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What do you expect?: fMRI of Expected Utility

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Abstract: Anticipated reward magnitude and probability comprise dual components of Expected Utility (EU), a cornerstone of economic and psychological theory. However, the neural mechanisms that compute EU have not been characterized. Using event-related functional MRI, we examined neural activation as subjects anticipated monetary gains and losses varying in magnitude and probability. Group analyses indicated that while the subcortical nucleus accumbens (NAcc) shows activation proportional to anticipated gain magnitude, the cortical mesial prefrontal cortex (MPFC) activated according to anticipated gain probability, as well as EU. Individual difference analyses indicated that while NAcc activation correlated with self-reported positive arousal, MPFC activation correlated with probability estimates. These results suggest that mesolimbic brain regions support the computation of EU in a distributed fashion – while subcortical regions compute an affective component, cortical regions compute a probabilistic component, and may integrate the two.

Introduction

All organisms, from bees to bridge players, must forecast the future in order to decide what to do next. To choose optimally, they must consider both the potential value of different courses of action and the probability that each will lead to a desired outcome. These considerations join in the concept of Expected Utility (EU), which has played a prominent role in both economic and psychological theory (von Neumann and Morgenstern, 1944; Rotter, 1972; Bandura, 1977). Originally proposed by D. Bernoulli in 1738 to account for gamblers' reluctance to accept risky bets with infinite potential payoffs, EU can be calculated as a product of the (nonlinear scaled) magnitude and probability of anticipated future outcomes (Bernoulli, 1738 / 1954; Mas-Colell et al., 1995). Currently, the extent to which neural mechanisms that compute these variables are unitary or separable remains unclear. Additionally, while computation of EU has traditionally been conceptualized as involving reflective acts of deliberation, recent evidence suggests that affective reactions may also figure into the equation (Loewenstein et al., 2001; Slovic et al., 2002).

The goal of this study was to identify neural substrates that support the computation of EU, and to characterize their psychological functions. By definition, the brain must compute EU prior to incentive outcomes. The spatial and temporal resolution of event-related functional magnetic resonance imaging (fMRI) affords researchers the opportunity to ask where and when these computations might occur. While prior fMRI research has examined brain activity during anticipation of incentives (Breiter et al.,

2001; Knutson et al., 2001a; O'Doherty et al., 2002), investigators have not yet simultaneously varied expected incentive valence, magnitude, and probability and observed their combined effect on anticipatory brain activation. Generally, we predicted that EU-computing regions should show increased activity during anticipation of large magnitude, high probability gains.

Comparative theorists have proposed that regions innervated by mesolimbic dopamine projections play a critical role in the computation of EU (Gallistel, 1986; Shizgal, 1997), so specific predictions focused on mesolimbic regions. Because fMRI studies of humans indicate that anticipation of monetary gains proportionally increases blood oxygen level dependent contrast (hereafter, "activation") in the subcortical nucleus accumbens (NAcc) (Breiter et al., 2001; Knutson et al., 2001a), we predicted that anticipation of large magnitude gains (but not losses) would increase NAcc activation. Becuase fMRI studies also indicate that gain outcomes instead activate the mesial prefrontal cortex (MPFC) (Delgado et al., 2000; Elliott et al., 2000; Knutson et al., 2001b), and because outcomes involve a collapse of probability, we predicted that increased gain probability would increase MPFC activation, even during anticipatory delays. Because midbrain dopamine neurons that project to the NAcc and MPFC have also been implicated in the computation of variables related to EU (Schultz et al., 1997; Montague and Berns, 2002), we examined midbrain activity during anticipation of gains and losses. Finally, we examined whether NAcc activation covaried with individual differences in positive aroused reactions (e.g., feelings of excitement) to gain cues, and whether MPFC activation instead covaried with the perceived probability of obtaining gains.

