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Dissociating Valuation and Saliency Signals during Decision-Making

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There is a growing consensus that the brain computes value and saliency-like signals at the time of decision-making. Value signals are essential for making choices. Saliency signals are related to motivation, attention, and arousal. Unfortunately, an unequivocal characterization of the areas involved in these 2 distinct sets of processes is made difficult by the fact that, in most experiments, both types of signals are highly correlated. We dissociated value and saliency signals using a novel human functional magnetic resonance imaging decision-making task. Activity in the medial orbitofrontal, rostral anterior cingulate, and posterior cingulate cortices was modulated by value but not saliency. The opposite was true for dorsal anterior cingulate, supplementary motor area, insula, and the precentral and fusiform gyri. Only the ventral striatum and the cuneus were modulated by both value and saliency.

Keywords: attention, decision-making, motor preparation, saliency, valuation

Introduction

There is a growing consensus in behavioral neuroscience that the brain makes simple decisions by assigning values to the different stimuli under consideration and then comparing those values to make a choice (Montague and Berns 2002; Rangel et al. 2008). This has motivated much interest in locating the neural substrates of value computations at the time of choice. Multiple studies have investigated this question using human functional magnetic resonance imaging (fMRI) and monkey and rat electrophysiology (Wallis and Miller 2003; Padoa-Schioppa and Assad 2006; Kable and Glimcher 2007; Plassmann et al. 2007; Tom et al. 2007; Hare et al. 2008) and have found that activity in areas such as the medial orbitofrontal cortex (mOFC), anterior cingulate cortex (ACC), and ventral striatum (VStr) correlate with behavioral measures of stimulus value at the time of choice. These results have been widely interpreted as evidence that these areas are involved in the valuation stage of the decision-making process.

Unfortunately, identifying neural activity associated with value signals is difficult because in many experimental paradigms value and saliency signals are highly correlated: the higher valued items also attract more attention, engage higher levels of motor preparation, and lead to higher levels of emotional arousal (Maunsell 2004; Roesch and Olson 2004). As a result, without further controls, one cannot conclude that a correlation between neural activity and value implies that this activity is truly involved in value coding for the purposes of decision-making. It is important to emphasize that this potential confound is not a mere theoretical curiosity, since activity correlated with value has been found in areas traditionally associated with visual processing such as V1 (Serences 2008), areas involved in motor preparation such as the supplementary motor area (SMA) (Wunderlich et al. 2009), and areas involved in visual attention such as lateral intraparietal cortex (Platt and Glimcher 1999). Some studies have attempted to control for these types of confounds (e.g., Plassmann et al. 2007), but the existing controls have not been able to rule out this confound in all the areas that have been shown associated with valuation at the time of decision-making in human fMRI studies.

Here, we present the results of a novel human fMRI decision-making task designed to dissociate value and saliency signals at the time of choice, thus addressing this problem. Value signals provide a measure of the desirability of the stimuli, which is given by the expected amount of reward that they generate if consumed (Montague and Berns 2002; Glimcher et al. 2005; Rangel et al. 2008). Value signals are positive for appetitive stimuli and negative for aversive stimuli. In contrast, saliency signals provide a measure of the importance of the stimulus, which plays an important role in allocating attentional, motivational, and other computational processes in the brain. Saliency signals are larger for stimuli that are likely to have a larger impact in the organism, such as highly appetitive or highly aversive consumption items.

The basic idea of the experiment is simple. Subjects are shown appetitive and aversive foods, spanning a range from "strongly disliked" to "strongly liked," and are asked to indicate through a button press whether or not they want to eat them at the end of the experiment. The presence of both appetitive and aversive stimuli of varying degrees of preference allows us to separate value from nonvalue signals: Whereas an area encoding for value should exhibit monotonically increasing activation from the very aversive to the very appetitive stimuli, an area associated with salience should exhibit a stronger response to strongly liked and strongly disliked items than to "weakly liked" and "weakly disliked" items.

Several studies have provided evidence for a dissociation between these 2 types of signals at the time of stimulus consumption (Anderson et al. 2003; Small et al. 2003), or in Pavlovian paradigms in which no decisions are made (Jensen et al. 2007; Cooper and Knutson 2008; Matsumoto and Hikosaka 2009). However, only 2 animal studies to date have attempted to control for this important confound during decisions (Roesch and Olson 2004; Lin and Nicolelis 2008). Roesch and Olson (2004) collected recordings from neurons in the macaque orbitofrontal cortex (OFC) and premotor cortex in a simple binary decision paradigm. They found value signals in OFC and motivational attentional-arousal signals in premotor cortex. Lin and Nicolelis (2008) found similar motivational attentional-arousal signals in rat basal

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forebrain neurons. However, a whole brain search aimed at dissociating both types of signals in humans at the time of decision-making has not been carried out to date, and it is unknown if areas such as the cingulate cortex are associated with value or saliency processes.

