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Chapter 7 1

Motivation and Cognitive Control: Going 2

Beyond Monetary Incentives 3

Marie K. Krug and Todd S. Braver 4

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Introduction 24

Motivation appears to have strong influences on cognitive processing and behavior 25
 in humans. The study of motivation–cognition interactions has become a recent 26
 focus of cognitive neuroscience research in order to better understand where, 27

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28 why, and how such interactions occur in the brain. In this chapter, we focus on an
29 often-overlooked issue that is relevant to this area of study. In human studies, mon-
30 etary rewards are most often used as an incentive to motivate behavior. Money is
31 considered a secondary reward, in that its reward value must be learned through
32 association with other directly reward stimuli. On the other hand, in the animal litera-
33 ture, primary rewards (e.g., food and liquid), which directly satisfy biological drives,
34 are often used to study learning and motivation (Rolls, 1999). The rationale behind
35 using monetary incentives in human experimental studies is that money is universally
36 understood in terms of its economic and reward value. However, the results are often
37 generalized to suggest that the effects apply to all rewards, including primary rewards,
38 when that may not necessarily be true. Here we suggest that nonmonetary (primary)
39 rewards offer not only a more direct comparison to the animal literature but also
40 provide additional experimental, conceptual, and theoretical leverage in understand-
41 ing the neural mechanisms of motivation–cognition interactions.

42 The structure of the chapter is as follows. First, we provide a brief review of the
43 extant literature on monetary incentives and their effects on cognitive processes,
44 suggesting that the effects can be somewhat complex, but seem to have specificity
45 in modulating cognitive control. Next, we discuss current literature that has com-
46 pared different types of incentives in terms of whether common or distinct neural
47 circuits are engaged. Finally, we provide some suggestions regarding promising
48 research directions and questions that can be explored through the use of primary
49 incentives.

50 **Monetary Incentives and Cognitive Performance**

51 It is universally assumed that people are motivated by money. In fact, it is common
52 practice for research participants to be compensated (regardless of their performance
53 on the experimental task) for their participation in a research study. The wording
54 often used to describe these payments (primarily at the request of Institutional
55 Review Boards) is that participants are being compensated “for their time.” Yet such
56 practices also reflect an implicit assumption that participants recruited for a paid
57 (rather than unpaid) study will (a) be more likely to agree to participate; (b) be more
58 motivated to show up for the experiment (and be on time!); and (c) perform the
59 experimental task to the best of their ability. However, the focus of this chapter is
60 not on monetary payments give to participants as a flat hourly or experimental rate,
61 but rather additional monetary earnings that can be attained only when performance
62 is at a certain level (usually defined by response time (RT), accuracy or a combination
63 of both).

64 Before delving into the nuances and issues involved with using money as an
65 incentive, an initial question to consider is whether monetary incentives even
66 improve general cognitive task performance. Indeed, it is important to consider that
67 there are situations where monetary incentives are not advantageous. For example,
68 Gneezy and Rustichini (2000) suggest that when the amount of monetary incentive

is very low, monetary incentives can actually result in worsened task performance. 69
In one of their experiments subjects were paid a flat rate (in Israeli currency; NIS) 70
to perform an IQ test. Each subject was randomly assigned to one of four groups. 71
Subjects in the first group were not given the opportunity to earn additional money 72
based on performance. In the other three groups, subjects were told that they would 73
earn additional money for each question that they answered accurately. The three 74
incentives groups were paid at different rates (low, medium, and high). Subjects in 75
the low incentive group actually answered significantly *fewer* questions than the 76
no-incentive group. Gneezy and Rustichini suggest that this occurs because once a 77
monetary incentive is introduced, subjects are entering into an incomplete contract, at 78
which point their level of effort becomes contingent upon the amount of additional 79
money they can earn. 80

The Gneezy and Rustichini (2000) results point to the detrimental effects that can 81
arise, in some cases, from paying a very small amount of money, which can produce 82
behavioral performance that may be worse than offering no monetary incentive at all. 83
Another, related perspective is that extrinsic rewards (such as money) decrease 84
intrinsic motivation and interest in the task at hand, which could translate to worsened 85
task performance (see Bonner & Sprinkle, 2002 and also Moller & Deci 2014, 86
for a discussion of this topic). The distinctions and relationships between intrinsic 87
and extrinsic motivation form a large literature that is beyond the scope of this 88
chapter; however, it is worth pointing out that it is also an area that may be amenable 89
to investigation from a cognitive neuroscience perspective, although such work is 90
just in its infancy (Murayama, Matsumoto, Izuma, & Matsumoto, 2010). A final, 91
contrasting perspective comes from the growing literature on “choking under pressure” 92
(Beilock, 2010), which documents situations in which large reward incentives 93
can also disrupt task performance, potentially through over-motivation effects that 94
shift the balance between cognitive and affective brain systems (Mobbs et al., 2009). 95
In general, these types of findings stress the importance of carefully considering 96
both the motivational signals and the cognitive control processes being affected 97
when investigating motivation–cognition interactions, a point which we develop 98
further below. 99

The fact that enhanced cognitive and behavioral performance is not a ubiquitous 100
outcome of offering motivational incentives is one that has been confirmed through 101
quantitative reviews of the extant literature (although these have been mostly conducted 102
from a behavioral economics perspective). For example, Bonner, Hastie, 103
Sprinkle, and Young (2000) reviewed 131 experiments in 85 different studies 104
(across several fields of research) to investigate the effects of monetary incentives 105
on task performance (similar reviews and conclusions were drawn by Smith & 106
Walker, 1993 and Camerer & Hogarth, 1999). They estimated that only about 1/2–1/3 107
of these experiments were characterized by an improvement in task performance 108
due to monetary incentive (and, as in Gneezy & Rustichini, 2000), some of the 109
experiments showed worsened performance in monetary incentive conditions). 110
They specifically investigated the influence of task type and type of payment scheme 111
on improvements in task performance. In regards to task type, Bonner and Sprinkle 112
categorized their tasks (in order of increasing complexity) as (1) vigilance and 113

114 detection, (2) memory, (3) production and simple clerical, (4) judgment and choice,
115 and (5) problem solving, reasoning, and game playing. Their low complexity vigilance/
116 detection tasks and memory tasks showed positive effects of monetary incentives
117 83 % and 69 % of the time, respectively.

118 They concluded that incentives appear to improve performance most reliably when
119 the gap between skill and task demand/complexity is low (i.e., simple tasks). When
120 tasks are simple, participants have the knowledge and skill set required to perform the
121 task well. Consequently, when offered monetary incentives, these participants will be
122 more likely to exert extra effort, and their extra effort will be effective in improving
123 performance (Bonner et al., 2000; Bonner & Sprinkle, 2002). While most of the
124 relevant cognitive neuroscience literature that we will be focusing on consists of
125 tasks that fall into the same category of complexity as their “low complexity” vigi-
126 lance and memory categories, it is important to note that use of monetary incentives
127 in more complex tasks may not reliably yield incentive effects.

128 Bonner et al. (2000) also investigated the type of payment/incentive scheme that
129 works best for improving task performance. Quota schemes, where subjects are
130 paid a set amount until a certain performance goal is met, at which point they receive
131 a bonus, are the most effective (69 %), followed by piece-rate schemes (57 %),
132 where subjects are paid a set amount for each unit (such as a task trial). Bonner et al.
133 reason that quota schemes, in addition to providing the opportunity to win money,
134 also give participants a specific goal that helps increase motivation and performance
135 beyond a piece-rate scheme. While piece-rate schemes tend to be the standard
136 method for delivering monetary incentives in the psychology and cognitive neuro-
137 science field, quota schemes should be strongly considered.