Methods

Twelve healthy volunteers (6 women and 6 men, right-handed, mean age 22) participated in the study. Prior to enrolling, volunteers were screened for physical and mental disorders (including neurological damage and abnormal cardiac function) via a medical interview. All subjects gave written informed consent, and the experiment was approved by the Institutional Review Board of the Stanford University Medical School. Before entering the scanner, subjects received a verbal description of the task, completed a practice version (10 min) to minimize learning effects in the scanner, and were tested on what each of the incentive cues indicated. Subjects were also physically shown the money that they could earn by performing the task successfully in the scanner, and all reported believing that they would receive cash contingent on their performance at the end of the experiment. Once in the scanner, anatomical scans were acquired. Subjects then engaged in four 10 min blocks of the incentive task during functional scan acquisition. Following the scan, subjects rated their affective reactions to the different cues on 7-point Likert scales, estimated the probability of success for each cue type, and were tested a second time to ensure that they understood the meaning of each cue.

Probabilistic monetary incentive delay (MID) task. The probabilistic variant of the MID task included 288 8-sec trials. During each trial, subjects saw one of eighteen shapes formed by varying three features (cue; 2000 ms), then focused on a fixation cross (x) while waiting for a variable anticipatory delay period (anticipation; 2000–2500 ms), and then responded with a button press to the appearance of a solid white square (target; 160-

310 ms). Following a short delay, subsequent feedback notified subjects whether they had won or lost money as well as their cumulative total (outcome; 2000 ms) (see Figure 1). Each of 18 trial types was presented 16 times in an individually randomized order.

Cue features were counterbalanced and signaled the incentive value of each trial: shape (circle, square) indicated valence (potential gain or loss); position of a vertical line (left, middle, right) indicated magnitude ($0.00, $1.00, $5.00); and position of a horizontal line (high, middle, low) indicated probability of success (high, medium, low). Expected probability was manipulated by altering the average target speed via an adaptive timing algorithm that followed subjects' performance, such that they would succeed on approximately 80% of high probability trials, 50% of medium probability trials, and 20% of low probability trials overall. Before playing, subjects were instructed which cue features indicated that they had a high, medium, or low chance of success, but were not informed of percentage estimates. fMRI volume acquisitions were time-locked to cue onsets.

fMRI acquisition. Imaging was performed using a 1.5-T General Electric MRI scanner with a standard quadrature head coil. Twenty-four 4-mm-thick slices (in-plane resolution 3.75 X 3.75 mm, no gap) extended axially from the mid-pons to the top of the skull, which provided adequate spatial resolution of subcortical regions of interest (e.g., midbrain, ventral striatum), and omitted only the base of the cerebellum or crown of the skull in some subjects. Functional scans of the whole brain were acquired every 2 sec (TR = 2 sec) with a T2*-sensitive in-/out- spiral pulse sequence (TE = 40 ms, flip = 90°)

specifically designed to minimize signal dropout at the base of the brain (Glover and Law, 2001). High-resolution structural scans were subsequently acquired using a T1-weighted spoiled grass sequence (TR = 100 ms; TE = 7 ms, flip = 90°), which facilitated subsequent localization and coregistration of functional data.

fMRI analysis. Analyses focused on changes in activation specifically during anticipatory delay periods, (i.e., after subjects saw cues, but before they responded to targets), but analysis of cue periods yielded similar results. All analyses were conducted using Analysis of Functional Neural Images (AFNI) software (Cox, 1996). For preprocessing, voxel time series were sinc interpolated to correct for nonsimultaneous slice acquisition within each volume, concatenated across runs, and corrected for three-dimensional motion. Visual inspection of motion correction estimates confirmed that no subject's head moved more than 2.0 mm in any dimension from one volume acquisition to the next. Preprocessed time series were submitted to a regression model which consisted of six regressors indexing residual motion, twelve regressors modeling baseline, linear, and quadratic trends for each of the four runs, one regressor of noninterest which "highlighted" anticipatory delays by contrasting them with the remainder of each trial to covary out general anticipation effects. Fully orthogonalized regressors of interest contrasted cued (1) VAL: positive versus negative valence, (2) MAG: $5.00 versus $0.00 magnitude, (3) PRB: 80% vs. 20% probability; (4) VAL X MAG, (5) VAL X PRB, (6) MAG X PRB, and (7) EU: VAL X MAG X PRB.