Two aspects of the study are worth highlighting from the outset. First, while our experiment allows us to dissociate value signals from those that are associated with motor preparation, attention or arousal, it does not allow us to dissociate between areas involved in the latter set of processes. Nevertheless, given the importance for behavioral neuroscience of characterizing the neural substrates of stimulus valuation, distinguishing areas that have the properties of value signals from those that are associated with alternative correlated computations is crucial for correctly interpreting both existing and future results. Second, our results show that many previous studies were correct in interpreting activity in areas such as the mOFC, ACC, and posterior cingulate cortex as value signals, since their activity correlates with value but not saliency measures. We emphasize that such ex post confirmation of existing results does not detract from the importance of carrying out this experiment, since ruling out this important confound would have been impossible without actually carrying out the necessary controls.

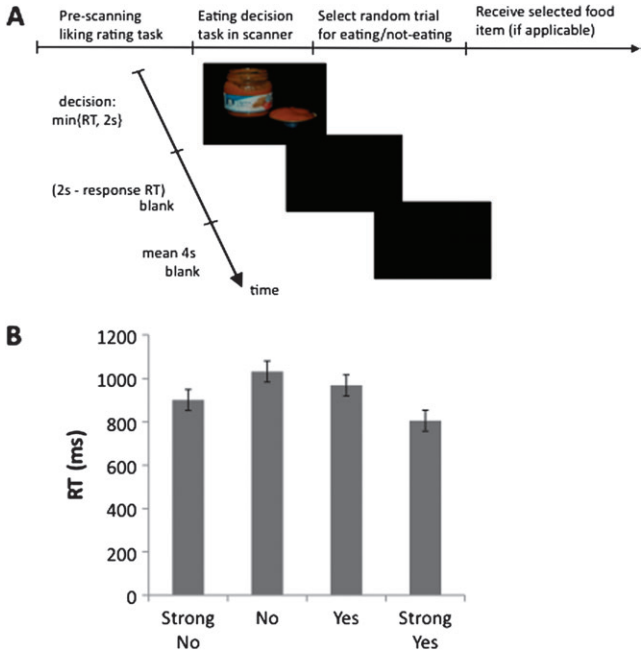

Figure 1. (*A*) Experimental design. (*B*) Reaction times by value (as measured by the subjects' responses). Error bars indicate ±1 standard error.

Materials and Methods

Subjects

Twenty subjects participated in the experiment (16 males, ages 19–52 years). All subjects were right-handed, healthy, had normal or corrected-to-normal vision, had no history of psychiatric diagnoses, neurological or metabolic illnesses, and were not taking medications that interfere with the performance of fMRI. Subjects also reported not having a history of eating disorders and were screened for liking some of the foods described below and disliking others. Subjects were told that the goal of the experiment was to study food preferences and gave written consent before participating. The review board of the California Institute of Technology (Pasadena, CA) approved the study. Subjects received $35 for their participation.

Stimuli

Subjects made decisions on 60 different food items. The set of food items was selected based on prior behavioral pilot data to span positive and negative preferences for most subjects. Thirty items were selected from a set of pictures that was rated as appetitive by most subjects. These included sweet and salty snack foods such as potato chips and candy bars. Thirty additional items were selected from a set of pictures that was rated as aversive by the majority of subjects. Examples include various types of canned meat such as liverwurst and various types of baby food. The foods were presented to the subjects as color pictures (72 dpi) using video goggles.

Task

Subjects performed 2 tasks: a liking-rating task prior to the fMRI session and a food choice task during the scanning session.

During the liking-rating task, subjects were asked to provide ratings (−2 = NOT AT ALL to 2 = VERY MUCH) for each of the 60 food items that they would encounter during the scanning task. The ratings were anchored to the question "How much would you like to eat this item at the end of the experiment?"

The food choice task is described in Figure 1*A*. Subjects were instructed not to eat immediately before arriving for the experiment and to have eaten no more than a light meal in the 4 preceding hours. In each trial, subjects were asked to make a binding decision about whether or not they wanted to eat the current food item at the end of the experiment. The decisions were binding because subjects knew that at the end of the experiment, a trial would be selected at random and that their response on that trial would be implemented. Thus, they would have to eat the food item shown in that trial if they said "Yes," and they would not be allowed to eat it if they said "No." On each trial, they were presented with a picture of an item and had up to 2 s to enter one of 4 responses: "Strong No," "No," "Yes," or "Strong Yes." Note that this feature of the design allowed us to measure the choice and the strength of preference simultaneously. Furthermore, the 4 responses were used to define value and saliency measures as follows. The value signal takes values from −2 (=Strong No) to +2 (=Strong Yes). The saliency signal takes a value of 1 (=No, Yes) or 2 (=Strong No, Strong Yes). Each of the 60 items was shown 4 times in the scanning task, twice per session in 2 consecutive sessions.

