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Reward Improves Cancellation and Restraint Inhibition Across Childhood and Adolescence

Katia J. Sinopoli^{a,d,e}, Russell Schachar^{b,c,e}, and Maureen Dennis^{b,e,f}

^aPhysiology and Experimental Medicine, The Hospital for Sick Children, 555 University Ave., Toronto, Ontario, Canada, M5G 1X8

^bNeurosciences and Mental Health, The Hospital for Sick Children, 555 University Ave., Toronto, Ontario, Canada, M5G 1X8

^cPsychiatry Department, The Hospital for Sick Children, 555 University Ave., Toronto, Ontario, Canada, M5G 1X8

^dPsychology Department, The Hospital for Sick Children, 555 University Ave., Toronto, Ontario, Canada, M5G 1X8

^eFaculty of Medicine, University of Toronto, 500 University Ave., Toronto, Ontario, Canada, M5G 1V7

^fDepartment of Psychology, University of Toronto, 500 University Ave., Toronto, Ontario, Canada, M5G 1V7

Abstract

Inhibitory control allows for the regulation of thought and action, and interacts with motivational variables, such as reward, to modify behavior adaptively as environments change. We examined the effects of reward on two distinct forms of inhibitory control, cancellation and restraint. Typically developing children and adolescents completed two versions of the stop signal task (cancellation and restraint) under three reward conditions (neutral, low reward, and high reward), where rewards were earned for successful inhibitory control. Rewards improved both cancellation and restraint inhibition, with similar effects of reward on each form of inhibitory control. Rewards did not alter the speed of response execution in either task, suggesting that rewards specifically altered inhibition processes without influencing processes related to response execution. Adolescents were faster and less variable than children when executing and inhibiting their responses. There were similar developmental effects of reward on the speed of inhibitory control, but group differences were found in terms of accuracy of inhibition in the restraint task. These results clarify how reward modulates two different forms of regulatory behavior in children and adolescents.

Keywords

Inhibition; reward; cancellation; restraint; development

Corresponding author: Katia Sinopoli, BrainFit Lab, University of Toronto, Faculty of Medicine, 160-500 University Ave., Toronto, ON M5G 1V7; Physiology and Experimental Medicine, The Hospital for Sick Children, 555 University Ave., Toronto, ON M5G 1X8, Phone: 416-978-8591, Fax: 416-946-8570, katia.sinopoli@sickkids.ca.

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Inhibitory control (IC) is a regulatory mechanism that facilitates adaptive interactions with the environment by aligning current thought and action with priorities of changing goals and stimuli (Logan, 1994). IC involves rapid, voluntary, internally generated acts that oppose excitatory “go” signals for responding. Motor inhibition functions include (but are not limited to) *canceled* or stopping an ongoing response, and withholding or *restraining* a prepotent response before it is initiated. Acts of IC interact with other adaptive processes such as performance monitoring and error adjustment (Logan, 1994; Verbruggen & Logan, 2008a), and occur within a motivational context of reward, non-reward, and punishment. The present study examined how reward affects IC cancellation and IC restraint in typically developing children and adolescents.

Like other regulatory mechanisms such as working memory or performance monitoring, IC improves over development. The latency to cancel a response becomes faster throughout childhood and adolescence, with only limited slowing in older adults (Williams, Ponesse, Schachar, Logan, & Tannock, 1999). Restraint inhibition, in contrast, peaks around age 12 years (Levin, Culhane, Hartmann, Evankovich, & Mattson, 1991). Age-related improvements in both types of IC are thought to reflect maturation of frontostriatal circuitry (Liston et al., 2006; Rubia, Smith, & Taylor, 2007) which includes non-linear decreases in cortical gray matter accompanied by linear increases in myelination (Giedd et al., 1999; Gogtay et al., 2004; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999). What is not understood is how reward modulates different forms of IC throughout development. As with substrates of the IC system, the neural substrates of the reward system, including dopaminergic networks, are also immature in children and adolescents (Geier & Luna, 2009; Meng, Ozawa, Itoh, & Takashima, 1999). However, in typically developing children, the effect of reinforcers on cancellation and restraint have been variously reported as facilitatory (Desman, Petermann, & Hampel, 2008; Huang-Pollock, Mikami, Pfiffner, & Burnett, 2007; Kohls, Peltzer, Herpertz-Dahlmann, & Konrad, 2009; Scheres, Oosterlaan, & Sergeant, 2001), impairing (Wodka et al., 2007), or as having no effect on either process (Iaboni, Douglas, & Baker, 1995; Oosterlaan & Sergeant, 1998; Slusarek, Velling, Bunk, & Eggers, 2001).