Anticipatory and regressors of interest were convolved with a gamma-variate function that modeled a canonical hemodynamic response prior to inclusion in regression models (Cohen, 1997). Maps of t-statistics for regressors of interest were transformed into Z-scores, coregistered with structural maps, spatially normalized by warping to Talairach space, slightly spatially smoothed (FWHM = 4 mm) to minimize the effects of anatomical variability, resampled at 2 mm^3, and combined into a group map using a meta-analytic formula (average Z*sqrt(n)) (Knutson et al., 2000). Foci activation thresholds were determined by False Discovery Rate ($Z>3.24$, $p<.05$, corrected) (Genovese et al., 2002), and required a minimum cluster of 4 contiguous voxels. Volumes of interest (VOIs) were specified by imposing 6 mm diameter spheres at peak activation foci in regions of interest in the midbrain, NAcc, and MPFC. Activation time-courses were extracted and averaged from these VOIs by trial type. Trial averaged activation values at a 4 second lag were then analyzed with 2 (VAL) X 3 (MAG) X 3 (PRB) analyses of variance (ANOVAs) for each VOI. Significant interactions were verified with Tukey's HSD tests ($p<.05$, corrected).

Behavior and Affect. Hits were calculated as percentage correct responses per condition. Ratings of cue-elicited valence and arousal were mean-deviated within-subject and rotated by 45 degrees to derive measures of positive and negative arousal (i.e., PA=arousal/sqrt(2) + valence/sqrt(2); NA=arousal/sqrt(2) - valence/sqrt(2)). Actual and estimated hit rate as well as cue-elicited affect for each trial type were analyzed with 2 (valence) X 3 (magnitude) X 3 (probability) repeated measures ANOVAs. Significant main effects or interactions were verified with Tukey's HSD tests ($p<.05$, corrected).

Estimated hit rate and affect were also correlated across subjects with activation in volumes of interest.

Manipulation checks established that cues had their intended effects on behavior and affect. Behaviorally, cue probability features predicted performance ($F(2,20)=984.87$, $p<.001$), indicating the effectiveness of the adaptive timing manipulation. Mean hit rates (SEM) were 23.40% (0.74) for 20% trials, 51.74% (0.85) for 50% trials, and 77.50% (0.61) for 80% trials. Subjects' hit rate estimates also showed a main effect of probability ($F(2,20)=70.47$, $p<.001$), indicating that they were aware of cue meaning. Mean hit rate estimates (SEM) were 17.05% (3.80) for 20% trials, 50.5% (4.22) for 50% trials, and 77.2% (5.48) for 80% trials. Additionally, reaction time for hits did not differ between gain and loss trials of the same magnitude, as illustrated by main effects of magnitude ($F(2,20)=4.65$, $p<.05$) and probability ($F(2,20)=31.12$, $p<.001$), but not valence, on reaction time.

On the other hand, a combination of cue valence and magnitude elicited differential affective reactions, as predicted. Cue-elicited positive arousal showed main effects of cue valence ($F(1,10)=69.85$, $p<.001$) and magnitude ($F(2,20)=39.14$, $p<.001$), qualified by the predicted interaction of cue valence and magnitude ($F(2,20)=29.00$, $p<.001$), as well as a separate interaction of cue magnitude and probability ($F(4,40)=5.06$, $p<.005$). Tukey's HSD tests indicated that subjects responded with more positive arousal to gain and loss cues than to nonincentive cues and with more positive arousal to gain cues than to loss cues of equivalent magnitude. Cue-elicited negative arousal showed main effects

of cue valence ($F(1,10)=57.79$, $p<.001$) , magnitude ($F(2,20)=73.75$, $p<.001$), and probability ($F(2,20)=30.07$, $p<.001$), qualified by the predicted interaction of valence and magnitude ($F(2,20)=28.67$, $p<.001$). Tukey's HSD tests indicated that subjects reacted with greatest negative arousal to large and small magnitude loss cues relative to all other conditions, and to cues indicating a low probability of success, followed by medium and high probability cues.