Trial ordering was fully randomized within and across subjects, with pseudorandomized intertrial blank-screen intervals to ensure identical full-task time across subjects. To avoid activation artifacts caused by the assignment of responses to buttons, the mapping of responses to buttons was counterbalanced (in the left-to-right directions) across subjects.

fMRI Data Acquisition

The functional imaging was conducted in a Siemens 3.0-T Trio MRI scanner. We acquired gradient echo T_2^*-weighted echo-planar images (EPIs) with blood oxygen level–dependent (BOLD) contrast. To optimize functional sensitivity in the OFC, we used a tilted acquisition in an oblique orientation of 30° to the anterior commissure–posterior commissure line (Deichmann et al. 2003). We also used an 8-channel phased array coil that yields a 40% signal increase in signal in the mOFC over a standard head coil. Each volume comprised of 44 axial slices. A total of 700 volumes (2 sessions, ≈16-min each) were collected in an interleaved-ascending manner. The imaging parameters were as follows: echo time, 30 ms; field of view, 192 mm; in-plane resolution and slice thickness, 3 mm; repetition time, 2.75 s. Whole-brain high-resolution T_1-weighted structural scans (1 × 1 × 1 mm) were acquired from every subject.

fMRI Data Preprocessing

The T_1-weighted structural scans for each subject were coregistered with their mean EPI and averaged together to permit anatomical localization of the functional activations at the group level. Image

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analysis was performed using SPM5 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK). Temporal normalization was applied to the scans with a time of acquisition of 1.9375 referenced to the last volume. To correct for subject motion, the images were realigned to the last volume, spatially normalized to a standard T_2^* template with a resampled voxel size of 3 mm and spatially smoothed using a Gaussian kernel with a full-width at half-maximum of 8 mm. Intensity normalization and high-pass temporal filtering (using a filter width of 128 s) were also applied to the data.

General Linear Model

We estimated a mixed-effects general linear model of the BOLD activity in the following 3 steps.

First, for each subject, we estimated a general linear model with AR(1) and the following independent variables for each of the 2 sessions:

(R1) Indicator variable for item presentation during nonmissed decision trials,
(R2) Indicator variable for item presentation parametrically modulated by the value signal (coding: −2 = "Strong No," −1 = "No," +1 = "Yes," +2 = "Strong Yes"),
(R3) Indicator variable for item presentation parametrically modulated by the saliency signal (coding: +1 = "Yes"/"No," +2 = "Strong Yes"/"Strong No"),
(R4) Indicator variable for item presentation during missed decision trials, and
(R5–R11) Six movement regressors and session constants.

Regressors R1–R3 were modeled using boxcar functions with durations equal to the subject's response time in that trial. R4 was modeled using a boxcar function with a duration of 2 s. Each of the regressors of interest (R1–R4) was convolved with a canonical hemodynamic response function.

Second, we calculated the following first-level single-subject contrasts: 1) regressor R2 versus baseline and 2) regressor R3 versus baseline.

Finally, for each of these first-level contrasts, we estimated a second-level mixed-effects analysis by computing a 1-sample *t*-test on the single-subject contrast coefficients. All figures and tables report results at a level of $P < 0.001$ uncorrected with an extent threshold of 5 contiguous voxels. Anatomical localizations were carried out by overlaying the t-maps on a normalized structural image averaged across subjects, with reference to an anatomical atlas (Duvernoy 1999).

Post Hoc ROI Analyses 1

In order to measure the strength of the signals encoded in the regions identified by the whole-brain analysis, we carried out an independent region of interest (ROI) analysis. This allowed us to test, for example, if areas in which activity correlated with value also exhibited activity correlated with saliency and vice versa. The following procedure was used to compute the effect size plots shown in Figures 2*B*, 3*B*, and 4*B*. First, we extracted an estimate of the particular regressor of interest (i.e., the estimated "beta" value) for each subject *i* from a voxel that was identified using the GLM estimates from all other subjects except for *i*. In particular, for each subject *i*, we identified a peak voxel for the contrast of interest by selecting the voxel within the anatomical area of interest that exhibited peak activity for that contrast in a mixed-effects analysis that included all subjects except for *i*. Second, the set of extracted beta values (one for each subject) were then averaged, and 2-sided *t*-tests were used to test the significance of the regressor of interest. For the effect size plot in Figure 4*B*, we used the peak voxels from the associated reported conjunction analysis (but the procedure was identical otherwise).