138 Overall, the results of these literature reviews imply that standard monetary incen-
139 tives delivered under a piece-rate scheme should improve performance on basic, sim-
140 ple vigilance, memory and, most likely, cognitive control tasks. It is important to
141 consider that this may only be true if the monetary incentive is large enough that
142 subjects are motivated to increase their efforts to achieve that amount of money
143 (Gneezy & Rustichini, 2000). Fortunately, in typical cognitive psychology and neuro-
144 imaging experiments, there are often a high number of task trials, so good perfor-
145 mance on many trials would result in an accumulation of a significant amount of
146 money (even if the amount per trial is low) and may be less likely to result in the
147 detrimental effects on performance seen in Gneezy and Rustichini (2000). The amount
148 of money that is considered “too low” to elicit an increase in effort probably also
149 depends on other factors in addition to the exact monetary value, such as the difficulty
150 of the task or individual differences such as personality traits or wealth status (Bonner
151 & Sprinkle, 2002; Tobler, Fletcher, Bullmore, & Schultz, 2007).

152 A final consideration is how incentive conditions are indicated. There are
153 important complexities regarding how and when incentive cues are presented that
154 must also be considered. In behavioral experiments, particularly in cognitive
155 psychology and neuroscience, the incentive conditions are usually explicitly cued
156 for participants prior to or at the start of the task trial. However, there is also grow-
157 ing evidence that suggests implicit or subliminal reward cues can also be quite
158 effective, particularly at increasing task effort (Aarts, Custers, & Marien, 2008;

Bijleveld, Custers, & Aarts, 2012; Capa & Custers, 2014). In some cases subliminal cues may be even more effective than supraliminally presented cues, depending on the nature of the cognitive task and when (during the duration of the task trial) the cues are presented (Zedelius, Veling, & Aarts, 2011). When a high reward cue is presented before a target word set in a working memory task, performance improves (regardless of whether the reward cue is presented subliminally or supraliminally). However, presenting a reward cue while the words are being maintained disrupts performance, but only if it is presented supraliminally (Zedelius et al., 2011).

The source of the distinction between supraliminal and subliminal reward cueing is still a matter of investigation, but one interpretation is that conscious processing of reward cues can sometimes divert resources from task-related cognitive processing (Bijleveld et al., 2012; Zedelius et al., 2011), which is similar to a common explanation of “choking” effects. Thus, while subliminal cues are thought to induce a general increase in effort, supraliminal cues can evoke conscious processing of the cue, rumination and implementation of specific strategies, which may or may not result in improvements in task performance (Bijleveld et al., 2012; Bijleveld, Custers, & Aarts, 2010; Capa & Custers, 2014; Zedelius et al., 2011). Taken together, these results suggest the importance of delving more deeply into the mechanisms by which motivational incentives exert their influence on specific cognitive processes, which has led to greater interest in cognitive neuroscience-based research approaches.

A Focus on Cognitive Control 179

The main goal of cognitive neuroscience research on motivational incentives is not just to understand the factors that optimize performance of a behavioral task, but rather to (a) identify which particular cognitive and neural mechanisms are modulated by incentives and (b) characterize the nature of interactions between the brain regions that process incentives and those that implement task-relevant processing.

Earlier neuroscience studies of reward incentives arising from the animal literature provide a strong foundation for current theorizing. A number of studies have shown that, when performing difficult working memory tasks such as the delayed response task (Watanabe et al., 2001) or memory-guided saccade task (Kawagoe, Takikawa, & Hikosaka, 1998, 2004), monkeys have faster and more accurate performance on reward-cued trials compared to non-reward cued trials. Behavioral performance is also improved when preferred (compared to non-preferred) rewards are used (Watanabe et al., 2001) or when rewards are large compared to small in magnitude (Leon & Shadlen, 1999). These behavioral effects show a neural correlate in the activation pattern observed within dorsolateral prefrontal cortex (DLPFC) neurons. Specifically, DLPFC neurons that exhibit sustained firing and directionally specific activity patterns during the delay period of such tasks (and are thus thought to be involved with active maintenance of task-relevant information) have increased delay-related activity when a preferred reward or larger reward is expected for a particular trial (Leon & Shadlen, 1999; Watanabe, Hikosaka,

200 Sakagami, & Shirakawa, 2005). These findings have been taken to suggest that
201 DLPFC may be a site of integration of cognitive and motivational information
202 (Leon & Shadlen, 1999; Watanabe, 2007; Watanabe et al., 2005; Watanabe &
203 Sakagami, 2007).

204 In addition to lateral prefrontal cortex (PFC), the animal literature also impli-
205 cates the involvement of the striatum in reward processes and subsequent changes
206 in behavior. Dopaminergic midbrain neurons respond to primary reward stimuli,
207 stimuli predictive of reward (such as reward cues), and reward prediction errors
208 (Schultz, 2001, 2002; Schultz, Dayan, & Montague, 1997). These neurons project
209 to PFC and also to the dorsal (caudate and putamen) and ventral (nucleus accum-
210 bens) striatum. Like DLPFC, neurons in striatum respond to cues indicating reward
211 (Kawagoe et al., 1998, 2004; Schultz, 2002) and also to the value or relative prefer-
212 ence of a particular reward (Hassani, Cromwell, & Schultz, 2001; Schultz, 2002).
213 Indeed, caudate neurons may be even more sensitive to changes in cue-reward con-
214 tingencies and differences in reward values than lateral PFC neurons (for a review
215 see Watanabe, 2007).

216 Studies examining motivation effects on cognition in human subjects have typi-
217 cally used monetary rewards, which can result in improvement in behavioral task
218 performance in various cognitive domains, ranging from visual selective attention
219 (Della Libera & Chelazzi, 2009) and perceptual target detection (Navalpakkam, Koch,
220 & Perona, 2009; Navalpakkam, Koch, Rangel, & Perona, 2010) to the color-word
221 Stroop (Veling & Aarts, 2010) and working memory (Heitz, Schrock, Payne, & Engle,
222 2008). A growing number of fMRI studies have helped elucidate the neural networks
223 underlying the effects of reward incentives on cognitive control task performance in
224 human participants, many of which have also used monetary incentives.

225 Small et al. (2005) and Engelmann, Damaraju, Padmala, and Pessoa (2009) used
226 Posner-type visual attention tasks, Padmala and Pessoa (2011) used a response con-
227 flict task, and the remaining studies used working memory tasks (Beck, Locke,
228 Savine, Jimura, & Braver, 2010; Gilbert & Fiez, 2004; Locke & Braver, 2008;
229 Pochon et al., 2002; Taylor et al., 2004). Many included a manipulation of difficulty,
230 such as working memory load (Gilbert & Fiez, 2004; Pochon et al., 2002; Taylor
231 et al., 2004), or presence/absence of response conflict (Padmala & Pessoa, 2011)
232 and some had different (e.g., high vs. low) levels of reward (Beck et al., 2010;
233 Engelmann et al., 2009; Gilbert & Fiez, 2004; Pochon et al., 2002; Taylor et al.,
234 2004). All except Taylor et al. (2004) used a piece-rate reward scheme, and the dol-
235 lar amounts of monetary reward (either the total amount that could be earned or the
236 amount that could be earned per trial) were explicitly indicated to the participants in
237 all studies except Pochon et al. (2002). It is important to note that Pochon et al. was
238 also the only experiment that did not report significant behavioral incentive effects
239 (although incentive effects were only at the trend level in Small et al. (2005), sug-
240 gesting that an explicit indication of the amount of monetary reward to be earned
241 (either as a per/trial rate or the total amount that can be won) may be necessary to
242 motivate participants.

243 In summary these experiments show a consistent pattern, in which incentives
244 increase activity specifically in the cognitive control-related brain regions that were

postulated to be the key loci for optimal task performance. For example, in Small et al. (2005), monetary incentives enhanced activity in regions necessary to optimize task performance for both validly cued trials (increased expectancy-related activity in posterior cingulate cortex, PCC) and invalidly cued trials (increased disengagement-related activity in inferior parietal lobule). Use of a load manipulation in some experimental designs has been used to provide additional evidence that regions recruited to help process more difficult task conditions are the same regions also recruited to improve performance under incentive conditions. For example, Taylor et al. (2004) found overlapping regions activated by both increases in load and monetary incentive in frontal and parietal cortex during the delay period of the object working memory task. They also found an interaction between reward value and load in DLPFC (driven by a greater effect of load for high reward trials). Gilbert and Fiez (2004) found that right DLPFC activity increased during the delay in response to both reward trials and increases in working memory load in a verbal working memory task. Similarly, Pochon et al. (2002) found that DLPFC was activated in response to increases in load and the reward condition during the n-back working memory task.