Results

Group analyses of FMRI data indicated that mesolimbic regions responded to different components of EU (see underlined regions in Table 1). The main effect of VAL activated foci in regions of interest including the left insula, left NAcc, and right caudate head. The main effect of MAG activated a large number of foci, including dorsolateral prefrontal cortex, anterior cingulate, supplementary motor area, bilateral insula, bilateral caudate head, thalamus, and midbrain. In addition, the main effect of MAG deactivated foci in the left MPFC and right parahippocampal gyrus. The VAL X MAG interaction activated foci in the bilateral NAcc, as predicted, in addition to bilateral MPFC, bilateral caudate head, dorsomedial thalamus, as reported previously (Knutson et al., 2001a).

The main effect of PRB activated foci in the bilateral MPFC, as predicted, while deactivating foci in the anterior cingulate, left insula, bilateral caudate head, and right putamen. The interaction of VAL X PRB did not activate any of the regions of interest, while the interaction of MAG X PRB deactivated only the bilateral caudate head and right putamen (not listed in Table 1). Finally, the interaction of VAL X MAG X PRB

(EU) activated foci in the left MPFC, left anterior cingulate, and left medial temporal gyrus (see Figure 2).

Target foci in the midbrain (corresponding to MAG), NAcc (corresponding to VAL X MAG), and MPFC (corresponding to PRB and EU) were used to construct volumes of interest (VOIs) for individual difference analyses. VOI analysis of midbrain activation yielded only a main effect of magnitude ($F(2,22)=9.61$, $p<.001$). Tukey's HSD tests indicated that activity was greater for anticipation of large than small incentives. The apparent symmetry of this effect for anticipation of gains and losses was inconsistent with computation of EU.

VOI analysis of left NAcc focus (associated with VAL X MAG) yielded main effects of magnitude ($F(2,22)=14.83$, $p<.001$) and probability ($F(2,22)=3.69$, $p<.05$), qualified by the predicted interaction of valence by magnitude ($F(2,22)=6.14$, $p<.05$). Tukey's HSD tests indicated that anticipation of large gains elicited greater activation than anticipation of small gains and nongains, replicating prior findings. Anticipation of large losses also elicited greater activation than anticipation of small losses, but anticipation of large gains elicited greater activation than anticipation of large losses, consistent with computation of the utility term (i.e., VAL X MAG) of EU. On the other hand, VOI analysis of the right NAcc focus instead yielded only main effects of MAG ($F(2,22)=9.53$, $p<.005$), and PRB ($F(4,44)=4.93$, $p<.05$), inconsistent with EU computation.

VOI analysis of the left MPFC focus (associated with PRB) yielded the predicted main effect of PRB ($F(2,22)=6.70$, $p<.05$). Tukey's HSD tests indicated that anticipation of high probability incentives elicited greater activation than anticipation of low probability incentives. Thus, left MPFC activation was consistent with calculation of the probability term of EU. Right MPFC activation showed only a nonsignificant trend for a main effect of PRB.

VOI analysis of the left MPFC focus associated with EU yielded the predicted interaction of VAL X MAG X PRB ($F(4,44)=2.69$, $p<.05$), but Tukey's HSD did not reveal significant difference between specific conditions. Similarly, VOI analysis of the anterior cingulate focus associated with EU yielded a VAL X MAG X PRB interaction ($F(4,44)=3.18$, $p<.05$), but Tukey's HSD did not reveal significant differences between specific conditions

Psychologically, if the NAcc supports a more affective computation involving projection of an outcome's promise, then individuals who show the strongest NAcc activation to large gain cues (which elicit the greatest activation) should also report having the most positive aroused reactions. On the other hand, if the MPFC supports a more reflective computation involving consideration of an outcome's probability, then individuals who show the greatest discrepancy in MPFC activation for high versus low probability cues should instead show the largest difference between the perceived probability of success on high versus low probability trials.