Post Hoc ROI Analyses 2

In order to provide further verification that the BOLD responses varied with the behavioral choices as suggested by the previous analyses, we estimated an additional GLM model with AR(1) (all omitted details are as in the main GLM):

(R1) Indicator variable for item presentation receiving a "Strong No" response,
(R2) Indicator variable for item presentation receiving a "No" response,
(R3) Indicator variable for item presentation receiving a "Yes" response,
(R4) Indicator variable for item presentation receiving a "Strong Yes" response,
(R5) Indicator variable for item presentation during missed decision trials, and
(R6–R12) Movement regressors and session constants.

We then extracted beta values for regressors R1–R4 using the same procedure described above, which is necessary to guarantee that the ROI analysis is independent from the whole-brain analysis. The resulting effect size plots are reported in Figures 2*C*, 3*C*, and 4*C*.

Results

The basic idea of the experiment is simple (Fig. 1*A*). In every trial, subjects were shown a picture of either an appetitive (e.g., potato chips and candy bars) or an aversive food (e.g., canned meats and baby foods) and had to decide if they wanted to eat that food. At the end of the experiment, one of the trials was selected at random and the decision made by the subject on that trial was implemented. Importantly, subjects made their choices using a 4-point scale ("Strong No," "No," "Yes, "Strong Yes").

The behavioral response allowed us to define 2 signals of interest. First, the value of an item was given by the magnitude of the response: −2 = "Strong No," −1 = "No," +1 = "Yes," and +2 = "Strong Yes." Second, we define a "saliency signal" given by the absolute value of this response coding: +1 = "Yes"/"No" and +2 = "Strong Yes"/"Strong No." The term saliency is meant to capture the variety of psychological processes (such as attention, motor preparation, and arousal) that might be activated more strongly for highly liked or disliked items, than for weakly liked or disliked ones.

Behavioral Results

Figure 1*B* shows that the saliency of the stimulus had an effect on response times: strong responses (high-saliency) were significantly faster than weak responses (low-saliency; $t_{77} = -4.22$, $P < 0.0001$). Positive responses, regardless of strength, were also significantly faster than negative responding ($t_{77} = -2.98$, $P = 0.004$).

Brain Activity Correlated with Value

Activity in the mOFC, rostral anterior cingulate cortex (rACC), and dorsal posterior cingulate cortex (dPCC) was positively correlated with value (Fig. 2*A*; for a complete list of activations, see Table 1). No areas exhibited negative correlation with value at our omnibus threshold of $P < 0.001$ uncorrected.

We carried out 2 independent post hoc effect size analyses in these ROIs (for details, see Materials and Methods) because previous studies have argued that these areas are associated with value computation at the time of choice (Wallis and Miller 2003; Padoa-Schioppa and Assad 2006; Kable and Glimcher 2007; Plassmann et al. 2007; Tom et al. 2007; Hare et al. 2008). An effect size analysis, depicted in Figure 2*B*, showed that activity in these areas was correlated with value but not with saliency. Note also that value signals increased monotonically with the behavioral responses. To verify that this is the case, we independently estimated the average BOLD response by

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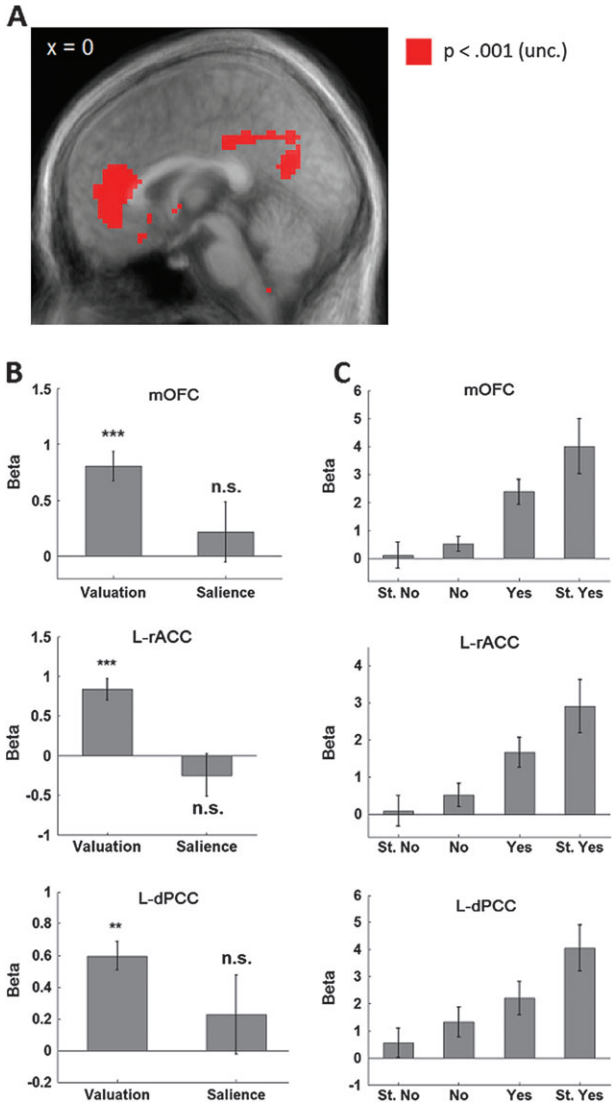