A few motivation–cognition studies (Beck et al., 2010; Engelmann et al., 2009; Locke & Braver, 2008; see also Jimura, Locke, & Braver, 2010) have focused not just on the brain regions modulated by incentives but also the temporal dynamics of such effects. A critical approach in this regard is the use of a mixed blocked/event-related fMRI design (Visscher et al., 2003). This type of design allows for separation of sustained, task-block state-related activity, as well as transient activity associated with individual trials or even events within a trial (e.g., cue vs. target). Engelmann et al. (2009) found that incentives increased cue-related activity in various frontoparietal regions (anterior cingulate cortex (ACC), middle frontal gyrus (MFG), frontal eye fields (FEF), etc.) and PCC. These same regions, as well as some additional regions (visual cortex, inferior temporal gyrus) were also engaged during the presentation of the target. They also found increased sustained, block-related activity in several frontoparietal regions (inferior parietal sulcus (IPS), FEF, right MFG). However, Beck et al. (2010) and Locke and Braver (2008) found that monetary incentive conditions were characterized primarily by increased sustained, block-related activity in cognitive control regions, rather than transient trial-related activity. Specifically, Beck et al. reported increased sustained activity in dorsal and anterior PFC, as well as parietal cortex in response to monetary incentive conditions while Locke and Braver (2008) reported sustained increases in DLPFC, parietal cortex, and ACC. In both Beck et al. (2010) and Locke and Braver (2008), the sustained activity was largely right-lateralized. It is suggested that this sustained activity (as opposed to individual trial-related transient activity) may be more helpful for maintaining task goals related to the monetary incentive, which was not delivered until the end of the experiment.

A key question raised by the finding of increased, incentive-related activation in cognitive control brain regions is: what is the neural source of such effects? An appealing account, which is suggested by the animal literature, is that in highly salient motivational conditions these regions may receive enhanced excitatory drive

290 signals arising from primarily subcortical, reward-processing regions. Indeed, in
291 addition to activation of the cognitive control regions, many of the aforementioned
292 fMRI studies have also shown activation in reward-processing regions. Locke and
293 Braver (2008) report activation of reward-related regions when individual differ-
294 ences are considered. Pochon et al. (2002) found that the reward condition activated
295 caudate. Beck et al. (2010) reported sustained activity in the right caudate and, at a
296 more liberal threshold, right lateral orbitofrontal cortex (OFC). Engelmann et al.
297 (2009) found cue and target-related activation in right substantia nigra/dopaminergic
298 midbrain, caudate, and putamen as well as increased sustained activity in both
299 caudate and putamen. Taylor et al. (2004) and Small et al. (2005) both found reward-
300 related activation in lateral OFC. In Taylor et al. (2004), this occurred during the
301 “probe” phase of the working memory trial, when subjects had to judge whether an
302 item was part of the target set. For Small et al., in the reward condition, OFC activity
303 was positively correlated with the cue benefit score, which is a measure of “cue
304 expectancy,” of the degree to which a directional cue biases spatial attention in a
305 visual spatial attention task. Lastly, Padmala and Pessoa (2011) found dorsal and
306 ventral striatal activity in response to the reward cue. Activation of OFC and striatal
307 regions in these paradigms in particular is not surprising, considering evidence for
308 their roles in coding the subjective reward value of a stimulus and reward-related
309 learning, respectively (O’Doherty, 2004).

310 One theory that nicely integrates these findings (as well as findings from the animal
311 literature discussed above) is that motivation may work specifically to influence
312 cognition via dopaminergic-mediated interactions between reward processing and
313 cognitive control brain regions (Braver, 2012; Braver, Gray, & Burgess, 2007; Pessoa
314 & Engelmann, 2010). A phasic DA-mediated gating signal, activated in response to
315 reward cues, could result in a shift to a more “proactive” control strategy, character-
316 ized by sustained, task-related activation of PFC and implementation of preparatory
317 cognitive control (Braver, 2012; Braver et al., 2007). Pessoa and Engelmann (2010)
318 suggest that motivation does not simply increase arousal (leading to changes in
319 global, nonspecific improvements in performance) but instead targets task-specific
320 frontoparietal and sensory regions. They propose that activation of dopaminergic
321 reward regions enhances signal-to-noise ratio in PFC. Experiments with human
322 subjects have generally been consistent with this dopamine (DA)/PFC theory, par-
323 ticularly in regards to the idea that task-specific control regions are recruited under
324 incentive conditions and that preparatory control in particular is enhanced.

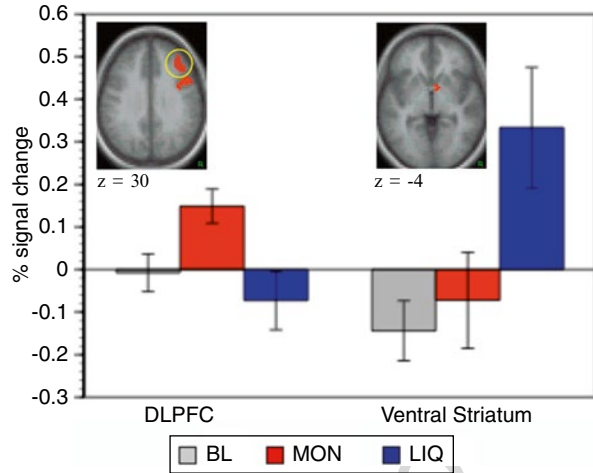
325 Future work in this area needs to focus more specifically on interactions between
326 reward-processing and cognitive control regions in order to test the DA/PFC theory
327 and also to understand motivation–cognition interactions more generally. One
328 excellent demonstration of this approach is Padmala and Pessoa (2011). The goal of
329 the study was to use connectivity and mediation analyses to draw a link between
330 increased activation in the cognitive control network during processing of reward
331 cues and the enhancement of cognitive control processes during target processing
332 (task was a picture-word response conflict paradigm that included response congru-
333 ent, response incongruent, and neutral targets). The results were highly informative.

Reward cue-related activity was found in frontoparietal cortex. During the target phase a motivation (reward vs. no-reward) x trial-type (incongruent, neutral) interaction was observed in medial PFC, such that reduced activation was observed on incongruent trials compared to neutral trials, particularly in the reward condition. These cue and target effects were correlated across participants and were mediated by reduced activation in the fusiform gyrus, suggesting attenuated processing of task-irrelevant information (which likely led to lowered conflict-related medial PFC activity in response to incongruent targets on reward-cued trials). Finally, additional reward-cue activity was observed in subcortical reward regions (i.e., dorsal and ventral striatum) that also showed enhanced connectivity with parietal regions on reward compared to no-reward trials. Thus, through a clever experimental design, examination of multiple events within a task trial, and a focus on functional connectivity and mediation effects, Padmala and Pessoa provide new information regarding both the mechanisms by which cognitive control is implemented and moreover, how motivation can influence this process. In a similar vein, this group has also looked at network analyses to more directly investigate overall changes in brain connectivity. While this type of analysis has typically been performed on resting state data, Kinnison, Padmala, Choi, and Pessoa (2012) have shown that during an incentive-cued response conflict paradigm, reward-cued trials result in increased integration (i.e., higher global efficiency and decreased decomposability) between cortical and subcortical brain regions, in comparison to control (no-incentive-cued) trials. Future experiments should also continue to investigate changes in connectivity at the network level under motivational conditions.

Monetary vs. Nonmonetary Incentives: Common or Distinct Effects?

