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Human Striatal Responses to Monetary Reward Depend On Saliency

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Summary

While the striatum has been implicated in reward processing, an alternative view contends that the striatum processes salient events in general. Using fMRI, we investigated human striatal responses to monetary reward while modulating the saliency surrounding its receipt. Money was maximally salient when its receipt depended on a correct response (active) and minimally salient when its receipt was completely independent of the task (passive). The saliency manipulation was confirmed by skin conductance responses and subjective ratings of the stimuli. Significant caudate and nucleus accumbens activations occurred following the active compared to passive money. Such activations were attributed to saliency rather than the motor requirement associated with the active money because striatal activations were not observed when the money was replaced by inconsequential, nonrewarding stimuli. The present study provides evidence that the striatum's role in reward processing is dependent on the saliency associated with reward, rather than value or hedonic feelings.

Introduction

Given the wide variety of stimuli that activate the striatum, its previously suggested predominance in reward processing (Schultz et al., 2000) has come under question. In addition to processing reward-related stimuli, both the striatum and its midbrain dopamine inputs respond to other events, including aversive, novel, and intense stimuli (Horvitz, 2000; Legault and Wise, 2001; Ravel et al., 1999; Setlow et al., 2003; Williams et al., 1993). Similar nonreward activations of the human dorsal and ventral striatum have also been demonstrated, including striatal responses to aversive stimuli, monetary punishment, and cues predicting such negative events (Becerra et al., 2001; Jensen et al., 2003; Knutson et al., 2000, 2003). Human striatal activations have been reported following neutral (with respect to valence) stimuli as well, if the stimuli are particularly arousing and unexpected (Zink et al., 2003). All of the aforementioned stimuli that activate the striatum have the common property of "saliency." A salient event in this context refers to a stimulus that is arousing (Horvitz, 2000) and to which attentional and/or behavioral resources are preferentially redirected (Redgrave et al., 1999), especially when the stimulus is unexpected. Intrinsic properties of a stimulus can give rise to its saliency if the properties are particularly striking, e.g., high intensity. Alternatively, an otherwise nonarousing event may acquire saliency by virtue of its importance under precise environmental or experimental conditions. For example, a target in a given task is more salient when there are consequences associated with a correct response than when the target requires an inconsequential response.

The contention that the striatum responds to saliency is compatible with the body of research linking the striatum with reward processing, but because previous human studies did not separate the rewarding quality from the saliency of the stimuli, the issue of reward value versus saliency remains unresolved. For example, neuroimaging studies have demonstrated that the dorsal and ventral striatum are involved with processing primary rewards such as gustatory stimuli (Berns et al., 2001; McClure et al., 2003; O'Doherty et al., 2002, 2003; Pagnoni et al., 2002), confirming animal research which used primary rewards to activate the striatal cells and midbrain dopamine neurons projecting to the striatum (Schultz, 1998; Schultz et al., 2000). However, in addition to their hedonic properties, primary rewards, such as juice or food, are also arousing, i.e., salient, because they possess an intrinsic behavioral significance given that receipt of these rewards requires physical consumption (i.e., received in the mouth and swallowed). Neuroimaging studies have demonstrated that conditioned rewards like money elicit a striatal response (Breiter et al., 2001; Delgado et al., 2000; Elliott et al., 2000, 2003; Knutson et al.; Knutson et al., 2000, 2001a, 2001b, 2003), but these studies are confounded with saliency in a different manner. The intrinsically arousing properties of money are typically diminished in experimental paradigms because the money is delivered as an abstract visual representation instead of actually handed to the subject during scanning. Consequently, money becomes salient in an experimental paradigm because of its importance within an engaging paradigm rather than its intrinsic properties. To our knowledge, prior studies have not presented money to subjects completely independent of a task. From previous studies using monetary reward, it is unclear whether the observed striatal activations are related to the rewarding quality of the money or the saliency surrounding the money. The current experiment sought to differentiate the human striatal response to monetary reward from saliency.

Using event-related functional magnetic resonance imaging (fMRI), we investigated if a differential striatal response occurred to monetary rewards when the delivery of money was salient, i.e., arousing, compared to when money was delivered in a nonsalient manner. Money was rendered maximally salient by being contingent on the subject's performance and minimally salient when receipt of the money was unrelated to the task (Figure 1). During the scanning session, subjects per-

