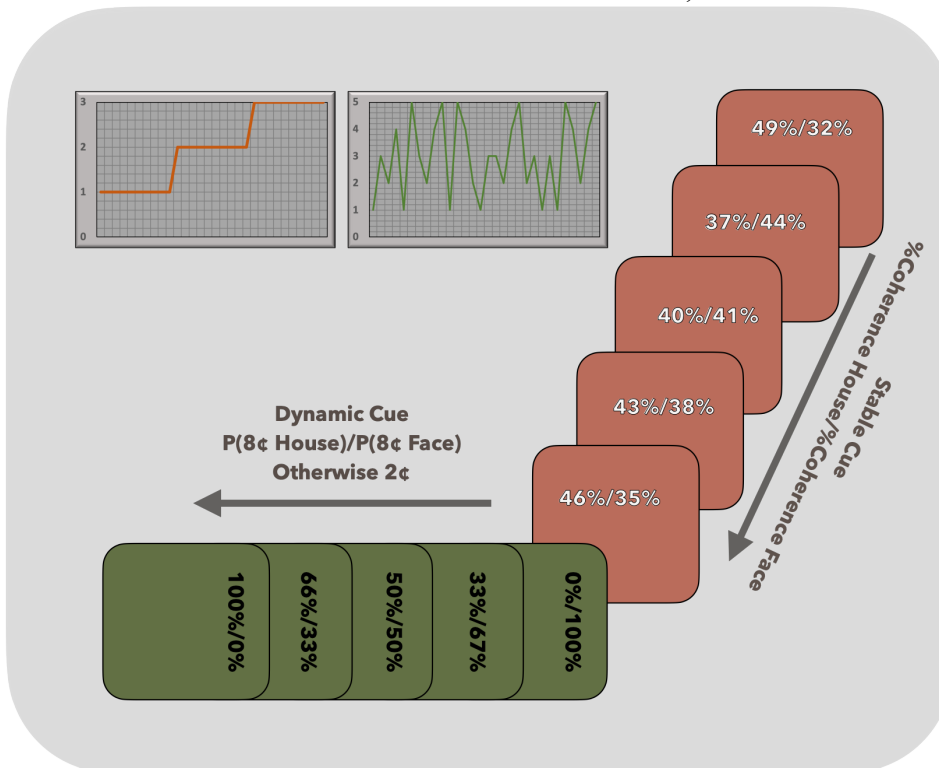
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APPENDIX A: TASK STRUCTURES



Task 1 Structure. Green = Run Level and Condition; Peach = Trial Level and Condition



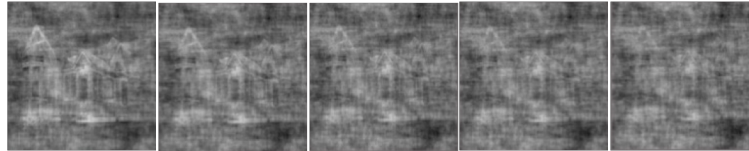
Task 2 Structure. Green = Run Level and Condition; Peach = Trial Level and Condition



Saliency 1-5

Saliency 5-1

Saliency 1



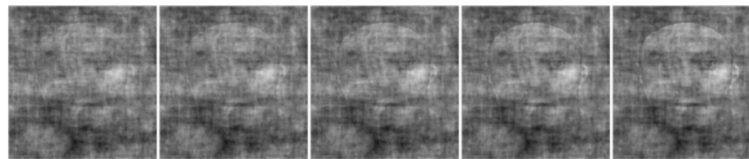
F1:H5

F2:H4

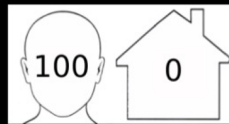
F3:H3

F4:H2

F5:H1



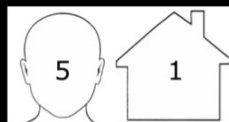
Task 1



Likelihood of receiving 8 cents for Face and House.
Otherwise 2 cents.

5F:1H

Task 2



Clarity level of face and house.

100F:0H

Examples. Stimulus types; Examples of target coherence manipulation, Example of run and trial cue for task 1 and task 2. Face stimuli were provided by the Max-Planck Institute for Biological Cybernetics in Tuebingen, Germany (Troje & Bülthoff, 1996).

APPENDIX B: POST-EXPERIMENT DEBRIEFING

(Administered following each session)

Please answer these questions honestly. There are no correct or incorrect answers.