Individual difference analyses supported both hypotheses. Subjects with greater left NAcc activation to the +$5.00 cues also reported greater positive arousal in reaction to those cues ($r=0.52$, $p<.05$, one-tailed), replicating prior reports that NAcc activity predicts positive arousal during gain anticipation (Knutson et al., 2001a; Bjork et al., 2004). Subjects who showed a greater disparity in MPFC activation in response to high versus low probability +$5.00 cues also estimated a greater difference between the likelihood of succeeding on high versus low probability trials ($r=0.63$, $p<.05$, one-tailed; Figure 2).

Discussion

In this initial study of the neural correlates of EU, distinct mesolimbic regions preferentially responded to different components of EU. Specifically, while anticipated gain magnitude activated the NAcc, anticipated probability instead activated the MPFC, as did their interaction. Additionally, individual difference analyses suggested that while NAcc activation correlated with positive arousal during gain anticipation, MPFC activation instead correlated with anticipated gain probability. Together, these findings add human support to theories that mesolimbic regions play a role in EU computation (Shizgal, 1997).

Novel features of the design enabled us to rule out alternate accounts of mesolimbic activation. First, the event-related construction of trials allowed specific interrogation of brain activation prior to incentive outcomes. Second, inclusion of valence as a factor allowed us to rule out sensory stimulation, arousal, salience, attention, and motor

preparation hypotheses, since analyses of behavior and affect suggested that all of these demands were equated across gain and loss conditions. Third, an adaptive timing component ensured that cued probabilities approximated subjects' actual probability of success throughout the experiment.

Group analysis indicated that two mesolimbic regions -- the NAcc and MPFC -- showed activation patterns consistent with computation of components of EU. However, VOI analyses suggested that the observed patterns of activation responded to gains more robustly than losses, since most significant differences were observed for large gains but not for losses. This result agrees with animal research suggesting that anticipated gains and losses may be processed by distinct subcortical mechanisms (Panksepp, 1998). In the realm of gains (Kahneman and Tversky, 1984), the findings suggest that the NAcc is the best candidate for computing the utility term, while the MPFC is a better candidate for computing the probability term. These findings thus contrast with theories that posit a primary role for the NAcc rather than the MPFC in the computation of probability (Breiter and Rosen, 1999; Berns et al., 2001).

In the economic literature, EU is often inferred from choice behavior (e.g., observed choices between gambles). However, to avoid circularity and truly predict choice, a definition of EU should not include the behavior that it predicts. Brain imaging technology now offers the possibility of substituting neural signals as more proximal predictors of choice. In order to isolate brain activity specifically associated with anticipation of incentives in this study, we sought to control behavioral choice. Thus, this

study cannot address whether EU predicts choice behavior or not (or which components do so). However, the findings now identify and characterize neural targets for future research that endeavors to predict individual choice behavior (Erk et al., 2002; Paulus and Frank, 2003).

Overall, the findings support a stage model of EU computation, in which people subcortically imagine potential gains, and then cortically correct for their future likelihood of occurrence. According to this proposed model, the NAcc computes gain prediction, while the MPFC computes gain prediction errors (Knutson et al., 2003). Such a model implies that organisms with diminished frontal lobe functioning such as very young or old humans and members of other species might have no problem anticipating gains, but might find it more difficult to adjust when events betray their expectations. Indeed, data from adults with selective MPFC lesions suggests that they do not show deficits in anticipating gains, but rather in framing this information in the context of other possible outcomes (Camille et al., 2004), as illustrated by the famous example of acquired impulsivity in frontal-lesioned patient Phineas Gage (Bechara et al., 2000; Camille et al., 2004).