As discussed above, theorizing on the effects of reward incentives on behavior (and neural activity) in human cognitive neuroscience is based upon the animal literature. In these animal studies, rewards are usually primary (food or liquid(s)), while in human studies discussed above, secondary (namely, monetary) incentives have been used as the reward. Thus, an initial important question, when considering the use of monetary incentives vs. primary incentives to motivate human cognitive performance, is whether and how monetary incentives differ from other types of incentives in terms of their effects on behavioral performance and neural activity. In particular, one question of obvious interest relates to how monetary incentives compare to primary incentives that have intrinsically appetitive reward value. To our knowledge, Beck et al. (2010) provide the only study to date that has examined this question from a neuroscience perspective and within the context of cognitive task performance. Thus, we provide a more detailed summary of its findings, before continuing to examine other studies that have compared incentive category effects during basic reward processing tasks.

Fig. 7.1 Anatomical double dissociation in incentive category specific sustained activation. Sustained activation selective to the liquid incentive condition was observed in subcortical reward processing regions, as representatively shown for the ventral striatum (7, 0, -4), whereas the cortical cognitive control regions showed monetary incentive-selective sustained effects (here shown for the DLPFC (35, 36, 22)). Figure from Beck et al. (2010, p. 8)



374 In Beck et al. (2010), participants performed the same working memory task
 375 under both liquid and monetary incentive conditions. The monetary condition was
 376 relatively standard, with the design and results summarized in the previous section.
 377 In the liquid condition, fast and accurate performance on incentive-cued trials was
 378 immediately rewarded with a squirt of apple juice. For incentive-cued trials where
 379 the performance criterion was not met, subjects received a neutral liquid instead.
 380 Liquid was not administered during no-incentive cued trials. Behaviorally, perform-
 381 ance improved on the incentive trials in a similar manner for the liquid condition
 382 compared to the monetary incentive condition, suggesting that the use of primary
 383 liquid rewards produces comparable changes in performance on this cognitive task.

384 Comparison of neural activity patterns across the two incentive conditions
 385 yielded a very different set of findings. Although the monetary incentive condition
 386 was selectively characterized by increased sustained activity in a primarily right-
 387 lateralized frontoparietal control network, sustained cortical activity effects were
 388 not as widespread in the liquid incentive condition (although there was sustained
 389 activation common to both tasks in a few cognitive regions such as left inferior and
 390 anterior PFC and right parietal cortex). However, the liquid incentive condition was
 391 characterized by sustained activation in subcortical reward-processing regions, such
 392 as the dorsal and ventral striatum (Fig. 7.1).

393 The liquid condition was also markedly characterized by increased transient,
 394 rather than sustained, activation of cortical cognitive control regions (bilateral
 395 ventrolateral prefrontal cortex (VLPFC), bilateral DLPFC, right anterior PFC,
 396 and bilateral inferior parietal cortex). Overlap analyses specifically showed that
 397 right DLPFC/inferior frontal gyrus, right anterior PFC, and right parietal cortex
 398 showed both money-selective sustained activation and liquid-selective transient
 399 activation, a clear shift in the temporal dynamics of activity in these control
 400 regions across the two incentive conditions (Fig. 7.2b). Time course analyses of
 401 this transient activity showed that, for the liquid condition, incentive cued trials

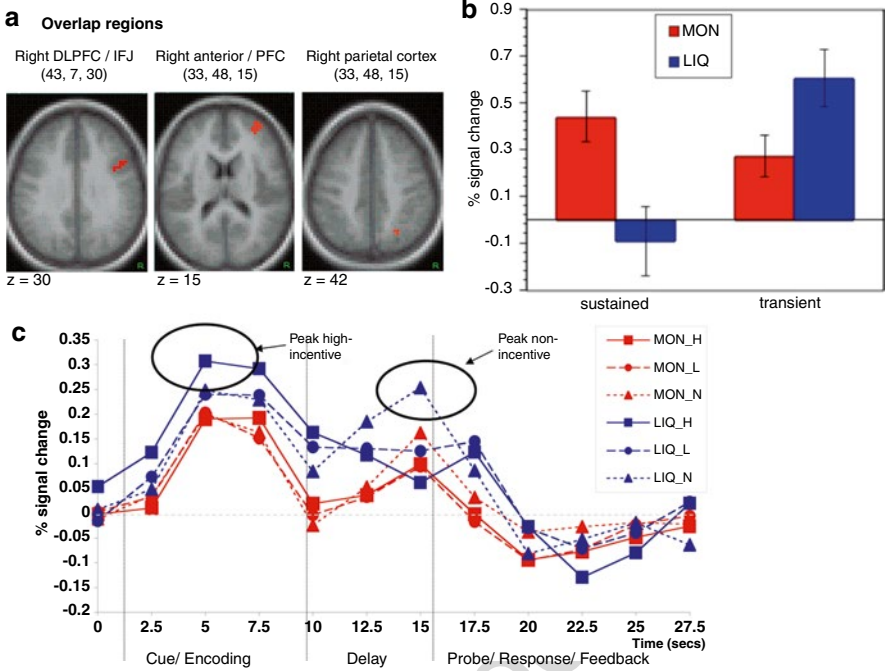


Fig. 7.2 Flexibility in activation dynamics of cognitive control regions related to incentive category. (a) Overlapping regions showing selective sustained effects in the monetary incentive condition and selective transient effects in the liquid incentive condition. (b) Overlapping regions showing a shift from sustained to transient activation across the monetary and liquid incentive conditions. Percent signal change is averaged for all three overlapping regions. (c) Timecourses for incentive trials and no-incentive trials within the monetary incentive and liquid incentive conditions. Timecourses are averaged for the three overlapping cognitive control regions. In the liquid condition, there is a shift in within-trial activity dynamics from late in the trial (no-incentive trials) to earlier in the trial (incentive trials). (MON_H: money high-incentive trials, MON_L: money low-incentive trials, MON_N: no-incentive trials during the monetary incentive condition; LIQ_H: liquid high-incentive trials, LIQ_L: liquid low-incentive trials, LIQ_N: no-incentive trials during the liquid incentive condition). Figure from Beck et al. (2010, p. 9)

showed activity that peaked at the time of cue-processing or encoding of the stimulus set, while in no-incentive cued trials, activity peaked later (at the time of the probe presentation), suggesting better preparatory, or proactive control, on trials where good performance would be rewarded and more reactive control processes on no-incentive trials (for a discussion of proactive vs. reactive control, see Braver et al., 2007) (Fig. 7.2c).

In summary, the results from Beck et al. (2010) suggest the possibility that monetary and liquid incentives influence cognitive processing through distinct neural mechanisms. However, it may be premature to draw more general conclusions based on it until further research in this area is conducted. Moreover, in apparent discrepancy with the Beck et al. (2010) results, studies of basic reward processing

413 suggest more similarities than differences in the brain regions engaged by different
414 types of reward incentives. This literature is briefly reviewed next.

415 A few studies have directly compared monetary and liquid rewards within
416 participants, similar to the approach taken by Beck et al. (2010), but using simpler
417 instrumental tasks. Kim, Shimojo, and O'Doherty (2011) focused on cue-related
418 expectations for juice or monetary rewards of different values and found overlap-
419 ping value-related responses in ventromedial PFC (vmPFC). In a similar study,
420 focusing more specifically on reward prediction errors (in a probabilistic learning
421 task) overlapping activity was observed in the dorsal striatum (caudate nucleus),
422 while activity in ventral striatum (nucleus accumbens) was stronger for money than
423 juice (Valentin & O'Doherty, 2009). Levy and Glimcher (2011) used an intricately
424 designed reward-choice paradigm (using liquid, food, and money rewards) to quan-
425 tify, both behaviorally and neurally, the subjective value representation of each type
426 of reward. The subjective value of money activated vmPFC, striatum, and PCC,
427 while the subjective value of food activated vmPFC, striatum, and hypothalamus.
428 Follow-up analyses confirmed that vmPFC (and possibly also striatum) are com-
429 monly activated in response to the value of both types of reward, and this region(s)
430 is/are most likely the site where different rewards are represented and compared on
431 a common scale.