1. Do you have any questions or concerns about the study?

2. Did you maintain your gaze at the center of the screen for the entire task?

3. Did you notice any patterns with respect to the images you saw on the screen? If so, describe.

4. How difficult was the **first experiment** you completed on the following scale?
 - a. 1 (Too easy)
 - b. 2 (Not very difficult)
 - c. 3 (Reasonably difficult)
 - d. 4 (Very difficult but do-able)
 - e. 5 (Too difficult)

Why?:

5. How difficult was the **second experiment** you completed on the following scale?
 - a. 1 (Too easy)
 - b. 2 (Not very difficult)
 - c. 3 (Reasonably difficult)
 - d. 4 (Very difficult but do-able)
 - e. 5 (Too difficult)

Why?:

6. What were the strategies you used to complete each task?

7. **For the following question, the word “detect” is defined as which image(s) you could see, not necessarily which image you tended to select more.**

Please select the following statement you most agree with:

- a. The houses were generally easier for me to detect (see) than the faces
- b. The faces were generally easier for me to detect (see) than the houses
- c. I detected (saw) faces and houses equally
- d. I detected (saw) cars more easily than faces or houses

Was this different between experiment 1 and 2? If yes, describe how below:

8. Please select the following statement you agree with most:

- a. Most of the time, when I selected car, I was actually trying to find the face
- b. Most of the time, when I selected car, I was actually trying to find the house
- c. Sometimes, when I selected car, I was trying to find a face, and other times, I was trying to find a house. My selection of car did not depend on which picture I was looking for.
- d. I never selected a car

Was this different between experiment 1 and 2? If yes, describe how below:

9. How frequently did you pay attention to the outcome that came after each trial?

- a. Not at all
- b. Occasionally
- c. Sometimes
- d. Frequently
- e. Always

Was this different for experiment 1 and 2? If yes describe how below:

10. Please select the following statement you agree with most:

- a. When the outcome was shown, I mainly wanted to know which image I chose in that trial, rather than how much I won.
- b. When the outcome was shown, I mainly wanted to know how much I won in that trial, rather than which image I chose.
- c. When the outcome was shown, I wanted to know which image I chose and how much I won equally.
- d. I did not attend to the outcome.

Was this different between experiment 1 and 2? If yes describe how below:

11. For the **first experiment** you completed, how frequently did feedback about the **image** (what you chose on each trial), change your behavior in future trials?
- a. Not at all
 - b. Occasionally
 - c. Sometimes
 - d. Frequently
 - e. Always

If you could rate the percentage of time feedback about the **image you chose** changed your behavior from 0-100 in the **first experiment**, what would you say?

12. For the **second experiment** you completed, how frequently did feedback about the **image** (what you chose on each trial), change your behavior in future trials?
- a. Not at all
 - b. Occasionally
 - c. Sometimes
 - d. Frequently
 - e. Always

If you could rate the percentage of time feedback about the **image you chose** changed your behavior from 0-100 in the **second experiment**, what would you say? _____

13. For the **first experiment** you completed, how much did feedback about the **reward** (how much you earned after each trial), change your behavior in future trials?
- a. Not at all
 - b. Occasionally
 - c. Sometimes
 - d. Frequently
 - e. Always

If you could rate the percentage of time feedback about the **reward** changed your behavior from 0-100 in the **first experiment**, what would you say?

14. For the **second experiment** you completed, how much did feedback about the **reward** (how much you earned after each trial), change your behavior in future trials?
- a. Not at all
 - b. Occasionally
 - c. Sometimes

- d. Frequently
- e. Always

If you could rate the percentage of time feedback about the **reward** changed your behavior from 0-100 in the **second experiment**, what would you say?

15. For the **first experiment** you completed, consider the trials when the **image you picked** was not the one you intended to pick. How much did this bother you?
- a. Not at all
 - b. A little bit
 - c. Somewhat
 - d. A Moderate amount
 - e. Very Much
 - f. There were no trials where I picked an image that was different from what I intended on picking.
16. For the **second experiment** you completed, consider the trials when the **image you picked** was not the one you intended to pick. How much did this bother you?
- a. Not at all
 - b. A little bit
 - c. Somewhat
 - d. A Moderate amount
 - e. Very much
 - f. There were no trials where I picked an image that was different from what I intended on picking.
17. For the **first experiment** you completed: consider the trials when the **reward** you expected was not the one you received. How much did this bother you?
- a. Not at all
 - b. A little bit
 - c. Somewhat
 - d. A Moderate amount
 - e. Very much
 - f. There were no trials that I earned a reward that was different from what I expected in that trial.
18. For the **second experiment** you completed: consider the trials when the **reward** you expected was not the one you received. How much did this bother you?
- a. Not at all
 - b. A little bit
 - c. Neutral
 - d. A Moderate amount
 - e. Very much