The discrepancies between studies appear related to a set of methodological issues. Some studies lack a neutral reward condition (Huang-Pollock et al., 2007; Iaboni et al., 1995; Oosterlaan & Sergeant, 1998; Slusarek et al., 2001), or confound the influence of both rewards and punishments on response execution and IC processes (Shanahan, Pennington, & Willcutt, 2008; Slusarek et al., 2001). Other concerns include the generalizability of findings: one study showed that rewards and punishments ameliorated IC as well as feedback about the “correctness” of the response (Desman et al., 2008), and another showed that reinforcement decreased the latency to cancel a response by only 5-13 milliseconds (Scheres et al., 2001). The Kohls et al. (2009) study of rewarded restraint involved children, leaving developmental questions about adolescence unexplored. To date, no study has compared how rewards affect restraint and cancellation inhibition in the same study and with methodologically comparable paradigms. The present study analyzed whether cancellation and restraint inhibition were modifiable by reward in typically developing children and adolescents by utilizing comparable experimental paradigms. In addressing the methodological criticisms of previous studies, only successful IC trials were rewarded, and these effects were compared to performance during a neutral, non-reward condition.

Cancellation inhibition is often measured with the stop signal task (SST; Logan & Cowan, 1984; Logan, 1994). The SST consists of a primary visual choice reaction time task (responding quickly to one of two “go signals”), and a secondary task where participants are instructed to stop responding to go signals when the auditory “stop signal” occurs (Logan &

Cowan, 1984; Logan, 1994). The stop signal is presented at various delays following the onset of the go signal such that the response is cancelled rather than withheld. The latency of IC (i.e., the stop signal reaction time, SSRT) is estimated as a measure of the efficiency of IC (Logan, 1994). Restraint inhibition is typically measured with the go/no-go (GNG) task in which participants respond as quickly as possible to a go stimulus and inhibit their responses to a no-go stimulus, each occurring on separate trials. Responses to the no-go stimulus (commission errors) index failed IC. Although similar neural substrates such as the ventrolateral prefrontal cortex or basal ganglia may be important for both cancellation and restraint (Dillon & Pizzagalli, 2007; Leung & Cai, 2007; Xue, Aron, & Poldrack, 2008), distinct pathways appear to mediate each form of inhibition. Specifically, cancellation may engage a predominately bottom-up, rapid control system involved in the detection of salient sensory stimuli (i.e., the stop signal; e.g., Chevrier, Noseworthy, & Schachar, 2007; see Downar, Crawley, Mikulis, & Davis, 2002), while restraint may be mainly dependent on a top-down system driven by regulatory centers in the dorsal aspects of the prefrontal cortex (e.g., Kelly et al., 2004). If restraint and cancellation differ in their measurement, developmental trajectory, and neurological underpinnings, then how each is modifiable by reward might be dissociable as well.

The present study employed the cancellation and restraint versions of the SST (Schachar et al., 2007) in order to make task procedures comparable over different inhibition operations. Critics of the GNG task argue that because a similar modality is required to discriminate between go and no-go stimuli (i.e., both are cues arising from the same modality occurring on separate trials), the act of inhibition may be confounded with the process of selective attention, making demands on IC weaker in the GNG task than in the SST (Aron & Poldrack, 2005; Rubia, Smith, Brammer, & Taylor, 2003). To make the SST and GNG tasks methodologically comparable, Schachar and colleagues (2007) developed a restraint (i.e., GNG) version of the SST where the delay between the onset of the go and stop signal is zero. Thus, the concurrent presentation of the go and stop signals interrupts the *preparation* of a response rather than interrupting an ongoing response (Schachar et al., 2007). In this manner, prepotent responding to the go signal is withheld, similar to the GNG task. Importantly, the no-go signal in the restraint version of the SST is an auditory tone, which minimizes the task demands on selective attention.