432 A less common example of a primary reward is presentation of erotic pictures.
433 Sescousse, Redoute, and Dreher (2010) directly compared monetary and erotic
434 rewards. They had subjects perform a visual discrimination task under monetary
435 incentive and erotic picture incentive conditions. Their analyses focused on activation
436 during the outcome (reward delivery) phase of the trial. Monetary rewards activated
437 anterior lateral OFC, while erotic rewards activated posterior lateral OFC, medial
438 OFC, and bilateral amygdala. Both types of rewards activated ventral striatum, mid-
439 brain, ACC, and anterior insula. The authors concluded that in addition to activating a
440 common reward network, only erotic rewards activate bilateral amygdala, and erotic
441 and monetary rewards activate different subregions of OFC, providing evidence that
442 the OFC represents abstract rewards in more anterior locations and primary rewards
443 in posterior subregions. Because incentive cues for this task also indicated a probabil-
444 ity of reward (in other words, if subjects performed well on that trial, they would have
445 a certain percentage chance of receiving the reward), Sescousse et al. (2010) were able
446 to look at reward prediction errors. They found that prediction errors for both types
447 of rewards activated a common network including ventral striatum, anterior insula,
448 and rostral ACC.

449 Studies that directly compare different types of primary and secondary rewards
450 are few compared to studies that have focused on reward-related activity during
451 delivery of a specific type of reward. Thus, meta-analyses are a useful approach to
452 more quantitatively compare the patterns observed in studies involving different
453 classes of rewards. Sescousse, Caldu, Segura, and Dreher (2013) recently performed
454 a large meta-analysis of this type, examining 87 neuroimaging studies to account
455 for these findings and help determine common and reward-specific brain regions in
456 response to receipt of monetary, food/liquid, and erotic rewards. They found that
457 all three types of rewards commonly activated a large reward-processing network

consisting of bilateral striatum (particularly ventral striatum/nucleus accumbens), 458
bilateral anterior insula, mediodorsal thalamus, bilateral amygdala, and vmPFC. 459
They stress the importance of considering anterior insula as a key component of 460
reward processing and discuss its role in affective processing and/or awareness of 461
rewards (see discussion, Sescousse et al., 2013). 462

However, some differences between reward types were also observed. Monetary 463
reward activated bilateral ventral striatum and anterior OFC more than food and 464
erotic rewards, providing corroboration for the idea that more anterior regions of 465
OFC in processing of abstract secondary rewards (Sescousse et al., 2010, 2013). 466
The authors suggested that greater activation in ventral striatum in response to mon- 467
etary rewards may be a consequence of differences in experimental design used in 468
most of the monetary rewards studies in comparison to the primary reward studies; 469
in monetary reward studies there was more likely to be a motor response component 470
(and passive viewing is more likely to be used in food/drink and erotic reward stud- 471
ies), and monetary reward studies were more likely to use a probabilistic reward 472
design, enhancing reward prediction error signals. Food rewards activated dorsal 473
anterior insula and somatosensory cortex. Activity in these regions is most likely 474
related to sensory processing of food and liquid stimuli. Erotic rewards activated 475
bilateral amygdala, ventral anterior insula, and the extrastriate body area (a region 476
involved in the visual processing of body stimuli) more so than money or food, and 477
lastly, both types of primary rewards (erotic pictures and food/liquid stimuli) acti- 478
vated middle insula more than monetary rewards (Sescousse et al., 2013). 479

The behavioral results from these and other studies suggest that participants 480
exhibit similar hedonic and motivational responses when performing for primary 481
and secondary rewards. In Sescousse et al. (2010), hedonic ratings of monetary 482
rewards and erotic pictures were not significantly different, and in Valentin and 483
O'Doherty (2009), pleasantness ratings of stimuli associated with high probability 484
of money and high probability of juice were not rated differently. In Levy and 485
Glimcher (2011), there was a lottery aspect to the behavioral task; subjects had to 486
choose between a certain low amount of reward vs. a risky, higher amount of reward. 487
While there was a lot of variability in degree of risk aversion between subjects, 488
within subjects risk aversion for food, water, and money was fairly consistent. 489
Regarding performance and motivated behavior, as discussed above, in Beck et al. 490
(2010) monetary rewards and liquid rewards resulted in comparable improvement 491
in cognitive task performance. In Sescousse et al. (2010), performance of the visual 492
discrimination task did not differ as a function of type of reward. 493

Interestingly, the literature on basic reward processing suggests mostly compar- 494
able effects of monetary and primary rewards in terms of neural circuitry. This stands 495
in potential contrast with the results of Beck et al. (2010), which point to the promi- 496
nent differences between monetary and primary rewards during motivated cognitive 497
control tasks. How can this apparent discrepancy be explained? Two obvious sources 498
of differences are that the Beck et al. study was the only one to (a) focus on incentive 499
category effects during higher cognitive processing and (b) examine the temporal 500
dynamics of brain activity in terms of sustained vs. transient reward-related modu- 501
lation. Thus, further research will be necessary to more clearly understand the 502

503 importance of these two dimensions. However, as we discuss next, the neural activity
504 differences between liquid and monetary incentive conditions could also be poten-
505 tially accounted for by another aspect of the experimental design used in Beck et al.
506 (2010) that highlights an important methodological consideration related to the use
507 of primary incentives.

508 Importantly, a key potential distinction between primary and secondary reward
509 incentives relates to how such rewards are delivered. Specifically, in studies using
510 monetary incentives, information regarding rewards is typically presented visually
511 (or auditorily) and provides a symbolic indicator about the value of rewards that will
512 actually be delivered at the end of the experiment (or often even later, when checks
513 are mailed or deposited). Thus, the reward feedback during task performance is
514 indirect and delayed. In contrast, in studies using primary rewards, these rewards
515 can be directly delivered to the participant (e.g., via tubing inserted into the partici-
516 pant's mouth), and potentially consumed instantaneously, providing direct reward
517 value following each trial (note that in the case of erotic rewards, the visual presenta-
518 tion of images are also "directly consumed" and thus may also have immediate
519 appetitive reward value).

520 Thus, in Beck et al. (2010), as described above, the two incentive conditions were
521 distinguished in terms of the timing of reward feedback delivery, with the liquid
522 rewards delivered directly and instantaneously following each trial, while monetary
523 reward feedback was indirect and only directly delivered at the end of the experi-
524 ment. This difference between the two conditions points to a potential limitation of
525 the experimental design and may also provide an explanation of the differences in
526 brain activity observed. In particular, because the monetary rewards were not directly
527 delivered until the end of the experiment, they may not have activated reward-
528 processing regions as strongly or as effectively as primary rewards. Moreover, the
529 more abstract and indirect nature of the monetary rewards may have resulted in more
530 sustained cognitive processing, with subjects maintaining a representation of task
531 winnings during performance, or at the very least, actively maintaining the incentive
532 value of the task context in working memory during the money condition (see Beck
533 et al. for a more detailed discussion of this topic). Because the primary rewards were
534 consumed immediately and directly, there may have been a reduced need for a cogni-
535 tive representation of the reward during the liquid condition. Consequently reward
536 regions may have been recruited more strongly, tonically, and consistently, provid-
537 ing a better (or, at the very least, different) mechanism for motivation–cognition
538 interaction. In particular, the sustained, direct activations of reward regions may
539 have triggered a different (more transient, proactive) implementation of cognitive
540 control on a trial-by-trial basis.