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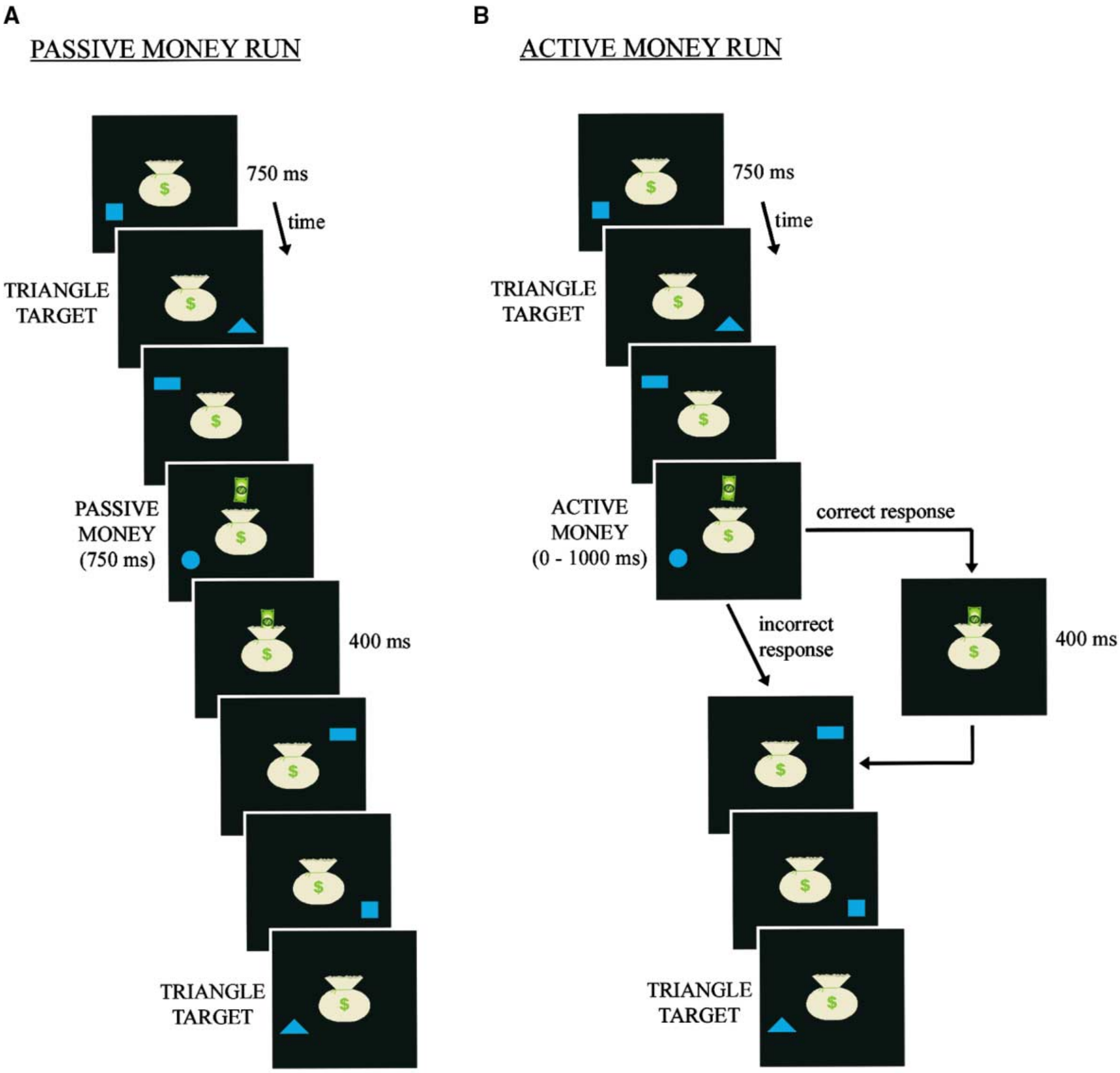

Figure 1. Experimental Design

(A) Passive money run. Subjects performed a target detection task in which blue shapes appeared pseudorandomly, one at a time, in one of four screen locations, and subjects were instructed to press button #1 each time a triangle appeared ("triangle target"). Occasionally a money bill ("passive money") appeared above the money bag, which was positioned in the center of the screen for the entire run. The money automatically dropped into the bag.

(B) Active money run. Subjects performed the same target detection task described in (A). Occasionally a money bill ("active money") appeared above the money bag. Subjects were required to press button #2 to trigger the money to fall into the bag. Failure to accurately respond resulted in the money disappearing without dropping into the bag. For both runs, after the scanning session, subjects received all the money that dropped in the bag. Each scanning session consisted of two other runs, passive blob run and active blob run (not shown), which were identical to the passive money run and active money run, respectively, except the money bills were replaced by a valueless, nongeometrical shape (blob). Subjects did not receive compensation for accurately responding to the active blobs, but they were instructed to perform as accurately as possible.

formed four runs of a target detection task. In one run, a money bill occasionally appeared and automatically dropped into a money bag positioned in the center of the screen, whereas in a separate run, subjects were required to momentarily interrupt the ongoing target detection task by accurately responding to the money bill with a button press to trigger its fall into the bag. As a control for the differential attentional and motor requirement in response to the money, two more separate runs were implemented in which the money bills were replaced with valueless, nongeometric shapes (blobs) in both conditions, i.e., active and passive. We hypothesized that greater striatal (both dorsal and ventral) activity would be observed following money presentation when receipt of the money was dependent on the subject's behavior (salient) compared to when the receipt was independent of the task (nonsalient). To confirm the saliency manipulations, we acquired skin conductance