We predicted that rewards, which promote approach and consumption (Schultz, 2006), would improve IC across tasks. Given the immaturity of both the reward and inhibition systems, we hypothesized that there would be age-related differences in the way in which rewards affect inhibition processes. Hyperactivity or hypersensitivity to rewarding stimuli is evident during adolescence, leading to a bias towards highly rewarding stimuli (see Galvan, 2010; Geier & Luna, 2009), suggesting that rewards may facilitate IC to a greater degree in the adolescent group. However, a hypersensitivity to rewards can be maladaptive when paired with an immature IC system, leading to decisions that are riskier and more impulsive than those made by children or adults (Ernst, Pine, & Hardin, 2006; Fareri, Martin, & Delgado, 2008; Geier & Luna, 2009), suggesting that rewards may induce more impulsive behaviors in the adolescent group, which in turn may lead to a greater number of inhibition errors compared to the child group.

Method

Participants

We recruited 66 healthy children and adolescents aged 7 to 17 years old through flyers and community advertisements. Brief telephone interviews were conducted at recruitment with each participant's parent to exclude participants with neurological or psychiatric disorders, mental retardation, learning disabilities, or sensory or motor impairments. Nine participants

cancelled or missed their appointments. To confirm that our participants were typically developing children and adolescents with no significant behavioral impairments, parent ratings of each participant's behavior were assessed with the Conners 3rd Edition Rating Scales (Conners 3; Conners, 2008). The Conners 3 assess behaviors and symptoms of attention-deficit/hyperactivity disorder (ADHD) as well as other difficulties related to inattention and/or hyperactivity such as executive dysfunction and oppositionality. Scales of interest included the Diagnostic and Statistical Manual of Mental Disorders, 4th edition text revision (DSM-IV-TR; American Psychiatric Association, 2000) Scales, which assess behaviors related to ADHD, conduct disorder, and oppositional defiant disorder, and DSM-IV-TR Symptom Counts which reflect the criteria needed to make a diagnosis of either of these disorders. Participant data were excluded from further analyses if parent ratings revealed significant elevations (T-score of 65 or greater) on the DSM-IV-TR Scales *and* if ratings met criteria for any disorder on the DSM-IV-TR Symptom Counts. Based on these criteria, 13 participants were excluded. The remaining 44 participants (22 female, 22 male; mean age, 12.44 years) were divided into two age groups based on a median split: a TEEN group (N=22, aged 13 to 17 years), and a CHILD group (N=22, aged 7 to 12 years).

All participants were administered the Vocabulary and Matrix Reasoning subscales of the Wechsler Abbreviated Scale of Intelligence (WASI), and overall score was used to exclude participants with IQ scores under 75. Demographic information was recorded at recruitment, including household income, parental occupation, and parental education. The socioeconomic status (SES) of each participant was computed using the Hollingshead Four-Factor Index (Hollingshead, 1975), which includes parental occupation and education. Family Hollingshead scores were calculated for each participant by averaging the SES scores of both parents, or was based on data from one parent when this was the only information available.

Prior to testing, informed consent was obtained from each parent, and assent was obtained from each participant. The experiment was conducted with approval of the Research Ethics Boards at the Hospital for Sick Children and the University of Toronto.

Stop Signal Tasks

The SST is based on a formal model that conceptualizes performance as a race between go processes (triggered by the go signal) and stop processes (triggered by the stop signal; Logan & Cowan, 1984; Logan, 1994; Verbruggen & Logan, 2008a). As go and stop processes “race” against each other, the process that “wins” the race determines the outcome (Logan & Cowan, 1984; Logan, 1994). Because inhibition is unobservable, the race model allows for the measurement of the latency of IC (i.e., the SSRT) and the factors that affect the probability and latency of stopping the ongoing response (Logan, 1994).