541 These ideas regarding the timing of reward delivery dovetail well with other
542 findings related to the temporal discounting of delayed vs. immediate rewards.
543 For example, McClure, Ericson, Laibson, Loewenstein, and Cohen (2007) examined
544 temporal discounting of liquid rewards. When the choice was between immediate
545 juice and delayed delivery of juice, the nucleus accumbens, subgenual cingulate
546 cortex, medial OFC, PCC, precuneus, and ACC were activated. Choices between
547 two delayed options activated visual, motor, and cognitive prefrontal regions such
548 as DLPFC. The brain regions recruited were very similar to those found in a

previous study (McClure, Laibson, Loewenstein, & Cohen, 2004) that investigated 549
temporal discounting of money. It is important to note that this close correspon- 550
dence in brain regions activated during temporal discounting of juice and money 551
occurred, despite the fact that the timescales used in these two experiments were 552
very different; in McClure et al. (2007), a “delay” for juice receipt was on the 553
order of minutes, while in McClure et al. (2004), the timescale for money receipt 554
was much longer. In a follow-up experiment, McClure et al. (2007) lengthened 555
their delay times to see how this would affect discounting-related brain activity 556
for receipt of juice. They found that when the delays were recalibrated such that 557
the “shortest” time delay was 10 min, limbic areas characteristic of immediate 558
reward delivery were not activated at all. 559

The findings from McClure et al. (2004, 2007) are also instructive for interpreting 560
the differences in temporal dynamics observed in Beck et al. (2010). Because liquid 561
rewards are valued and delivered on a more immediate timescale, this could have 562
contributed to the greater activation of subcortical limbic systems, as well as the 563
motivation-induced transient recruitment of cognitive control regions in the liquid 564
condition. Thus, an important direction for future research would be to include liq- 565
uid reward conditions in which the rewards are delayed until after the experiment. 566
A key question is whether such a manipulation leads to an increase in sustained, 567
right-lateralized activity in cognitive control regions, as might be expected from 568
the monetary incentive and temporal discounting literature. Relatedly, by directly 569
comparing monetary and liquid incentive effects under such conditions (see Levy & 570
Glimcher, 2011) for a similar approach used during risky decision-making), it 571
would be possible to more clearly determine whether money and primary rewards 572
are inherently and qualitatively different when used as rewards, or instead whether 573
the differences observed in Beck et al. (2010) can be fully attributed to differences 574
in the timing of reward receipt in these experiments and/or differences in how the 575
brain values these rewards based on time (see also commentary, Lamy, 2007). 576

The results of McClure et al. (2004, 2007) and Beck et al. (2010) also have impli- 577
cations regarding the optimization of task design and reward contingencies laid out 578
in Bonner et al. (2000). While Bonner et al. presents a review of the contingencies 579
upon which monetary incentives improve task performance, it is uncertain whether 580
these same conditions apply to primary rewards. We hypothesize that task complex- 581
ity should have similar consequences on incentive effects regardless of the type of 582
reward used, provided that the reward is equally as motivating as money (and, conse- 583
quently, subjects are willing to exert comparable amounts of effort to earn a liquid 584
reward, for example). On the other hand, use of a quota payment scheme may be 585
particularly effective for monetary rewards compared to primary rewards such as 586
liquid. With monetary incentives, even with a piece-rate scheme, the money is often 587
not received by the participant after each task trial, but rather at the end of the experi- 588
ment. Thus, with a quota scheme, the goal aspect can help motivate performance and 589
will help subjects maximize their total winnings, and the lack of immediacy of 590
reward attainment might not be much of a disadvantage. However, if liquids are used 591
as incentives it is hard to know if receiving a large amount of liquid, or a “liquid 592
bonus” once a certain goal had been met, would be more motivating than liquid 593
delivered under a piece-rate scheme. 594

595 **Use of Nonmonetary Reward in Cognitive Studies:**
596 **Conceptual and Methodological Advantages**

597 An important outcome of investigations into the potential similarities vs. differences
598 in the effects of monetary vs. nonmonetary incentives on behavior and brain activity
599 is that it contributes to our understanding of the motivational side of motivation–
600 cognition interactions. Indeed, if it were the case that common neural circuitry were
601 engaged across different types of motivational incentives, and they were also similar
602 in terms of their effects on behavioral performance (when equated for incentive
603 value), it would suggest that motivational signals are represented in a highly abstract,
604 domain-general format within the brain. In such a case, it is useful to consider
605 whether purely symbolic (i.e., hypothetical or imaginary) rewards can be substi-
606 tuted for real monetary incentives. Obviously, if this were true it would be advanta-
607 geous, from a practical and logistical perspective, to rely exclusively on symbolic
608 rewards to motivate participants, since symbolic rewards are clearly simpler (and
609 cheaper) to employ in experimental studies.

610 Indeed, in a few studies that have explicitly examined the use of symbolic
611 (i.e., hypothetical or imaginary) rewards, very similar effects on brain activity
612 and behavior have been observed when compared to the use of real monetary
613 rewards.

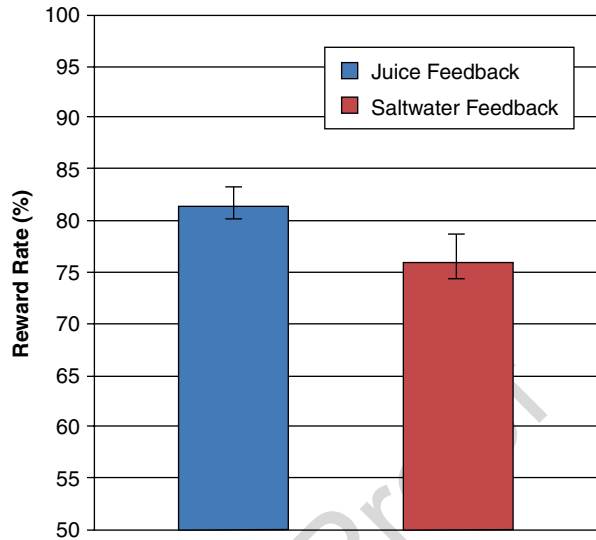
614 For example, in a study examining discounting of delayed rewards, Bickel,
615 Pitcock, Yi, and Angtuaco (2009) found no statistical differences in choice patterns
616 and brain activation (in both limbic and lateral prefrontal regions) in a hypothetical
617 money gain condition (none of the money would be given to the subject) relative to
618 a real money gain condition (in which one of the trials was randomly selected and
619 paid out to the participant). Likewise, in a simple associative learning study,
620 Miyapuram, Tobler, Gregorios-Pippas, and Schultz (2012) found graded responses
621 in the dopaminergic midbrain and medial OFC to cues (pictures of money) that
622 indicated different hypothetical reward values (participants were explicitly told that
623 the reward cues were symbolic only). Moreover, when participants imagined a
624 hypothetical monetary reward cue, similar responses in these same regions were
625 observed compared to when the cue was visually presented. Similar results were
626 also observed in Bray, Shimojo, and O'Doherty (2010). Common activation in
627 medial OFC was observed when participants received a real reward in a probabilis-
628 tic learning task and when they instead freely imagined a personally reward scen-
629 ario in the same context. Symbolic rewards also often have similar effects in
630 enhancing behavior and cognitive performance when compared to real rewards.
631 For example, Shen and Chun (2011) found that the use of arbitrary point incentives
632 led to the same degree of performance enhancement in a task-switching paradigm
633 (i.e., reduced switch costs) as did real monetary rewards. Moreover, adding money
634 to a point condition did not lead to further enhancements beyond points alone.
635 Together, these results suggest that there may be no special advantages to the use of
636 real monetary incentives for the study of motivation–cognition interactions.
637 Nevertheless, further work will be needed to explore this issue more thoroughly.

In contra-distinction to the relationship between monetary and symbolic rewards, we argue that there may be real advantages to the use of primary rewards for investigating motivational influences on cognitive processing. Primary rewards produce motivational effects that, by definition, are hard-wired, present across development and in all species (allowing for another advantage, better comparison between the human and animal literature). Primary rewards are also truly appetitive in that they are directly and immediately consumed. Thus, they enable more precise control over the timing and manipulation of reward delivery. Further, because they are processed automatically, they may more effectively drive core motivational neural circuits in a context-independent manner; that is, their effects on brain activation and behavior might be less dependent on symbolic processing, situational construal, or conscious awareness. Moreover, as we describe next, there are even additional advantages of primary reward incentives that warrant further investigation, which can ultimately lead to a more complete understanding of the “motivation” side of motivation–cognition interactions.