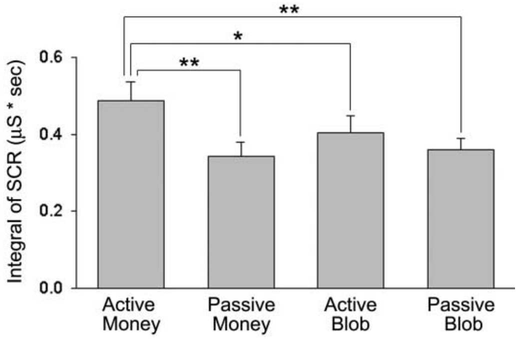

Figure 2. Group Skin Conductance Responses to Active Money, Passive Money, Active Blobs, and Passive Blobs

Plotted for each of the four events is the integral of the skin conductance response (SCR) signal computed over a 5 s interval starting at the stimulus of interest onset. Bars represent means and standard errors across subjects. The SCR to the active money was significantly greater than the SCRs to the passive money, active blob, and passive blob. SCRs to the passive money, active blob, and passive blob were not significantly different from each other. $^*p < 0.05$; $^{**}p < 0.005$.

responses (SCRs) and psychometric measures of pleasure and arousal from a second group of subjects outside the scanner.

Results

We were interested in the brain and behavioral responses to four event types: (1) active money: money requiring a button press to trigger its drop into the money bag; (2) passive money: money which automatically dropped into the money bag; (3) active blob: blob requiring a button press to trigger its drop into the bag; and (4) passive blob: blob which automatically dropped into the bag.

Subjective and Psychophysical Measurements of Arousal

To assess the saliency of the active money, a separate group of ten subjects performed the experimental task outside the scanner. Skin conductance responses (SCRs) and subjective ratings of arousal and pleasure were acquired that corresponded to the four events of interest (i.e., active money, passive money, active blob, passive blob). SCRs were significantly different between events types [$F(3,26) = 6.906$; $p = 0.001$]. Post-hoc comparisons (Student-Newman Keuls method) revealed that the active money elicited a significantly greater SCR compared to the SCRs following the presentation of the passive money ($p = 0.001$), active blob ($p = 0.019$), and passive blob ($p < 0.005$) (Figure 2). The SCR associated with the active blob was not significantly different than the SCR corresponding to the passive blob ($p = 0.296$) or passive money ($p = 0.210$), nor was the SCR significantly different following the passive money compared to the passive blob ($p = 0.546$). The rating scales for arousal and pleasure also yielded a significant effect of event type [$F(3,27) = 20.419$, $p < 0.001$; $F(3,27) = 6.474$, $p = 0.002$, respectively]. Post-hoc comparisons (Student-Newman Keuls method) revealed that the subjects rated the active money as significantly more arousing than all the other events ($p < 0.01$), including the passive money ($p < 0.001$). The active money was also rated as significantly more pleasant than the active blob ($p = 0.023$) and passive blob ($p = 0.002$). The active money and passive money were not rated significantly different in terms of pleasure ($p = 0.203$).

Behavior

Subjects in the fMRI experiment made less than one error per run on average. Responding to the active stimuli (money or blobs) with either a double button press or an incorrect button press followed by the correct button press within one second resulted in the money/blob falling into the bag, but we considered those types of responses as errors for the purpose of the analysis. The reaction times for the active money (mean = 467.5 ms, SE = 22.7 ms) were significantly shorter than the reaction times for the active blobs (mean = 530.3 ms, SE = 21.7 ms; $p = 0.001$, $t = 3.935$, d.f. = 15, paired t test).

fMRI Data

We considered separately the following two contrasts: (active money > passive money) and (active blob > passive blob); as well as the interaction: (active money-passive money) > (active blob-passive blob). Due to the a priori hypothesis concerning the striatum, the summary statistical maps were thresholded at $p < 0.005$ uncorrected for multiple comparisons (Friston, 1997), with a voxel extent greater than 10 voxels. Significantly activated striatal regions are presented in Table 1. Other brain regions are also presented; however, because we lacked an a priori hypothesis concerning nonstriatal regions, our threshold, $p < 0.005$ uncorrected, does not provide adequate protection against type I errors in the whole brain. As such, the nonstriatal brain activations are reported for completeness purposes only and will not be a focus of discussion.

Behaviorally Salient Monetary Rewards Activate the Striatum

Significant activations were observed in the striatum following the presentation of active money relative to passive money, in both the right and left caudate body ($p < 0.001$) and the right nucleus accumbens ($p < 0.005$) (Table 1; Figure 3). For each striatal activation, the effect size (at the peak voxel) was greatest for the active money compared to the other event types. We did not observe any significant activations in the putamen. No significant striatal activations were observed when active blobs were compared to passive blobs. The interaction, (active money-passive money) > (active blob-passive blob), revealed significant activations in the bilateral caudate body and the right caudate head. In the interaction contrast, activity in the nucleus accumbens did not reach significance at the designated $p < 0.005$ threshold.