Two versions of the SST were used to measure canceling and restraining a prepotent response (see Figure 1; Logan, 1994; Schachar et al., 2007). In both versions, the primary task involved the computerized presentation of one of two possible go signals (an X or an O) on each trial. Participants were instructed to respond to these stimuli as quickly as possible by making the appropriate button press on a handheld controller. The auditory stop signal (a 1000 Hz tone emitted from computer speakers) occurred randomly on 25% of trials, and participants were instructed to inhibit their responses to the go signal when they heard this tone. Logan (1994) reasoned that presenting the stop signal on only 25% of trials ensures that sufficient data on IC can be collected while minimizing expectation for the stop signal, which can result in slower go reaction time on the go trials as a strategy to increase the probability of inhibition.

In the cancellation version, the stop signal was presented at various delays following the go signal to allow for the interruption of an ongoing response. The initial delay period between the presentation of the go and stop signal was set at 250 milliseconds and was adjusted dynamically based on the participants' performance (Logan, 1994). Using this dynamic tracking of performance, the probability of inhibition on stop signal trials should converge on approximately 50%, regardless of whether or not participants slowed their go signal reaction time as a strategy to increase successful inhibition (Logan & Cowan, 1984; Logan, 1994). In the restraint (GNG) version of the task, the stop signal was presented at the same time as the go signal. Because the delay between the onset of the go and stop signal is zero, the response is inhibited during the preparation of the response and before being executed (Schachar et al., 2007).

The initial presentation of either version of the SST was a neutral or non-reward (NO) condition, where participants received no specific feedback about performance. Rather, at the end of each block, the words "Good work! Press a button to keep going" appeared in the middle of the screen. Following the NO condition, the participants were told that they would perform the task for a second time where they could receive 2 points each time they successfully inhibited their responses (low reward condition, LOW). They were also told that they would be performing the task for a third time, where they could win 10 points for each successful inhibition trial (high reward condition, HIGH), and if they could acquire 400 points by the end of the testing session, they would receive a prize (a \$10 gift certificate for the movies). Bonus points were offered for pushing the buttons as quickly as they could when they saw the go stimuli. Although no bonus points were actually rewarded, this instruction was introduced to reduce the tendency for participants to slow their go RT to ensure successful inhibition (and thus win more points). Points earned in the LOW and HIGH conditions were immediately represented on the screen in a visual analog scale (the scale was left empty in the NO condition). At the end of each block, a message appeared in the middle of the screen updating participants of how many points they had just won in that specific block (e.g., "You won 10 points."). Points earned were tallied by the examiner, and total scores (and the prize) were revealed at the end of the testing session. The reward conditions were always presented in the same ascending order of magnitude (NO, LOW, HIGH). The presentation order was not counterbalanced due to a concern that the LOW or NO conditions could have been perceived as punishments if they followed presentation of the HIGH condition. This would have effectively confounded the effects of rewards on IC with the effects of punishments, thus changing the main experimental manipulation.

All participants completed both the cancellation and restraint (GNG) versions of the SST three times in order to examine performance under three different reward conditions (NO, LOW, HIGH). Each reward condition consisted of 120 trials divided into 5 blocks of 24 trials each, with the stop signal randomly occurring on 30 trials. The first block in each task was a practice block, data from which were not utilized in subsequent analyses. The order of administration of each version was counterbalanced, with a break between, during which other tasks were administered.

Statistical Analyses

Age group differences in WASI and SES scores were examined with an analysis of variance (ANOVA), and chi-squared tests compared group differences in sex and handedness.

Consistent with previous studies (Band, 1997; Band, van der Molen, & Logan, 2003; Schachar, Levin, Max, Purvis, & Chen, 2004; Verbruggen & Logan, 2008b), participants were excluded from data analyses if the following conditions were met: less than 66% accuracy on go trials, mean go reaction time (MRT) less than 100 milliseconds, and for the cancellation version only, percent inhibition (reflecting the amount of responses that were

inhibited) less than 12.5% or greater than 87.5%. Based on these criteria, one participant was excluded from subsequent analyses of the cancellation and restraint data.