More broadly, the findings are consistent with the notion that subcortical circuits can generate affective reactions while cortical circuits simultaneously support more reflective considerations (MacLean, 1990; Panksepp, 1998). Indeed, individual difference analyses indicated that people who showed the greatest NAcc activation also experienced the most positive arousal during gain anticipation, while people who showed the greatest disparity

in MFPC activation estimated the largest difference in the probability of success on high versus low probability gain trials. Together, these findings suggest that affect and cognition may both inhabit the same historic formula, and take neuroscientists a step closer to understanding how these forces might combine to direct economic and social choices.

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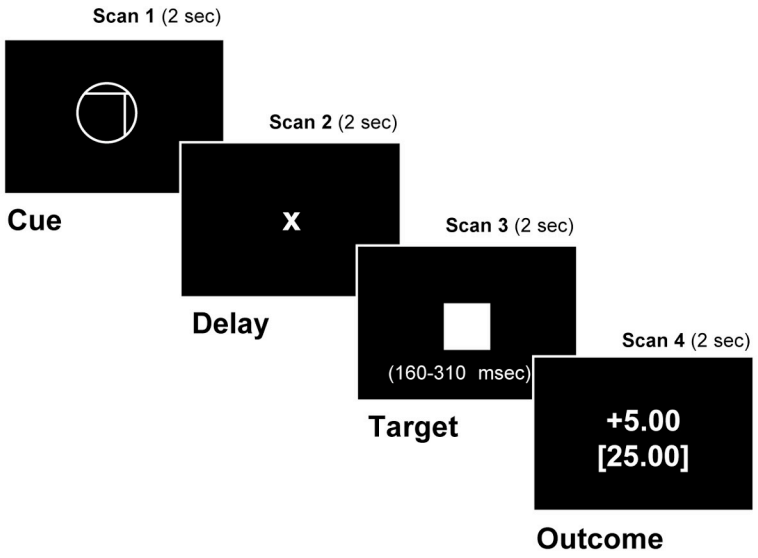
Figure Legends

Figure 1. Probabilistic MID Task trial structure.

Figure 2. Group maps illustrating the interaction of VAL X MAG (U), main effect of PRB (P), and interaction of VAL X MAG X PRB (EU). Maps are thresholded at $Z=3.24$ ($p<.05$, corrected False Detection Rate); warm colors signify activation while cool colors signify deactivation.

Figure 3. Volume of interest (VOI) analyses. (A) Activation time-courses taken from the NAcc VOI for gain trials of varying magnitudes (*+$5.00 vs +$0.00, $p<0.05$, two-tailed). (B) Correlation of self-reported positive arousal in response to +$5.00 cues with percent signal change in left NAcc VOI in response to +$5.00 cues (lag=4 sec; $r=0.52$, $p<0.05$, one-tailed). (C) Activation time-courses taken from the MPFC VOI for +$5.00 gain trials of varying probabilities (*80% versus 20% probability of success, $p<0.05$, two-tailed). (D) Correlation of percent hit estimate for high versus low probability trials with percent signal change in left MPFC VOI for high versus low probability +$5.00 gain trials (lag=4 sec; $r=0.63$, $p<0.05$, one-tailed).

Figure 1.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Cue
Scan 2 (2 sec)
x
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Scan 3 (2 sec)
(160-310 msec)
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Outcome

Figure 2.