Discussion

The key finding in the present study was a differential striatal response to monetary reward dependent on the

Table 1. Significantly Activated Brain Regions

Brain Regions	Cluster Size (voxels)	Peak MNI Corrdinates			Peak Z Score
		x	*y*	*z*	
Active Money > Passive Money					
Striatal regions					
Right caudate body	53	12	3	15	3.62
Left caudate body	73	−12	−6	15	3.43
Right nucleus accumbens	10	12	9	−6	3.00
Other brain regions					
Left postcentral/precentral gyrus	967	−45	−36	63	5.00
Right precentral gyrus	13	27	−27	75	2.86
Right cerebellum	150	21	−57	−24	5.03
Right cerebellum	81	12	−90	−21	3.83
Cingulate	362	0	−9	54	4.40
Anterior cingulate	13	−3	36	12	3.03
Right sup. temporal/inf. frontal gyrus (includes insula)	225	63	3	0	4.09
Left sup. temporal/inf. frontal gyrus (includes insula)	37	−48	15	−12	4.03
Left middle frontal gyrus	52	−57	12	27	3.78
Right supramarginal gyrus	10	66	−27	30	3.03
Right amygdala	10	24	0	−15	3.17
Left amygdala	13	−21	0	−15	3.40
Active Blob > Passive Blob					
Striatal regions					
No significant striatal activations					
Other brain regions					
Left postcentral/precentral gyrus	692	−39	−36	66	5.21
Right cerebellum	93	9	−57	−12	4.24
Cingulate	155	0	−12	51	4.38
Left insula	42	−39	−3	6	3.77
Right supramarginal gyrus	99	60	−30	36	3.92
Right precuneus	10	6	−60	30	3.49
(Active Money-Passive Money) > (Active Blob-Passive Blob)					
Striatal regions					
Right caudate body	32	12	−3	12	3.31
Left caudate body	10	−12	3	12	2.99
Right caudate head	11	9	18	6	3.63
Other brain regions					
Left postcentral gyrus	15	−33	−42	66	3.27
Right cerebellum	57	15	−87	−21	4.70
Right cerebellum	10	33	−84	−21	3.40
Right superior temporal gyrus	13	63	6	0	3.22
Right inferior frontal gyrus	21	45	33	6	3.08
Right fusiform (O4)	11	48	−51	−21	4.47

Significance was measured at $p < 0.005$. MNI = Montreal Neurological Institute.

conditions underlying receipt of the money. We found that activity within the dorsal (caudate) and ventral (nucleus accumbens) striatum increased in response to monetary rewards that were contingent on subjects' behavior compared to monetary rewards that were received independently of the task. Importantly, no differential responses in the striatum were observed when the money bills in both conditions were replaced by valueless, nongeometrical shapes (blobs), suggesting that the striatal activations to the active money were not exclusively related to additional motor and attentional requirements associated with the active money. Furthermore, there was a significant interaction of stimulus type (money or blob) and response (active or passive) in the caudate and a nonsignificant trend in the nucleus accumbens. Because the motor aspect was the same for the active money and the active blob, and therefore cancelled out in the interaction, our results suggest that the striatal responses cannot be attributed solely to movement.

Instead of movement, we attribute the differential striatal activity between active money and passive money to differences in stimulus saliency. A salient stimulus is defined as arousing by virtue of either its inherent properties when they are striking or its importance based on the context in which it is presented. The active money elicited significantly greater SCRs and significantly higher arousal ratings than all the other events, providing solid evidence that the active money was the most salient condition. The active money was especially arousing because the receipt of the money was contingent on the subject's accurate response. Although the passive receipt of money represented the same reward value, it was not particularly salient. In the postscanning interviews, subjects reported that they noticed the receipt of the passive money but that they concentrated