Dependent variables of interest in both versions of the SST (and across reward conditions) were related to response execution and IC. IC measures included SSRT and percent inhibition. SSRT was estimated via the integration procedure (Logan, 1994). First, the go reaction times for trials in which there were no stop signals presented were collapsed and rank ordered. Then, the go reaction time that corresponded to the probability of inhibition was determined, and the SSRT was estimated by subtracting the mean delay from this new “integrated go reaction time”. For instance, if a participant inhibited 55% of their go responses when the stop signal was presented, then the 55th slowest go reaction time was used as the integrated go reaction time measure. This method can be used to estimate SSRT for both cancellation and restraint versions of the SST (Schachar et al., 2007). Response execution measures included MRT, standard deviation of go reaction time (SDRT), and accuracy on go trials (percent correct).

Performance on each task was compared separately for each dependent variable utilizing repeated measures ANOVAs, with reward condition (NO, LOW, HIGH) and task (cancellation, restraint) as the within-subjects factors, and group (CHILD, TEEN) and task order (cancellation administered first, restraint administered first) as the between-subjects factors. The only significant finding from analyses of sex differences was that females exhibited more variable go task performance than males on the cancellation task (data not shown), so we did not include sex in any further analyses.

Results

Participant Characteristics

Table 1 describes the participant characteristics. No participants were excluded based on WASI scores below 75. Although there was a significant difference in IQ scores between groups ($F(1, 42)=6.08$, $p=0.018$, partial $\eta^2=0.126$), individual and mean IQ scores were within the normal range (i.e., within 1 standard deviation of the mean). Family SES scores and handedness were similar between groups, as was the gender distribution.

Stop Signal Task Performance

SSRT—A repeated measures ANOVA revealed a significant main effect of reward on SSRT (linear effect, $F(2, 78)=10.401$, $p<0.001$, partial $\eta^2=0.211$; see Table 2). In both tasks, the latency to inhibit a response was faster in the reward conditions (LOW, HIGH) relative to the neutral (NO) condition. The TEEN group exhibited faster SSRT relative to the CHILD group ($F(1, 39)=18.528$, $p<0.001$, partial $\eta^2=0.322$), and this effect was evident on both cancellation and restraint tasks (age group by task interaction, linear effect, $F(1, 39)=5.715$, $p=0.022$, partial $\eta^2=0.128$). SSRT was faster in the cancellation task relative to the restraint task (linear effect, $F(1, 39)=263.686$, $p<0.001$, partial $\eta^2=0.871$). There was no effect of order of task administration, nor were there any other significant interactions.

Percent Inhibition—In the cancellation task, approximately 50% of inhibition trials were successfully inhibited across reward conditions (see Table 2), suggesting that the tracking algorithm was successful at limiting the probability of inhibition to approximately 0.5 across reward conditions. Not surprisingly, more responses were inhibited during the restraint task relative to the cancellation task (linear effect, $F(1, 39)=636.356$, $p<0.001$, partial $\eta^2=0.942$). Although there was no main effect of reward, there was a reward by task interaction (linear effect, $F(2, 78)=7.439$, $p=0.001$, partial $\eta^2=0.160$) indicating greater percent inhibition (and fewer commission errors) in the restraint task during the HIGH condition relative to both the

NO and LOW conditions. There was no main effect of order, but if the cancellation task was administered first, a greater percentage of responses were inhibited in the cancellation task in the NO and LOW conditions, and in the restraint task in the HIGH conditions (reward by task by order interaction, linear effect, $F(2, 78)=6.524$, $p=0.002$, partial $\eta^2=0.143$).

There was no overall effect of age group, but there was a significant reward by age group interaction (linear effect, $F(2, 78)=3.683$, $p=0.030$, partial $\eta^2=0.086$) revealing that the TEEN group was able to inhibit a greater percentage of responses relative to the CHILD group in the NO and LOW conditions. A significant task by age group interaction (linear effect, $F(1, 39)=4.698$, $p=0.036$, partial $\eta^2=0.108$) revealed that the CHILD group exhibited greater percent inhibition in the cancellation task compared to the restraint task, while the TEEN group exhibited greater percent inhibition in restraint compared to the cancellation task.