- f. There were no trials that I earned a reward that was different from what I expected in that trial.
19. For the **first experiment** you completed: how frequently did you attend to the cue that came **before the trial**?
- a. Not at all
 - b. Occasionally
 - c. Sometimes
 - d. Frequently
 - e. Always
20. For the **second experiment** you completed: how frequently did you attend to the cue that came **before the trial**?
- a. Not at all
 - b. Occasionally
 - c. Sometimes
 - d. Frequently
 - e. Always
21. For the **first experiment** you completed: how frequently did you recall the cue that came at the **beginning of the run**?
- a. Not at all
 - b. Occasionally
 - c. Sometimes
 - d. Frequently
 - e. Always
22. For the **second experiment** you completed: how frequently did you recall the cue that came at the **beginning of the run**?
- a. Not at all
 - b. Occasionally
 - c. Sometimes
 - d. Frequently
 - e. Always

APPENDIX C: ACTIVATION TABLES REWARD TASK 1

Activation Tables for Cortical (Uncorrected $p = .05$, Cluster Threshold = 50) and Subcortical (Uncorrected $p = .05$, Cluster Threshold = 5) regions from Reward Main Effect Task 1. Coordinates are center of mass (CM).

Task 1 Reward Main Effect Cortical Activation Table

#Voxels	CM			Region
	CM x	CM y	z	
244	0.7	-38.7	18.2	L Anterior Cingulate Cortex
208	26.4	53.5	-8.7	L Parahippocampal Area (ventromedial visual area)
189	-34.5	81.9	18.5	R Middle Occipital Gyrus/V3
188	25.3	91.4	14	L Middle Occipital Gyrus
134	-47.9	9.7	-16	R Superior Temporal Sulcus
97	22.8	69.1	51.4	L Medial Intraparietal Area/Superior Parietal Lobule
92	-26.5	48.4	-11.6	R Parahippocampal Area (ventral visual complex)
86	43.2	-11.7	-14.2	L Anterior Agranular Insula
67	26.7	8.7	43	L Premotor Cortex
66	-25.5	96.3	-2.1	R Primary Visual Cortex (V1)
63	47	68.4	3.1	L V5/MT+
55	-25.1	67.3	50.1	R Medial Intraparietal Area/Superior Parietal Lobule
51	11.2	68.3	-51.7	Left Cerebellum (VIII)

Task 1 Reward Main Effect Subcortical Activation Table

#Voxels	CM x	CM y	CM z	Region
35	8	-15.7	-1	L Ventral Caudate
25	-9.5	-13.3	3.4	R Ventral Caudate
8	7.5	19.5	12.3	L Thalamus
7	-29.9	7.2	-1.4	R Dorsolateral Putamen
6	32	5.3	-4.5	L Dorsolateral Putamen
6	11.8	-13.2	14.7	L Dorsal Caudate
5	28.4	11.3	-3	L Dorsolateral Putamen

APPENDIX D: ACTIVATION TABLES REWARD TASK 2

Activation Tables for Cortical (Uncorrected $p = .05$, Cluster Threshold = 50) and Subcortical (Uncorrected $p = .05$, Cluster Threshold = 5) regions from Reward Main Effect Task 2.

Task 2 Reward Main Effect Cortical Activation Table

# Voxels	CM x	CM y	CM z	Region
464	1.3	89.5	24.6	Bilateral Cuneus
365	33.9	-22.4	3.8	L Insula
358	-35.5	-24.5	0.9	R Insula
348	-3.3	-30.1	38	R Medial Frontal Gyrus (BA 8)
309	-33.9	60.7	44.5	R Medial Intraparietal Area
202	43.1	47.6	48	L Inferior Parietal Lobule
185	-13.3	67.7	41.3	R Precuneus
146	50.5	-6.8	27.5	L Precentral Gyrus
143	45.5	72	36	L Inferior Parietal Lobule
141	12.6	-60.8	29.1	L Superior Frontal Gyrus
135	2.6	-58.1	-9.6	L Ventromedial Prefrontal Cortex
128	-43.1	-36.8	23.9	R Dorsolateral Prefrontal Cortex
119	-44	-10.5	28.6	R Inferior Frontal Junction
111	1.7	20.5	-12.7	L Red Nucleus/Brain Stem
104	1.8	49.4	30.6	L Posterior Cingulate Cortex
98	41.7	-41.8	7.5	L Dorsolateral Prefrontal Cortex
97	13.6	71.9	39.8	L Superior Parietal Lobule
91	-39.8	75.8	-13.3	R Fusiform Gyrus
89	-22.8	-40.9	-15.3	R Orbitofrontal Gyrus (BA 11)
88	-8.3	24.9	58.4	R Primary Motor Cortex
69	35.4	44.3	-9.8	L Parahippocampal Gyrus
65	5.5	-44.5	-1.9	L Anterior Cingulate Cortex
62	7.5	63.7	20.3	L Parieto-occipital Gyrus
56	-11.6	35.3	70.3	R Primary Sensory Cortex
52	-11.8	93.1	0.4	R Calcarine Gyrus