Figure 2. (*A*) Regions in which activity was correlated with value included the mOFC (−6, 24, −21), rACC (−1 39, 3), and dPCC (−3, −33, 39). (*B*) Effect size plots for these 3 areas showing that activity correlated with value but not with saliency. Note that all effect size plots were constructed using a procedure that ensures independence from the procedure used to identify the ROIs. Significance levels for *t*-tests: $^{**}P < 0.01$, $^{***}P < 0.001$. (*C*) Effect size plots for these 3 areas as a function of the behavioral response.

behavioral choice. As shown in Figure 2*C*, activity in the mOFC, rACC, and dPCC increased monotonically with the positivity of the choice, consistent with value coding.

Brain Activity Correlated with Saliency

Activity in several areas, including the dorsal anterior cingulate cortex (dACC), SMA, precentral gyrus, posterior insula, and fusiform gyrus (Fig. 3*A*; for a complete list of activations, see Table 2) correlated positively with the saliency measure but not with value. No areas exhibited negative correlation with saliency at our omnibus threshold of $P < 0.001$ uncorrected. An independent post hoc effect size analysis showed that activity in these areas did not correlate with value (Fig. 3*B*).

Saliency signals should exhibit a *U*-shape with regard to the behavioral responses (i.e., activation should be larger for the

Table 1
Regions in which activity during the decision period was correlated with value

MNI-coordinate (*x*, *y*, *z*)	Number of voxels	Region of activation	Side	BA	*T*
9, −69, 27	232	Precuneus	R	7 m	6.31
−6, −69, 30	151	Precuneus	L	7 m	5.95
−39, −60, 9	29	Middle temporal lobe, subgyral	L		5.83
−6, −90, −3	41	Cuneus/lingual gyrus	L	17	5.65
0, 39, 3	193	Rostral anterior cingulate	L	32, 24	5.45
6, 42, 0	268	Rostral anterior cingulate	R	32, 24	5.40
9, −81, 18	103	Cuneus	R	17	4.98
24, 39, 54	25	Superior frontal gyrus	R	8	4.86
39, −60, −45	17	Cerebellar tonsil	R		4.69
−3, −33, 39	127	Dorsal posterior cingulate	L	31	4.58
−6, 24, −21	49	Medial rectal/frontal gyrus, mOFC	L	11	4.61
−48, −57, 45	63	Supramarginal gyrus	L	40	4.58
42, −63, 51	28	Angular gyrus	R	7	4.45
−51, −6, −24	12	Inferior temporal gyrus	L	20	4.17
9, −39, 36	104	Dorsal posterior cingulate	R	31	3.95
6, 24, −18	43	Medial frontal gyrus, mOFC	R	11	3.92
−6, 6, −9	15	VStr	L		3.86
−9, 9, −12	15	VStr	L		3.84
−21, −18, −18	5	Parahippocampal gyrus	L		3.60

Note: Height threshold: $T = 3.5794$, $P = 0.001$ (uncorrected). Extent threshold: $k = 5$ voxels. BA=Brodmann area.

"Strong Yes" and "Strong No" responses than the non-Strong responses). To verify that this was the case, we independently estimated the average BOLD response by behavioral choice. As shown in Figure 3*C*, activity in all these areas exhibited the required pattern. Note, also, that there were no significant activation differences between trials with "Strong Yes" and "Strong No" responses or between trials with "Yes" and "No" responses, which shows that the saliency measure used in the study is highly correlated with the computations performed in these areas.

Brain Activity Correlated with Both Value and Saliency

Only the cuneus and VStr exhibited activation that correlated positively with both the value and saliency signals. Figure 4*A* shows the result of a conjunction analysis identifying areas of the VStr in which activity was associated with both types of signals (Table 3). Independent post hoc analyses of the effect sizes and responses by behavioral choice using the previous methods led to the same conclusion (Fig. 4*B–C*).