MRT—Reward did not significantly affect the speed of response execution in either task (see Table 3). There was a significant reward by task by order interaction (linear effect, $F(2, 78)=4.894$, $p=0.010$, partial $\eta^2=0.111$) indicating that participants exhibited longer MRT in the NO condition of the cancellation task when the cancellation task was administered first. Faster MRT was observed in the restraint task (linear effect, $F(1, 39)=25.601$, $p<0.001$, partial $\eta^2=0.396$), especially if the cancellation task was administered first (linear effect, $F(1, 39)=7.503$, $p=0.009$, partial $\eta^2=0.161$). The TEEN group exhibited faster MRT relative to the CHILD group ($F(1, 39)=16.068$, $p<0.001$, partial $\eta^2=0.292$). There were no other significant interactions with age.

SDRT—Reward did not alter the variability of go responses, and there were no significant interactions with reward (see Table 3). Greater variability was observed in the cancellation relative to the restraint task (linear effect, $F(1, 39)=7.667$, $p=0.009$, partial $\eta^2=0.164$), and in the CHILD relative to the TEEN group ($F(1, 39)=13.652$, $p=0.001$, partial $\eta^2=0.259$). There was no significant effect of task order, nor were there any other significant interactions.

Percent Correct—Accuracy on the go task was significantly affected by reward (linear effect, $F(2, 78)=3.352$, $p=0.040$, partial $\eta^2=0.079$), with greater percent correct in the NO condition relative to the LOW and HIGH conditions (see Table 3). However, this effect seems to be mediated by task version and task administration order: if the cancellation task was administered first, greater accuracy was observed in the NO condition of the cancellation task, and poorer accuracy was observed in the NO and LOW conditions of the restraint task (reward by task by order interaction, linear effect, $F(2, 78)=21.845$, $p=0.040$, partial $\eta^2=0.079$). Greater accuracy was found in the cancellation than in the restraint task (linear effect, $F(1, 39)=6.252$, $p=0.017$, partial $\eta^2=0.138$), especially when the cancellation task was administered first (task by order interaction, linear effect, $F(1, 39)=24.316$, $p<0.001$, partial $\eta^2=0.384$). The TEEN group exhibited greater accuracy ($F(1, 39)=15.797$, $p<0.001$, partial $\eta^2=0.288$), in particular during the restraint task when the cancellation task was administered first, and during the cancellation task when restraint was administered first (task by order by age group interaction, linear effect, $F(1, 39)=18.311$, $p<0.001$, partial $\eta^2=0.319$).

Discussion

The present study explored the effect of reward on two different forms of IC (cancellation and restraint) in typically developing children and adolescents. Increasing the magnitude of reward earned for successful inhibition improved both cancellation IC (SSRT) and restraint IC (SSRT and percent inhibition). The lack of interaction between age group and reward suggests that reward facilitated the speed of inhibition (SSRT) to a similar degree across

children and adolescents, but the effect of reward on the percentage of responses inhibited seems to depend on age. Accuracy on the go task was also affected by reward; however, this effect was dependent on the order of task administration. Relative to younger children, adolescents were faster at inhibiting and executing responses, and were less variable and more accurate in their go responses. Adolescents also inhibited a greater percentage of responses in the NO and LOW conditions of the restraint task. Differences between task versions were found for the speed of IC and response execution, percentage of responses inhibited, variability of go responses, and accuracy of go responses (although this later measure is mediated by the order of task administration). These results bear on the effects of reward, age, and inhibition task.

Reward Effects

Reward decreased the latency of IC, and did so to a similar degree across cancellation and restraint tasks as shown by the lack of a significant interaction between SSRT and task version. Interestingly, facilitation of SSRT was similar between the LOW and HIGH conditions, suggesting that typically developing children and adolescents may perform at optimal levels with very minimal levels of reinforcement (Slusarek et al., 2001). On the other hand, rewards did not influence the speed or variability of response execution measures. These data provide counter-evidence for the claim that the speed of response execution is directly tied to the speed of SSRT (see Alderson, Rapport, & Kofler, 2007). There were fewer commission errors in the restraint task following administration of reward (i.e., percent inhibition increased), yet this finding may not reflect the experimental manipulations because it depends on task order.