Task 2 Reward Main Effect Subcortical Activation Table

#Voxels	CM x	CM y	CM z	Region
13	22.9	1.1	-1.3	L Ventromedial Putamen
10	11.4	10.4	13.2	L Thalamus
10	19	-2.5	18.7	L Dorsal Caudate
8	-7.2	14.4	-2.3	R Thalamus
8	-11.2	-19.6	7.1	R Dorsal Caudate
7	-14.4	-12.8	4.8	R Dorsal Caudate
6	11.2	21	13	L Thalamus
5	10.8	-13.9	-7.8	L Ventral Caudate
5	15.1	-20.8	3	L Ventral Caudate

APPENDIX E: ACTIVATION TABLES SALIENCE TASK 1

Activation Tables for Cortical (Uncorrected $p = .05$, Cluster Threshold = 50) and Subcortical (Uncorrected $p = .05$, Cluster Threshold = 5) regions from Salience Main Effect Task 1.

Task 1 Salience Main Effect Cortical Activation Table*

# Voxels	CM x	CM y	CM z	Region
978	40.4	60.3	44.4	L Inferior Parietal Lobule
809	54.3	45	-8	L Fusiform Gyrus
627	-38.1	67.5	41	R Superior Parietal Lobule
478	46.2	-15.1	33.3	R Frontal Eye Fields
470	3.3	73.6	15.4	R Cuneus
348	-7	-36.7	47	R Dorsomedial Prefrontal Cortex
288	-61.4	32.9	-10.8	R Superior Temporal Sulcus
255	-2.8	57.1	39.7	R Precuneus
245	-40.6	64.6	-18.5	R Inferior Temporal Gyrus
233	44.5	-45.8	-3.8	L Inferior Frontal Gyrus (BA 47)
228	-44.2	-18.3	34.7	R Inferior Frontal Junction
226	-30.3	47.6	-13.8	R Ventromedial Visual Area
198	20.6	-60.1	-7.5	L Orbitofrontal Cortex /Ventromedial Prefrontal Cortex
179	32.5	-21.7	-1.8	L Anterior Insula
137	-33.2	-22.7	-1	R Anterior Insula
132	-59.1	53.8	14.8	R Temporo Parietal Junction
123	-48.3	-33.3	23.3	R Dorsolateral Prefrontal Cortex
101	34.9	87.8	19.6	L Middle Occipital Area
97	33.5	23.1	65.9	L Primary Motor Cortex
96	17	-53.5	33.9	L Superior Frontal Gyrus
91	47.1	8.2	-36.4	L Anterior Inferior Temporal Lobe
91	2	31.6	68	L Primary Motor Cortex
88	0.3	24.5	37.2	Bilateral Posterior Cingulate Cortex
69	52.9	-32.8	15.2	L Dorsolateral Prefrontal Cortex
68	29.1	39.3	63	L Postcentral Gyrus
64	-17.2	84.8	-12.1	R V3
62	31.1	5.2	-11.9	L Parainsular Area
56	43.9	30.7	20.1	L Superior Temporal Gyrus
52	39	82.8	-35.6	L Cerebellum (Crus II)
50	14.9	-32.1	57.1	L Superior Frontal Gyrus