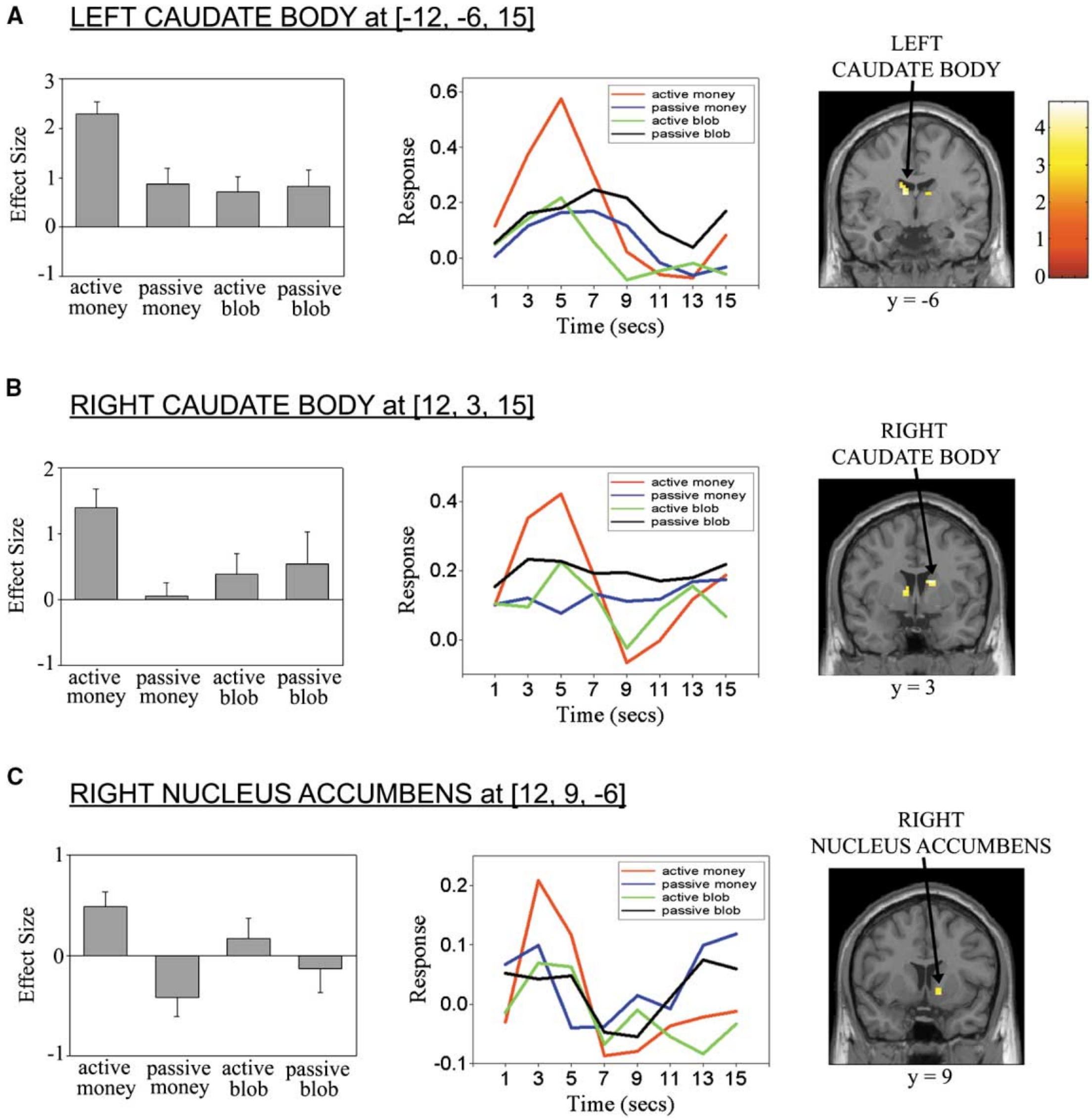

Figure 3. Significant Striatal Activations for the Contrast, Active Money > Passive Money

Significant ($p < 0.005$) striatal activations were observed in (A) the left caudate body, (B) the right caudate body, and (C) the right nucleus accumbens, shown here (right) overlaid on coronal sections of a structural template brain. Other activations in the brain are masked out. The z score scale shown in (A) also applies to activations in (B), (C), and (D). Plotted (left) are the effect sizes (parameter estimates) of active money, passive money, active blob, and passive blob, extracted from the peak voxel of the corresponding striatal cluster. The effect size is expressed as percentage of the global mean intensity of the scans. Bar plots represent averages and standard error across subjects. Also plotted (middle) are the event-related hemodynamic responses to active money, passive money, active blob, and passive blob extracted from the peak voxel of the corresponding striatal cluster.

on the ongoing target detection task. If we had simply presented passive money to subjects without an ongoing task, the money would have drawn the subjects' attention, perhaps leading them to either count the occurrences or try to predict future timing of money presentation. Such confounds were avoided by implementing an ongoing target detection task of relatively fast pace, which engaged the subject's attention and ensured that the passive money was less arousing than the active money. The active blobs were just as task relevant as the active money because both required the same response, i.e., a button press, but the active blobs were not very salient because there were no consequences associated with responses to them. Correct responses to the active blobs were relatively meaningless. Subjects responded significantly faster to the active money than to the active blobs, confirming that subjects viewed these two conditions differently. The faster reaction times and larger SCRs to the active money compared to active blobs are consistent with the rather obvious notion that money is more motivating, and therefore more salient, than amorphous shapes.

Because the reward value and the appearance of the money bills were identical in both conditions, active money and passive money differed only in their saliency, as defined above. One aspect of this saliency difference may have derived from the uncertainty surrounding the consequences of a response in the active condition. A large body of evidence exists showing that the dopamine and striatal responses to rewards and other salient events are dependent on temporal uncertainty (Berns et al., 2001; McClure et al., 2003; O'Doherty et al., 2003; Pagnoni et al., 2002; Schultz, 1998; Zink et al., 2003). We exploited this observation in the design of the current experiment by making the appearance of the active and passive money, as well as the blobs, unpredictable in all conditions. Due to the limitations of fMRI, it was not possible to differentiate between the brain response to the appearance of the money/blob and the receipt of the money/blob. The aforementioned uncertainty of gain associated with the active money was minimized by allowing sufficient time to respond to the money and allowing subjects to practice the task until they were comfortable and confident with their ability to gain the money in the active condition. Importantly, each subject did accurately respond to and receive all of the active money, indicating that uncertainty around the receipt of reward in the active money condition was minimal.