A recent pilot study in our lab provides a nice case study example of the potential utility of primary rewards for uncovering the relationship between motivational and cognitive processing, while also raising issues that provide avenues for further exploration. Participants ($N=36$) performed a cued task-switching paradigm in which pre-trial color cues indicated whether the current trial was an incentive (reward possible for fast and accurate responses) or no-incentive (no reward possible) trial. On incentive trials, the reward was a small monetary bonus that was cumulated and provided at the end of the experiment. However, at the end of each incentive trial a feedback signal was presented that indicated whether the reward had been obtained on that trial or not. Of note, feedback on the incentive trials was not presented visually, but rather delivered as a liquid (no liquid was given when the reward was not obtained). Participants performed the task in two blocks that were identical in all respects, except that they used different color cues and liquid feedback: in one block, reward feedback was signaled by a pleasant liquid (apple juice), whereas in the other it was signaled by an aversive liquid (saltwater). Critically, however, the valence of the liquid was incidental, as it signaled the identical information (successful task performance and attainment of the monetary reward) in both conditions. Nevertheless, liquid valence clearly had an impact on performance, as participants earned significantly more rewards in the juice condition relative to the saltwater ($t(35)=2.58$, $p=.01$) (Fig. 7.3). Thus, the results suggest that the liquid feedback modified the incentive properties of the task, presumably via their automatic (i.e., pre-existing, hard-wired) signaling of motivational significance.

There are a number of possible interpretations of the observed effects. One of the least interesting is that participants performed more poorly in the aversive liquid condition either because they were confused by the incongruent feedback or because they purposely performed worse to avoid receiving saltwater. However, this explanation is unlikely, since the liquid valence effect was relatively subtle (6 % difference in reward rate), relative to substantial performance improvement on incentive trials compared to no-incentive trials in both reaction time (156 ms faster in the juice feedback condition ($t(35)=7.230$, $p<.001$), and 144 ms faster in the saltwater

Fig. 7.3 Incidental liquid feedback affects reward rate in a monetary incentive task. Reward was achieved when trial response was both accurate and faster than an individually determined criterion RT. Reward rate was calculated as a ratio of the number of successful (rewarded) incentive trials compared to the total number of incentive trials. Mean reward rate was significantly greater for juice feedback compared to saltwater feedback. Error bars indicate standard error of the mean



683 condition ($t(35)=6.325, p<.001$) and accuracy (accuracy was 4.1 % higher in the
 684 juice condition ($t(35)=3.281, p=.002$), and 3.9 % higher in the saltwater condition
 685 ($t(35)=2.002, p=.053$)). Moreover, the main effect of trial type (indicating better
 686 performance on incentive vs. no-incentive trials; RT: $F=52.698, p<.001$; Accuracy:
 687 $F=9.906, p=.003$) did not interact with the type of liquid feedback. (F 's<1).
 688 Together these findings are inconsistent with the idea that participants were con-
 689 fused or purposely tried to perform more poorly on incentive-cued trials in the salt-
 690 water condition.

691 Another potential interpretation is that the motivational utility of incentive trials
 692 reflected both the monetary bonus and liquid feedback, with the two types of incen-
 693 tives integrated together into a “common currency” representation of subjective
 694 value (Levy & Glimcher, 2012; Montague & Berns, 2002; Rangel, Camerer, &
 695 Montague, 2008). Under this account, pleasant liquids add to the subjective value of
 696 incentive trials, while aversive liquids serve as a cost, subtracting from the estimated
 697 subjective value. Thus, according to this account, giving juice feedback would be
 698 expected to be equivalent—in terms of brain activity and behavior—to slightly
 699 increasing the monetary reward value of the trial, whereas giving saltwater feedback
 700 is equivalent to slightly decreasing the monetary reward value. A similar, but more
 701 complex interpretation is that the liquid and monetary rewards are integrated, but in
 702 a multiplicative, rather than additive manner (e.g., the liquid valence effect might be
 703 more prominent with smaller monetary rewards; cf., Talmi, Dayan, Kiebel, Frith, &
 704 Dolan, 2009). Nevertheless, both accounts lead to straightforward predictions that
 705 could be tested, for example, in imaging studies that orthogonally manipulate mon-
 706 etary reward values and liquid feedback within a factorial design.

707 Another key advantage of using primary rewards is that it would be possible to
 708 test whether their modulatory effect on behavior is directly related to the subjective

value of the incentive. Critically, subjective value is idiosyncratic, such that different individuals should have different preference profiles. Thus, in a paradigm such as the one described above, if a range of different rewards were used, the predicted reward earning level should track preference rankings, with the highest reward rate attained for the most preferred reward and the lowest rate earned for the least preferred reward. The opposite pattern should be observed with aversive liquids (e.g., lowest reward for most disliked liquid). Although, to our knowledge, no such studies have yet been conducted in the literature, consistent patterns have been observed in human imaging studies of basic reward processing. O'Doherty, Buchanan, Seymour, and Dolan (2006) observed that activity in the dopaminergic midbrain and ventral striatum appeared to track the preference rankings for a range of liquid rewards.

Another important alternative interpretation of our pilot data results is that they reflect the interaction of motivation with two distinct forms of instrumental control, one that is goal directed and the other that is habitual. The distinction between goal-directed and habitual behavioral control is prominent in motivational theories originating in the animal learning literature (Daw, Niv, & Dayan, 2005; Dayan, Niv, Seymour, & Daw, 2006; Dickinson & Balleine, 2002) but this distinction has not previously been a focus of examination in human studies of motivation–cognition interactions. However, the use of primary rewards may provide important leverage for understanding the contribution of these two mechanisms on brain activity and behavioral performance and brain activity. Specifically, incentive-cued paradigms may not only involve goal-directed or strategic, top-down implementation of cognitive control in response to the incentive cues but may also have a learned, low-level conditioning (i.e., Pavlovian) component that also contributes to behavior. Because performance feedback (the immediate outcome) is typically of the same affective valence as the over-arching reward outcome, these contributions to performance are usually confounded.

In the current study, however, the use of affectively valenced liquid feedback may have promoted the acquisition of cue-outcome associations that were dissociable from the explicit instrumental contingencies. In particular, the difference in performance observed across the two liquid feedback conditions suggest that cognitive processing was either (a) enhanced by the incidentally positive cue-outcome associations of the juice condition; (b) impaired by the incidentally negative cue-outcome associations of the saltwater condition; or (c) both (a) and (b). Interestingly, our first attempts to examine these alternatives (through the use of a neutral liquid) suggest that the effect of saltwater was stronger than the effect of juice, but further study is required. For example, one approach would be to use a design in which cue-outcome associations are acquired through learning (e.g., by using an intermixed rather than blocked design, with probabilistic cue-liquid feedback mappings). If differences in reward rate in the different cue conditions are still observed, even under conditions in which participants show no explicit awareness of the cue-liquid contingencies, it would be more suggestive of a Pavlovian conditioning influence.