49	-15.5	-69.9	9.6	L Superior Medial Frontal Gyrus
44	-33.3	14.7	-33.1	R Entorhinal Cortex
37	49.5	81.7	-7.7	L Posterior Inferotemporal area
37	-15.7	68.6	17.2	R Calcarine Gyrus
36	41.9	7.5	9.3	L Posterior Insula
35	-26	-62.9	-9.4	R Anterior Prefrontal Cortex
33	19.9	-66.8	13.9	L Anterior Prefrontal Cortex
31	-18.1	60.2	4.1	R Calcarine Gyrus
30	-36.5	88	11	R V4
29	-45.7	39.8	52.3	R Inferior Parietal Lobule
28	-7.7	44.6	18.9	R Reterosplenial Complex
26	-56.1	1.1	-31.1	R Anterior Inferior Temporal Gyrus
26	-47.7	61.3	-1.5	R VT/MT+
26	12.5	18.3	74.9	L Precentral Gyrus
25	-32.2	77	-37.6	R Cerebellum Crus I
25	-18.2	33.1	0.7	R Hippocampus
24	11.8	88.8	-33.6	L Cerebellum (Crus II)
24	-34.8	14.2	-9.6	R Posterior Insula
23	-59.3	21.3	-25.6	R Inferior Temporal Gyrus
23	-14.6	19.9	5.8	R Thalamus
23	25.9	-30.6	39.4	R Middle Frontal Gyrus
22	28.1	9.7	-26.8	L Hippocampus
22	14.5	19.5	8.2	L Thalamus
21	60.3	43	-22	L Inferior Temporal Gyrus

* Due to large cluster sizes that spanned several regions, cluster threshold was increased to uncorrected .03 for cortical regions and cluster size decreased to 20 voxels.

Task 1 Salience Main Effect Subcortical Activation Table

#Voxels	CM x	CM y	CM z	Region
58	12.7	20.5	6.7	L Thalamus
33	-14.5	19.1	7.2	R Thalamus
17	-4.6	-9.9	-0.9	R Ventral Caudate
16	11.3	-9.6	8.8	L Dorsal Caudate
8	10.7	-16.6	1.4	L Ventral Caudate

APPENDIX F: ACTIVATION TABLES SALIENCE TASK 2

Activation Tables for Cortical (Uncorrected $p = .05$, Cluster Threshold = 50) and Subcortical (Uncorrected $p = .05$, Cluster Threshold = 5) regions from Salience Main Effect Task 2.

Task 2 Salience Main Effect Cortical Activation Table

# Voxels	CM x	CM y	CM z	Region
618	-20.3	64.9	-43.2	R Cerebellum Crus 2
277	-38.7	80.1	20.7	R Intraparietal
274	-50.8	62.3	-4.3	R V5 MT+
263	-50	61	42.2	R Inferior Parietal Lobule
240	51.4	68.8	4.4	L Temporoparietal Junction
239	32.3	83	26.5	L Inferior Parietal Lobule
211	62.4	35.8	32.1	L Supramarginal Gyrus
206	40.8	-18.7	-3.1	L Superior Temporal Gyrus
196	27.9	-1.7	58.1	L Anterior Precentral/Posterior Middle Frontal Gyrus
189	31.7	64.4	-54	L Cerebellum VII
178	46.7	-5.8	24.2	L Rostral Precentral (BA 6)
164	6	-11.9	41.5	L Middle Cingulate Cortex
154	20.2	62.8	63.9	L Intraparietal Lobule/Superior Parietal Lobule
134	-45.7	-11.6	30.2	R Inferior Frontal Junction
125	-30.1	46.2	-10.8	R Parahippocampal Area
116	41.8	-33.1	17.1	L Dorsolateral Prefrontal Cortex
112	-35.6	-24.8	-7.5	R Anterior Ventral Insula
99	-12.8	29.8	45	R ventral BA 5/Middle Cingulate Cortex
82	27.9	69.9	-17.8	L Cerebellum (VI)
81	-47.3	59.8	-30.6	R Cerebellum Crus 1
79	8.4	39.2	51.9	L Middle Cingulate Cortex
73	-37.2	2.1	55	R Inferior 6-8 Transitional Area
73	-3.7	17.4	71.4	R Primary Motor Cortex
65	31.2	48	-8.7	L Parahippocampal Area
60	-60.6	29.6	43.1	R Supramarginal Gyrus
58	-1.1	44.7	-28.8	R Cerebellum
54	-41.3	-27.7	43.4	R Middle Frontal Gyrus
54	-16.4	62.6	64	R Ventral Intraparietal Area
53	24	48.9	-36.5	L Cerebellum (VIII)
50	21.1	-36.5	37.4	L Middle Frontal Gyrus

Task 2 Salience Main Effect Subcortical Activation Table

#Voxels	CM x	CM y	CM z	Region
27	-5.8	10.8	-0.4	R Thalamus
13	2.1	17.6	3.5	L Thalamus
10	15.8	-6.1	13.5	L Dorsal Caudate
8	-13	-15.3	8	R Dorsal Caudate
7	-17.8	-14.4	-1.8	R Ventromedial Putamen
6	-28.7	-5	5.7	R Dorsolateral Putamen
5	26.9	13.3	9.9	L Dorsolateral Putamen