The present experiment separates the rewarding quality of monetary rewards from its saliency. Previous studies of human brain responses to monetary rewards revealed that the caudate and nucleus accumbens were activated by both reward anticipation and reward outcome (Breiter et al., 2001; Delgado et al., 2000; Elliott et al., 2003; Knutson et al., 2000, 2001a, 2001b, 2003). Although the results of the present study are consistent with previously reported striatal responses to monetary reward, we do not believe they can be attributed to either reward outcomes or reward anticipation. The authors of the previous studies have argued that striatal activation results because money is rewarding; however, in these studies, the receipt of the money also occurred in a salient manner. In most monetary reward experiments, the receipt of the monetary reward was contingent on subjects' performance, and representation of the reward followed a correct response (Delgado et al., 2000; Elliott et al., 2000, 2003; Knutson et al., 2000, 2001a, 2001b, 2003). Breiter et al. (2001) demonstrated nucleus accumbens activation during a game of chance, in which the behavior of a "spinner" determined the rewarding outcome. Although it was not contingent on a response from the subject, receipt of the money was still arousing because it was the result of an engaging paradigm. The conditions under which money was received in previous studies makes it unclear if the striatal activations were related to reward effects or saliency. A recent study (Tricomi et al., 2004) investigated how brain responses to rewards were modulated by the contingency of a behavioral response, and the authors report dorsal, but not ventral, striatal activations. An important distinction in the present study was the specific manipulation of saliency, based on an attentional and behavioral switch, which may account for both the different striatal activations reported here (i.e., ventral striatum) and our different interpretation (i.e., saliency rather than goal-directed behavior).

For decades researchers have associated the dorsal and ventral striatum and their major dopaminergic inputs with processing rewards and reward-related stimuli (Schultz, 1998; Schultz et al., 2000); however, an alternative view contends that these structures respond to all salient events, rather than rewards specifically (Horvitz, 2000; Redgrave et al., 1999; Zink et al., 2003). Although both the ventral and dorsal striatum have been implicated in processing salient events, including rewards, some argue that the dorsal and ventral components of the striatum may have separate functions. For example, the ventral striatum has been implicated in the appetitive aspects of reward processing, while the dorsal striatum has been implicated in the consumatory aspects (Knutson et al., 2001b). A differential role for the dorsal and ventral striatum in processing salient nonrewarding events has been suggested as well. In a recent study, we specifically investigated striatal responses to the saliency of neutral events (Zink et al., 2003), and we concluded that the nucleus accumbens plays a role in coding unexpected arousing events, whereas caudate activity is more closely linked to the behavioral relevance of stimuli. In accordance with a theory postulated by Redgrave et al. (1999), the nucleus accumbens may respond when an attentional switch is elicited, whereas the caudate may respond when a behavioral switch is elicited. The results of the present study are consistent with this finding. The active money, which activated the nucleus accumbens and caudate, elicited both an attentional and behavioral switch because subjects had to momentary interrupt the ongoing task to respond to the active money.

Despite the present finding that task-related monetary reward modulates activity in the striatum, our results are still consistent with results of previous experiments which demonstrate a striatal and midbrain dopamingeric response to primary rewards (juice) presented outside of a task context (Berns et al., 2001; Mirenowicz and Schultz, 1994; Ravel et al., 2001). The primary rewards used in these studies are rewarding because of their taste and smell, yet they are also innately salient because of their physical nature; such rewards are tactile and are inherently significant by virtue of their receipt requiring a behavioral reaction (i.e., swallowing). Thus, it is virtually impossible to separate saliency from the rewarding quality of primary rewards. Conversely, monetary rewards are abstract and can be presented to subjects as a representation of money that they receive at a later time. The abstract nature of monetary rewards allows for a nonsalient presentation, which would be difficult to achieve with primary rewards.

Hedonism, i.e., pleasure, is related to saliency in that greater pleasure can be associated with greater arousal (Bradley et al., 2001). The striatal activations may have occurred because of a greater hedonic quality associated with the active money relative to the passive money, rather than greater saliency. This, the hedonic hypothesis, was not supported by our data. In order to quantify hedonic feelings toward the different events, a separate group of subjects performed the task, during which subjects rated their feelings of pleasure. Although subjects were significantly more aroused by the active money, there was not a significant difference in their ratings of pleasure to the active money compared to the passive money. Also, in debriefing interviews, subjects who were scanned did not report differences in their hedonic feelings toward the active money compared to the passive money. In addition to the rating scale data collected, we attribute the present results to the saliency because several previous studies in animals and humans have provided evidence that the striatum and its dopamine inputs do not code the hedonic impact of rewards. The hedonic reaction patterns of rats with 6-OHDA lesions of the dopamine fibers projecting to the dorsal and ventral striatum did not differ from the hedonic reaction patterns of control rats (Berridge and Robinson, 1998), and mice lacking dopamine preferentially respond for rewarding stimuli similarly to wild-type mice (Cannon and Palmiter, 2003). Dopamine neurons do not respond to primary rewards presented at regular time intervals (Ljungberg et al., 1992), and when a cue predicts a future reward, dopamine neurons respond to the cue and no longer respond to the reward itself (Schultz, 1998). Using human neuroimaging techniques, a similar striatal response occurs when receipt of money is cued; the striatum is activated by the cue rather than the money itself (Knutson et al., 2001b). Intuitively, if the striatum were responding to the hedonic impact of the money, striatal activations should occur in response to the presentation of the money. Together, these studies and the rating scale data suggest that the striatum is involved with processing a quality of reward other than the hedonic impact, and the present results demonstrate a role of the striatum in processing saliency.