Discussion

The results in this paper provide a clear dissociation between areas involved with valuation at the time of choice and saliency-like signals that might be associated with attention, motor preparation, or arousal. Activity in the mOFC, rACC, and dPCC correlated with value but not with saliency signals. In contrast, activity in the dACC, SMA, precentral gyrus, posterior insula, and fusiform gyrus correlated with saliency but not with value. Only activity in the VStr and the cuneus correlated with both.

Our results have implications for several areas of neuroscience. First, a growing number of studies has found that activity in the mOFC and rACC is correlated at the time of choice with behavioral measures of the value of stimuli in a wide variety of tasks (Wallis and Miller 2003; Padoa-Schioppa and Assad 2006; Kable and Glimcher 2007; Plassmann et al. 2007; Tom et al. 2007; Hare et al. 2008). This has been widely interpreted as evidence that these areas might be involved in the assignment

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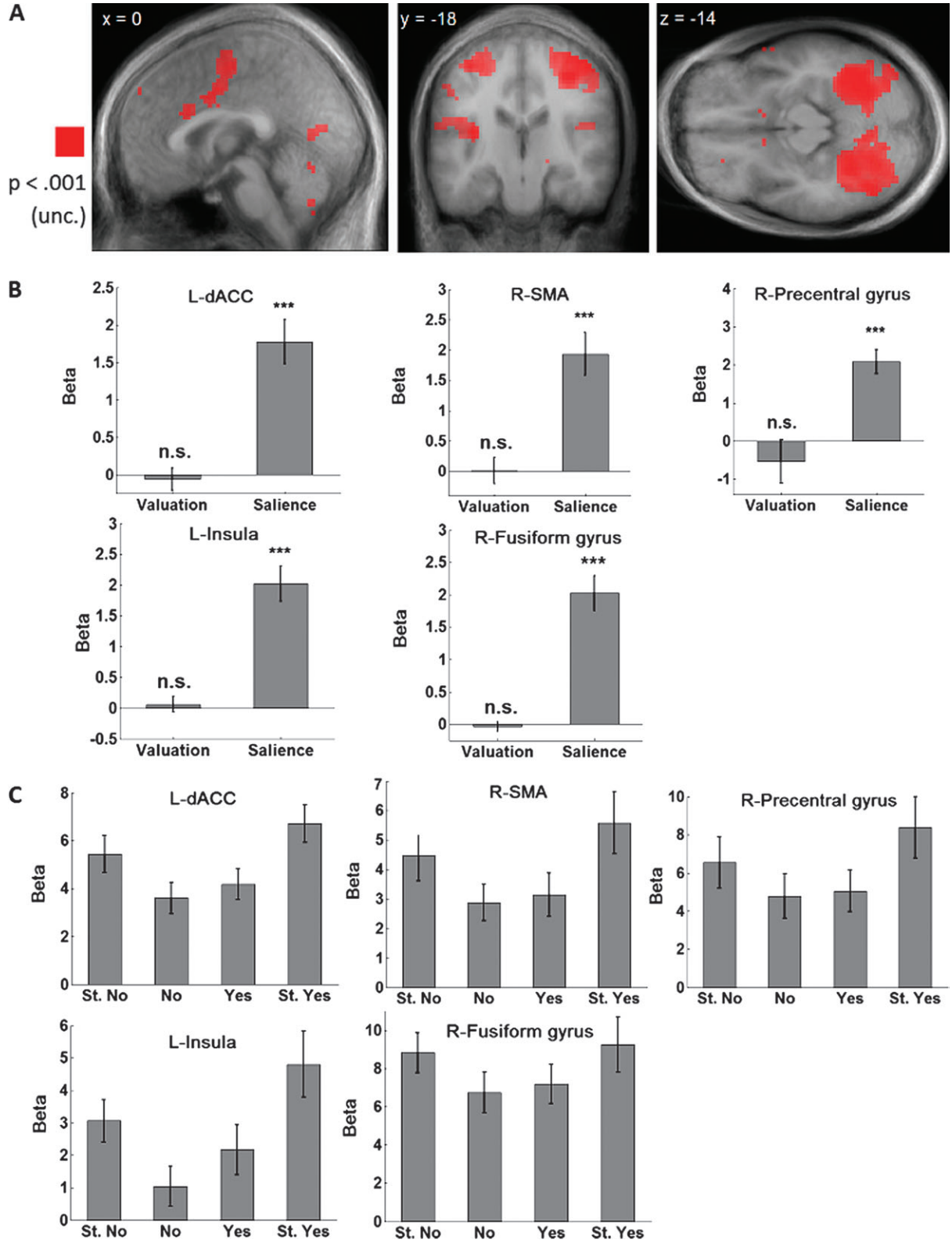

Figure 3. (*A*) Regions in which activity was correlated with the saliency measure included the dACC (−3, 0, 42), SMA (9, −12, 60), precentral gyrus (36, −18, 57), posterior insula (−33, −21, 15), and fusiform gyrus (30, −60, −18). (*B*) Effect size plots for these 5 areas showing that activity correlated with saliency but not value. Significance level for *t*-tests: $^{***}P < 0.001$. (*C*) Effect size plots for these areas as a function of the behavioral response.