In the animal learning literature, the most well-accepted means of testing for a Pavlovian contribution to instrumental behavior is through demonstration of a

754 Pavlovian instrumental transfer, or PIT, effect. In the standard PIT procedure, a
755 conditioning phase comes first, in which one cue (the CS+) is associated with a
756 reward outcome in a purely Pavlovian manner (i.e., no instrumental behaviors
757 are required), while another is associated with a neutral or aversive outcome (CS-).
758 The second phase consists of exposure to the instrumental task, also for reward
759 outcomes. In the key transfer phase, the instrumental task is performed again but in
760 the presence of the Pavlovian cues and with rewards withheld (i.e., in extinction).
761 Demonstration of a Pavlovian priming effect occurs if the instrumental task is
762 enhanced in the presence of the CS+ compared to the presence of the CS-. There has
763 been recent interest in demonstrating PIT effects in human studies of basic reward
764 and punishment (Bray, Rangel, Shimojo, Balleine, & O'Doherty, 2008; Geurts,
765 Huys, den Ouden, & Cools, 2013; Talmi, Seymour, Dayan, & Dolan, 2008). This
766 work has shown the amygdala and ventral striatum to be critical neural substrates for
767 PIT effects. However, to our knowledge, such effects have not been examined as a
768 potential mechanism of incentive effects in studies of motivation-cognition interac-
769 tions. Thus, this represents a ripe target for future research. For example, in our para-
770 digm, a strong test of PIT effects would require participants to acquire the
771 cue-feedback associations in a purely Pavlovian conditioning phase and a demon-
772 stration that the reward cues modulate task-switching performance even when
773 presented during an extinction phase.

774 Based on the dual-process framework described above, it is also possible the liquid
775 feedback effects on task-switching performance demonstrated in our pilot study
776 reflect goal-directed rather than habitual motivational control. Here again, the use of
777 primary rewards provides potential strong theoretical advantages in testing for a goal-
778 directed mechanism. In particular, one such test is the outcome revaluation procedure,
779 which also derives from the animal learning literature (Dickinson & Balleine, 2002).
780 In this procedure, two different reward incentives are each paired with a different
781 instrumental action. After an initial training/testing period with these incentives, the
782 subjective value of one incentive is modified for the individual, either through satia-
783 tion, deprivation, or some other physiological manipulation, while the other incentive
784 is left unaffected. Then, following this revaluation phase, the individual is tested again.
785 When the behavior is under goal-directed instrumental control, behavioral patterns
786 should be instantly changed for the revalued incentive, but remain constant for the
787 control incentive (which rules out a more general motivational or behavioral effect).
788 Although outcome revaluation procedures have only recently been examined in
789 human imaging studies, the results to date are promising.

790 In a study examining simple instrumental choice, Valentin, Dickinson, and
791 O'Doherty (2007) used the outcome revaluation procedure with liquid rewards to
792 show that OFC activation was sensitive to outcome-devaluation, suggesting that it
793 may serve as the neural substrate for goal-directed control. Mohanty, Gitelman,
794 Small, and Mesulam (2008) demonstrated that such motivational effects could also
795 influence higher order cognitive processing. In a spatial attention paradigm, behav-
796 ior in response to "donut" targets was altered when subjects were satiated on donuts
797 compared to a food-deprived state. Motivational state also altered activation in
798 reward-processing and task-relevant cognitive regions. These behavioral and neural

changes were not observed in response to non-appetitive stimuli (tools). In this study subjects were not performing the task to actually earn the food reward. However this type of deprivation vs. satiation design could easily be adapted to look at the effects of motivational state in response to specific rewards or reward cues and the subsequent effects on cognition. Manipulation of motivational state would be most easily accomplished using primary rewards rather than monetary incentives, given that individuals typically do not show satiation for monetary rewards. Thus, in our liquid feedback paradigm, evidence for a goal-directed mechanism would be obtained if selective satiation on the juice reward, induced after an initial performance phase, had immediate effects in reducing reward rates for juice cue trials.

Summary and Conclusions

In this chapter we have provided a new perspective on studies of motivation–cognition interactions, which emphasizes some of the potential concerns associated with the use of monetary incentives, as well as some of the potential advantages to using nonmonetary incentives, such as primary rewards, like food and liquids. We began by reviewing findings that suggest that motivational incentives do not always have a straightforward influence on task performance, sometimes yielding no effects, and other times causing paradoxical performance impairments. Such findings place a greater emphasis on better understanding the nature of motivation–cognition interactions, particularly in understanding the general vs. incentive-specific types of motivational signals that drive such interactions. A cognitive neuroscience approach is particularly useful for such investigations. This approach is targeted toward revealing the particular mechanisms of how, where, and why motivation–cognition interactions occur in the brain. We discussed findings suggesting that motivational effects on task performance appear to be strongly related to cognitive control, modulating activation in frontoparietal brain networks that are critically involved in working memory, attentional control, and task/goal representations. Moreover, the source of such effects may be enhanced through interactions between the frontoparietal cognitive control network and primarily subcortical reward networks, potentially mediated by the neuromodulator dopamine (which strongly targets both networks). We then discussed intriguing findings from a study conducted in our lab (Beck et al., 2010), which suggests that the modulation of reward and cognitive control networks in the brain appears to interact further with the type of motivational incentive used. Specifically, important dissociations were observed between monetary and primary liquid rewards in terms of the temporal dynamics of brain activity in both networks.

One potential interpretation of this result is that motivational effects on cognition are incentive specific, with different categories of reward engaging different neural circuits. However, a review of the basic reward processing literature on incentive category effects indicates that such assertions are not strongly supported. Instead, the findings suggest that a number of reward regions that appear to be fairly domain-general (e.g., vmPFC and ventral striatum) and are engaged commonly by

840 a variety of different incentive types. One potential resolution to this discrepancy is
841 that the difference between monetary and primary rewards may not necessarily
842 point to an incentive-specific motivational effect, but could rather reflect the different
843 dynamics of how primary and monetary rewards are delivered. In particular, pri-
844 mary rewards can be directly delivered and consumed immediately after successful
845 task performance, whereas monetary rewards are indicated during task performance
846 via abstract (typically visual) feedback cues and are only acquired after the exper-
847 iment is over. Yet we suggest that both types of interpretation, incentive-specific
848 effects and reward delivery dynamics, point to the need for further studies in this
849 domain, since to our knowledge, Beck et al. (2010) represents the only published
850 study examining incentive category effects during motivation–cognition interac-
851 tions using a within-study design.

852 Moreover, a key takeaway point of the Beck et al. (2010) study, and the literature
853 on domain-general activation of the reward-processing network by different types
854 of incentives, is that monetary incentives are not the only type of reward that can
855 induce motivational effects on cognitive task performance. Indeed, a growing litera-
856 ture suggests that such effects can even be observed by symbolic (i.e., hypothetical
857 or imagined) as well as real rewards. This is not to say that there are not interesting
858 effects that are specific to monetary rewards; there may in fact be a distinct behav-
859 ioral and neural signature of monetary rewards. However, future experiments need
860 to be carefully designed to answer this question. In addition to matching primary
861 and monetary rewards on reward delivery schedule, use of a symbolic “control”
862 condition will help separate out the neural and behavioral effects of money from
863 those induced by a salient symbol or abstract cue (Hubner & Schlosser, 2010).

864 Our primary suggestion of the chapter is that primary rewards offer distinct con-
865 ceptual and methodological advantages for investigating the nature of motivation–
866 cognition interactions, particularly in terms of understanding the distinct properties
867 of various motivational signals. We presented pilot data from our lab as a case-study
868 illustration of how primary rewards might be exploited in an experimental context,
869 by demonstrating how such rewards, when presented as a feedback signal, interact
870 with monetary incentive-related enhancements of task performance, presumably via
871 automatic signaling of motivational significance.

872 We then ended the chapter by discussing a number of promising directions for
873 further research in this area, using our pilot data as an example. In particular, we sug-
874 gested that the use of primary rewards opens experimental studies up to a number of
875 different avenues of fruitful exploration. We highlighted a variety of different meth-
876 odological approaches, including (a) factorial designs to understand whether various
877 incentive types are integrated into a common representation of subjective motiva-
878 tional value; (b) manipulation of idiosyncratic reward preferences to determine
879 whether cognitive performance actually tracks subjective value; (c) tests for Pavlovian
880 motivational influences on instrumental behavior, using the well-established PIT
881 effect; and (d) tests for a goal-directed motivational influence using outcome revalu-
882 ation procedures. In sum, we believe that such approaches provide clear “low-hanging”
883 fruit, by pointing the way toward effective research strategies for uncovering
884 more clearly how, why, and where motivational signals modify ongoing cognitive
885 processing in the brain.

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