Incentive learning involves the detection and estimation of the valence of appetitive stimuli (rewards), followed by signals about the magnitude of the incentive and prediction errors that allow for the adjustment of behavior (Geier & Luna, 2009). Although it is not possible to elucidate *how* rewards affected IC in the current study, a number of hypotheses can be made about potential mechanisms. Reward may have led to general increases in arousal, approach behaviors, or effort, leading to more efficient performance (indeed, associations have been found between dopamine-related reward signals and concurrent behavioral activation and arousal; see Salamone & Correa, 2002). However, reward must have affected processes beyond general arousal because there were no significant influences of reward on the speed of response execution or reward-related improvements in the variability of responses in the CHILD group.

Rewards might have sharpened attentional engagement, particularly during inhibition trials, which might have led to a more ready response to stop signals (Boehler et al., 2009). Whether or not the mechanism involved attention, rewards likely strengthened the established relationship between the stop signal and appropriate cancellation or restraint behaviors, perhaps by enhancing learning from prediction errors (Berridge, 2007; Kelley, 2004) and thereby, the association between the stop signal and the act of IC. Were this mechanism operative, however, one might have expected better IC in the NO condition of the second task performed (given that they just performed one version of the task under different reward conditions) but there were no task order effects or interactions between task order and age.

Alternatively, rewards may have enhanced the “liking” and/or “wanting” of the stop signal, thereby leading to faster IC. According to the hedonia hypothesis (see Volkow et al., 2006; Wise, 1980), rewards enhance the hedonic value associated with the stop signals, thereby leading to faster IC responses. Although we did not assess this directly, the participants did not anecdotally report increased pleasure during the reward trials; on the contrary, they enjoyed the tasks less as the session progressed and many were relieved at the end. The

incentive salience hypothesis (see Berridge, 2007) states that incentives, like rewards, cause a specific stimulus or action to be desirable, and labels a specific behavior as a rewarded outcome that an organism is motivated to perform. What rewards do, we believe, is “tag” conditioned stimuli that predict the value of the reward, and thereby increase the incentive salience (the “wanting”) of the stop signal to facilitate IC. In this view, reward’s effects on “liking” or learning contribute to the “wanting” of a stimulus. Generation of the incentive salience is a dynamic process and can be target-specific, with each stimulus acquiring its own incentive salience value (Berridge, 2007). The stop signal, arguably more salient during the LOW and HIGH conditions, becomes desirable because it is linked to a positive outcome (points that lead to a prize); in contrast, the go signal response is not rewarded, so it has less incentive salience and the net effect is a facilitation of SSRT but not response execution.

At the neural level, the mesocorticolimbic dopamine system may be responsible for adding incentive salience to the stop signal (Berridge, 2007). Rewards may directly influence the interaction between the cognitive control and dopamine-rich motivational centers of the brain, or may alter the activity in other areas responsible for the integration of IC and motivation (Padmala & Pessoa, 2010). We hypothesize that rewards for successful IC may operate on overlapping neural substrates that mediate each form of IC to effect the *preparation* of the inhibition function via stimulation of the reward pathway, resulting in faster cancellation and restraint IC. While the active suppression of motor responses is related to activity in the basal ganglia (Mink, 1996), successful cancellation and restraint also involve activation of the inferior frontal gyrus (IFG; e.g., Chevrier et al., 2007; Konishi, Nakajima, Uchida, Sekihara, & Miyashita, 1998; Konishi et al., 1999). Stop signals that signify increased rewards for successful inhibition are more salient than non-rewarding stop signals, which may enhance the preparation of inhibition via stimulation of bottom-up, IFG-mediated pathways that are important for the detection of salient information (see Chikazoe et al., 2009; Downar et al., 2002; Konishi et al., 1998; 1999; Smith & Jonides, 1998). Alternatively (or concurrently), reward signals may facilitate IC at the level of the basal ganglia by similarly altering the preparation of the motor response. Here, rewards may facilitate preparation of the IC response by enhancing the gating mechanism of dopamine in the striatum (see Beste, Willemsen, Saft, & Falkenstein, 2010; Horowitz, 2002).