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Table 2

Regions in which activity during the decision period was correlated with saliency

MNI-coordinate (*x*, *y*, *z*)	Number of voxels	Region of activation	Side	BA	*T*
30, −60, −18	505	Fusiform gyrus (O4)	R	37	8.31
−30, −54, −21	649	Fusiform gyrus (O4)	L	37	8.23
36, −18, 57	438	Precentral gyrus	R	4	7.18
−54, 0, 36	56	Precentral gyrus	L	4, 6	6.17
−30, −27, 57	275	Precentral gyrus	L	4	6.04
−33, −21, 15	25	Insula, posterior	L	13	5.61
12, −63, −51	61	Inferior semilunar lobule	R		5.38
9, −81, 18	203	Cuneus	R	17	5.29
9, −12, 60	172	SMA	R	6	4.95
27, −54, −51	13	Cerebellar tonsil	R		4.91
−36, 9, −18	15	Temporal pole	L	38	4.89
0, −3, 45	68	Dorsal anterior cingulate	R	32′, 24′	4.67
−3, 0, 42	42	Dorsal anterior cingulate	L	32′, 24′	4.49
−12, −81, 0	133	Lingual gyrus	L	17	4.29
−3, −12, 60	84	SMA	L	6	4.11
−9, 9, −14	6	VStr	L		4.00
45, −18, 21	15	Insula, posterior	R	13	3.87
12, 11, −15	11	VStr	R		3.79

Note: Height threshold: $T = 3.5794$, $P = 0.001$ (uncorrected). Extent threshold: $k = 5$ voxels. BA=Brodmann area.

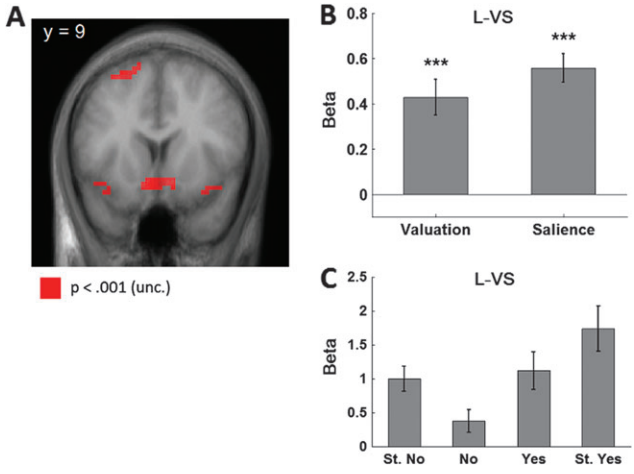

Figure 4. (*A*) Region of VStr (−9, 9, −12) in which activity was correlated with both value and saliency. (*B*) Effect size plots this area showing that activity correlated with both value and saliency. ***$P < 0.001$. (*C*) Effect size plots for this area as a function of the behavioral response.

Table 3

Conjunction analysis showing regions in which activity during the decision period was correlated with both valence and saliency

MNI-coordinate (*x*, *y*, *z*)	Number of voxels	Region of activation	Side	BA	*T*
12, −84, 3	62	Cuneus	R	17	5.02
−6, 12, −12	5	VStr	L		4.54
−9, −90, 3	37	Cuneus	L	17	4.04
9, 12, −15	7	VStr	R		3.74

Note: Height threshold: $T = 3.5794$, $P = 0.001$ (uncorrected). Extent threshold: $k = 5$ voxels. BA=Brodmann area.

of values to stimuli during decision-making. Our data, together with the findings by Roesch and Olson (2004), suggest that this conclusion is justified even though previous studies did not carry out the controls necessary to rule out the involvement of these regions in attentional, motivational, or arousal processes.