It should be noted that the signal measured in fMRI is an indirect measure of changes in cerebral blood flow, which tends to be more correlated with presynaptic activity than postsynaptic spiking (Logothetis et al., 2001). The BOLD signal cannot be associated directly with activity in specific cell types and is not a measurement of specific neurotransmitter release. We are unable to link the present results to specific neurons in the striatum (e.g., tonically active interneurons or medium spiny projection neurons) or direct changes in dopamine transmission. However, since the BOLD signal is more correlated with presynaptic activity, the observed activations within the striatum probably do not represent spike rates of striatal projection neurons. Tonically active interneurons (TANs) comprise $\sim$2% of all striatal cells, so it is unlikely that the TANs are solely responsible for the reported changes in striatal activity either. However, dopaminergic inputs, which do respond to salient events (Horvitz, 2000), may interact with convergent glutamatergic cortical inputs in the striatum by amplifying strong (salient-related) cortical inputs and dampening weak (nonsalient-related) cortical inputs (Horvitz, 2002; Nicola et al., 2000). This interaction could be responsible for the signal changes observed in the striatum in the present study.

In conclusion, we have demonstrated that striatal responses to monetary reward, as measured with fMRI, are contingent on the manner in which the money is received. Striatal activations (caudate and nucleus accumbens) resulted when the receipt of reward was dependent on subjects' performance (salient) but not when receipt of reward was independent of a task (nonsalient). The striatal response can be attributed to differences in the saliency of the two conditions because other qualities (i.e., reward value, appearance, temporal uncertainty) were identical. The active money was salient because of its behavioral importance. If the striatum were simply responding to the rewarding value of such stimuli, there should be no difference between active and passive receipt of money. The difference argues strongly for the role of saliency in modulating the reward response in the striatum. Although the present study focused specifically on the dorsal and ventral striatum, additional brain regions are activated in our contrasts of interest, suggesting that the striatum is one constituent in a large network of areas throughout the brain that process salient events.

Experimental Procedures

Subjects

Sixteen right-handed, healthy adults (ten males; six females), ages 18–32, were included in the fMRI experiment. Ten separate subjects (five males; five females), matched for handedness and age, performed the task outside the scanner during which SCRs and subjective rating scale data were acquired. Subjects in both groups had no history of neurological or psychiatric disorder and gave informed consent for a protocol approved by the Emory University Institutional Review Board.

Experimental Tasks

All stimuli presentations and recordings of reaction times were performed with the software, Presentation (Neurobehavioral Systems, Inc., San Francisco, CA).

Each scanning session consisted of four runs of slightly different tasks (Figure 1). While in the scanner, subjects performed a visual target detection task in every run. One of four blue shapes (square, rectangle, circle, or triangle) was presented in pseudorandom order in one of the four screen corner locations for 750 ms within a 2000 ms interstimulus interval. Subjects were instructed to press button #1 with their right index finger each time a triangle appeared. Each run consisted of 140 stimulus presentations, of which there were 25 triangle targets. Subjects were guaranteed $10 for participation in the study and received additional money during the scanning session (another $30). In the "active money run," a money bag was positioned in the center of the screen at all times. While performing the target detection task, occasionally a money bill unexpectedly appeared above the bag, and subjects were required to press button #2 with their right middle finger within 1 s of the money bill appearance to trigger the bill falling into the bag, which took 400 ms to drop. Subjects were told that all money in the bag represented actual money they would receive immediately following the scanning session. Prior to being put in the scanner and to ensure believability, subjects were shown the actual money that they could earn by correctly performing the task. If the subjects did not correctly respond to the money bill, it simply disappeared from the screen after 1 s rather than falling into the bag, and subjects did not earn money on that trial. In another run, the "passive money run," receipt of the money was not contingent on subject performance. Subjects were only instructed to press button #1 to the triangles in the target detection task. Each time a money bill appeared in this run, it automatically fell into the bag after 750 ms, taking 400 ms to drop, with no response from the subject, and subjects understood that the appearance of the money bill was not contingent on the target detection task. As before, money in the bag represented money that the subject received after the scanning session. The presentation of a money bill in both the active money run and the passive money run was unpredictable, occurring 12 times per run with 10–30 s between consecutive appearances. The exact value of each money bill was not disclosed to the subjects in order to avoid confounds due to counting or knowledge of the amount earned at a given time, but subjects were told the value of each bill ranged from $0.50–$4.00. As a control for the added attention and motor requirements of active money, each session included an "active blob run" and "passive blob run," which were identical to the active money run and passive money run, respectively, except the money bills were replaced with green nongeometrical shapes (blobs). Subjects were aware that the blobs did not have monetary value and that they would not receive extra money for correct responses in these runs, but they were instructed to perform as accurately as possible.