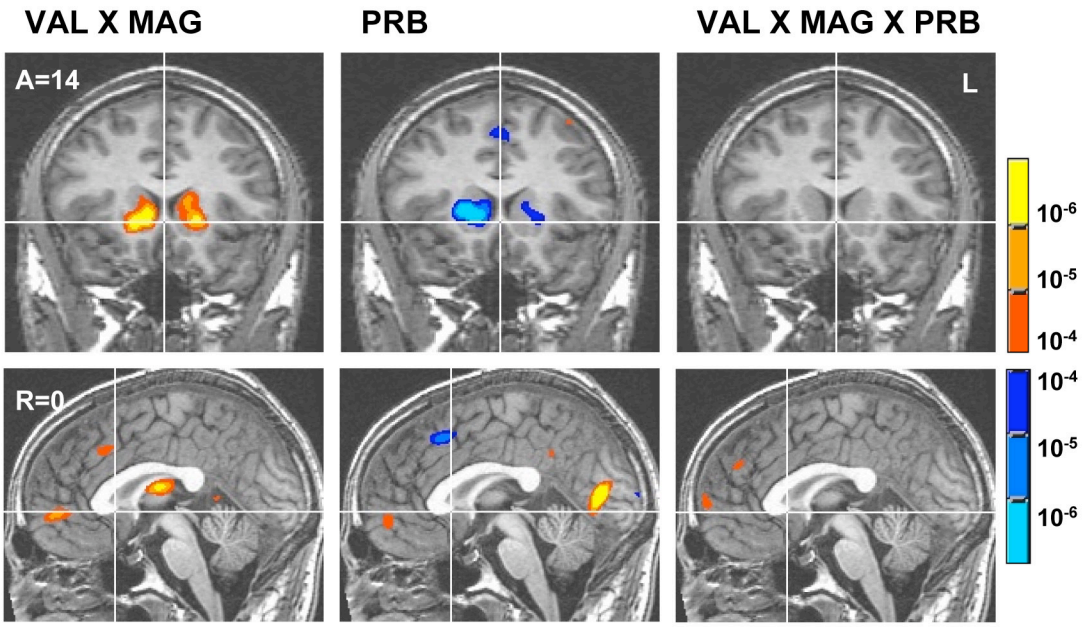

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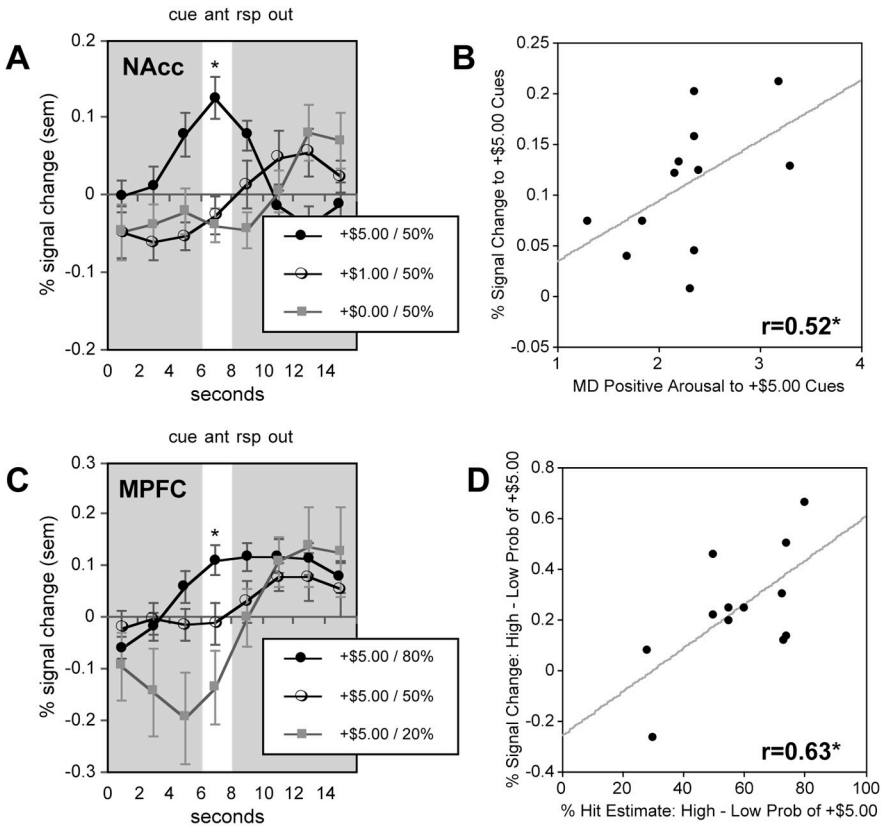
Figure 3.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r=0.63*