Second, our results contribute to the literature seeking to dissociate value and saliency signals. Several previous studies have presented evidence for and against such dissociations at the time of stimulus consumption (Anderson et al. 2003; Small et al. 2003), or in Pavlovian paradigms in which no decisions are made (Jensen et al. 2007; Cooper and Knutson 2008; Matsumoto and Hikosaka 2009). Although the computations made by the brain in these tasks might be very different from those made during decision-making, it is interesting to note some common results. Cooper and Knutson (2008) found that the VStr also correlates with both saliency and valence during the anticipation of probabilistic rewards. In a related study, Jensen et al. (2007) found both positive and negative prediction error signals in a similar region of VStr (although see Seymour et al. 2007 for results dissociating gain and loss encoding in the striatum). Small et al. (2003) found valence signals in OFC and anterior insula and saliency signals in the amygdala, cerebellum, pons, and middle insula during a gustation task. Anderson et al. (2003) found valence signals in response to odors in the OFC and saliency signals in amygdala. Thus, some of the findings from these alternative paradigms parallel the ones obtained here, which suggests that some common valuation and saliency-type processes might be activated at the time of decision and during consumption and reward anticipation.

Closer to our study, Roesch and Olson (2004) recorded from neurons in the macaque OFC and premotor cortex in a simple binary decision paradigm in which values and saliency were also orthogonalized. Consistent with our findings, they found valuation signals in OFC and motivational–attentional–arousal signals in premotor cortex. Lin and Nicolelis (2008) recorded from rat basal forebrain neurons in a go/no-go task. They found that activity in this area at the time of decision was modulated by the saliency of the stimulus not by its value. However, since they only had 2 stimuli (one positive and one negative), it is hard to fully interpret the nature of the signals identified in this area. The results in this paper extend these findings to humans and provide evidence for the dissociation of saliency and value signals during choice.

Third, our results provide new insights into the role of the striatum in decision making. Several previous studies have argued that this area is involved in the computation of value signals (Kable and Glimcher 2007; Knutson et al. 2007; Tom et al. 2007). Others have argued that it might be involved in saliency and the deployment of motor responses (Horvitz 2000; Tricomi et al. 2004; Zink et al. 2004). Our results show that common regions of the striatum are involved in both value and saliency computations at the time of decision-making. This suggests that the striatum might be a critical area where the value signals necessary to make choices come together with the motor signals necessary to implement them.

Fourth, a comparison of our results with the literature on risk coding also provides some novel insights about the role of the anterior insula in valuation and decision-making. Recent studies (Preuschoff et al. 2006, 2008) have shown activity in the anterior insula correlated with the amount of risk that individuals faced on a Pavlovian reward task with stochastic payoffs. Note that the risk signal in this task closely resembles a saliency signal, since it is high for stimuli with very high or very low probability of reward, and close to zero for stimuli with an average probability of reward. Together with our findings, this suggests that the anterior insula might be involved

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in identifying stimuli with extreme values for a wide class of stimuli and in a wide range of valuation-related tasks.

A few methodological and conceptual aspects deserve further discussion. First, by defining the saliency signal to be equal to the absolute value of the behavioral response, the study implicitly assumed that strongly disliked and strongly liked items induce attentional, motor preparation, or arousal responses of equal strength. Theoretically, this is equivalent to assuming that all these processes correlated with the "magnitude" of the value, regardless of its sign. While the previous literature does not offer a guide about whether or not this is a valid assumption, it is worth pointing out that the results in Figures 2*C*, 3*C*, and 4*C* are consistent with the notion of saliency employed here.

Second, the study does not assume that value is the only driver of attention, motor preparation, or arousal. For example, stimulus familiarity can influence attention, previous experience making decisions with a stimuli is known to influence the level of motor preparation, and visceral states can have strong effects on overall levels of arousal. The only assumption that this study makes is that these processes might also be influenced to some extent by a stimulus' value, which is consistent with the reaction time data shown in Figure 1*B*.

Third, a limitation of the study is that it cannot distinguish between different attentional, motor preparation, and arousal signals. However, it is important to emphasize that this is the first human neuroimaging study that is able to systematically rule out these confounds for areas, such as ventromedial prefrontal cortex and rACC, that have been traditionally associated with valuation. It is also possible to speculate about their respective roles based on the previous literature. The dACC, precentral gyrus, and SMA have been associated with the preparation and execution of motor responses (Bush et al. 2002; Rushworth et al. 2004) and thus might be a critical part of the motivational system. The insula has been shown to encode bodily states and thus is likely to be associated with arousal (Craig 2002). Finally, the fusiform gyrus has been shown to respond selectively to certain types of stimuli and thus might be involved in the deployment of attention (Vulleumier 2005).

More generally, the results presented here show the importance of including both appetitive and aversive stimuli in decision-making studies whenever possible. Since a large number of areas correlate with value when only appetitive or aversive stimuli are included, it is easy to misinterpret as valuation areas regions that are actually associated with attention, motor preparation, or arousal processing.

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