The money/blobs in each run never appeared at the same time as a triangle target in the ongoing target detection task; however, this information was not disclosed to the subjects to ensure that the subjects were monitoring the target detection task even when the money/blobs appeared. Subjects were given instructions for all four runs prior to entering the scanner, and the run order was counterbalanced across subjects. The four event types (active money, passive money, active blob, and passive blob) were sequestered to separate runs, rather than being intermixed within runs, to minimize subject confusion. Rather, each run started with an instruction screen for 10 s (corresponding scans were discarded prior to analysis), indicating which run type was beginning and reminding the subject of the instructions.

fMRI Imaging

Scanning was performed on a 3.0 Tesla Siemens Magnetom Trio scanner. For each subject, a T1-weighted structural image was acquired for anatomical reference, followed by four whole-brain functional runs of 155 scans each to measure the T2*-weighted blood oxygenation level-dependent (BOLD) effect (gradient-recall echo-planar imaging; repetition time: 2010 ms; echo time: 30 ms; flip angle: 90°; 64 $\times$ 64 matrix; field of view: 192 mm; 30 3.5 mm axial slices acquired parallel to the anteroposterior commissural line). Head movement was minimized with padding.

fMRI Analysis

The data were analyzed using Statistical Parametric Mapping (SPM2) (Friston et al., 1995b). For each subject, the first five scans in each run were excluded from the analysis to discount artifacts related to the transient phase of magnetization. Slice timing correction was used to adjust for time differences due to multislice imaging acquisition. Motion correction to the first functional scan was performed within subjects using a six-parameter rigid-body transformation. Each individual's anatomical image was coregistered to the mean of their functional images using a rigid-body transformation and then spatially normalized to the Montreal Neurological Institute (MNI) template conforming to the Talairach orientation system (Talairach and Tournoux, 1988) by applying a 12-parameter affine transformation followed by nonlinear warping using basis functions (Ashburner and Friston, 1999). The computed transformation parameters were applied to all the functional images, interpolating to a final voxel size of 3 $\times$ 3 $\times$ 3 mm^3. Images were subsequently spatially smoothed with a 8 mm isotropic Gaussian kernel.

A random-effects, event-related statistical analysis was performed with SPM2 (Friston et al., 1995a, 1999) in a two-level procedure. At the first level, a separate general linear model (GLM) was specified for each subject. The BOLD responses to different event types (triangle targets, active money, passive money, active blob, passive blob, and errors when applicable) were modeled with a basis function consisting of a synthetic hemodynamic response function (consisting of two γ functions shifted 2 s apart) and its first-order temporal derivative. At the model estimation stage, the data were high-pass filtered (threshold $=$ 128 s), and serial correlations were accounted for by an autoregressive model of the first order. Contrast images were calculated for each subject corresponding to: (1) active money $>$ passive money, (2) active blob $>$ passive blob, and (3) (active money-passive money) $>$ (active blob-passive blob). The individual contrast images were then entered into a second-level analysis, using a one-sample t test. Due to the a priori hypothesis concerning the striatum, the resulting summary statistical maps were thresholded at $p < 0.005$ (uncorrected for multiple comparisons), and striatal activations were reported at this threshold. The other brain activations are also reported for completeness; however, because we lacked an a priori hypothesis concerning nonstriatal regions, our threshold does not provide adequate protection against type I errors in the whole brain.

Psychophysical and Rating Scale Data Acquisition and Analysis

Outside of the scanner, a separate group of ten subjects performed the experimental task during which skin conductance responses (SCRs) were acquired. The analog signal was digitized using the MP150 digital converter (Biopac Systems, Goleta, CA) and fed into AcqKnowledge 3.7 recording software (Biopac Systems). The SCR data were sampled at 125 Hz, and a 1 Hz low-pass filter and 0.05 Hz high-pass filter were applied to the data during acquisition. To analyze the SCRs to our four stimuli of interest (active money, passive money, active blob, and passive blob), we computed the integral of the SCR signal over a 5 s interval starting at the stimulus of interest onset and performed a one-way repeated measures ANOVA on the resulting data. In addition to acquiring SCR data, immediately following each run of the experimental task, we collected ratings of subjects' subjective feelings toward the stimuli of interest in the corresponding run. Specifically, we assessed the two dimensions of pleasure and arousal using the Self-Assessment Manikin (Bradley and Lang, 1994), an affective rating system in which a graphic figure depicting values along the two dimensions on a continuously varying scale is used to indicate emotional reactions. The subject could select any of the five figures comprising each scale, or between any two figures, which resulted in a nine-point rating scale for each dimension. We performed a one-way repeated measures ANOVA on the rating scale data.

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