Age Effects

For appropriate preparation, initiation, and on-line control of behavior, a balance between IC and response execution processes needs to be established (Rubia et al., 2001). This balance seems to improve with development, with age-related changes in cancellation SSRT are distinct from age-related changes in go reaction time (Williams et al., 1999), suggesting two separable neural mechanisms in the maturation of speeded information processing. Relative to cancellation, restraint inhibition matures somewhat earlier in development, with adult levels in performance reached by age 12 years (Levin et al., 1991). Consistent with previous research (Hale, 1990; Johnstone et al., 2007; Williams et al., 1999), we found that adolescents exhibited faster and more accurate IC and response execution than younger children.

The development of IC may be related to age-related improvements in other processes such as the ability to sustain fixation and interference control (Ridderinkhof, van der Molen, Band, & Bashore, 1997), as well as developmental changes in regulatory processes such as working memory, decision-making, and performance monitoring (e.g., Roncadin, Pascual-Leone, Rich, & Dennis, 2007; Velanova, Wheeler, & Luna, 2009). The neural circuits subserving inhibition mature into adulthood (Rubia et al., 2007). Therefore, group differences in IC may likely be related to increased recruitment of the IFG and basal ganglia with age (Rubia et al., 2007) and/or increases in the integrity of the connections between frontal and striatal structures (Liston et al., 2006; Rubia et al., 2006). These changes may

result in better saliency detection of the stop signal (Chikazoe et al., 2009) and more efficient programming of motor responses (Horowitz, 2002) to improve cancellation and restraint. Moreover, the maturation of cognitive control centers in the prefrontal cortex may promote developmental changes in restraint (Kelly et al., 2004).

Like the inhibition system, reward circuitry, including the dopamine system, also matures with age (Meng et al., 1999; Segawa, 2000; Spear, 2000). Adolescents recruit the same neural circuitry as adults when encountering rewards (e.g., Bjork et al., 2004; Ernst et al., 2005; Galvan et al., 2006), but relative to adults, exhibit decreased activation of the ventral striatum when anticipating rewards (Bjork et al., 2004), but hyperactivation that is sustained and more diffuse in both the ventral striatum and orbitofrontal cortex with reward consumption (Ernst et al., 2005; Galvan et al., 2006; May et al., 2004). Hyperactivity in reward-related centers of the adolescent brain parallel the exaggerated dopaminergic response to rewards that is apparent during adolescence (Laviola, Macri, Morley-Fletcher, & Adriani, 2003); despite relatively low basal levels of dopaminergic output (Andersen & Gazzara, 1993). Strikingly, adolescents show increased activity in the ventral striatum in anticipation of a high reward, but decreased activity in the same region in anticipation of a low reward (Galvan et al., 2006). The adolescent reward system may then bias a still developing IC system towards actions that result in immediate rewards as a result of greater reward-seeking (Galvan, 2010; Geier & Luna, 2009), which is adaptive when the decision is appropriate but maladaptive when the behavior is based on immediate rewards (Geier & Luna, 2009). For instance, the hypoactive nature of anticipatory signals may drive high sensation seeking, which when paired with an immature IC system and hyperactive consummatory signals, may bias adolescents towards poor decisions marked by impulsivity and a lack of IC driven toward obtaining high-risk, short-term goals (Ernst et al., 2006; Fareri et al., 2008; Geier & Luna, 2009).

Thus, one might expect that the adolescent group would have had an exaggerated response to rewards given the apparent hyperactivity in their reward circuitry, perhaps leading to faster SSRT and/or more inhibition errors during the reward conditions. We found that adolescents exhibited greater percent inhibition than children during the NO and LOW conditions, reflecting a similar amount of commission errors in the HIGH condition between groups. These data seem to provide some evidence for the above hypothesis, suggesting that children require a high amount of reward to motivate their behaviour to adolescent levels, whereas adolescents respond positively to even low levels of reward. On the other hand, there was no interaction between age group and reward condition for SSRT, suggesting that reward affected the speed of IC to a similar degree across the developmental span studied here. The data do not allow us to decide between a range of possibilities that may account for this apparent discrepancy, but a direct comparison to an adult participant group may have shown the exaggerated SSRT response to reward hypothesized to be present in adolescents.

Inhibition Task Effects

The behavioral literature suggests that cancellation and restraint are different forms of inhibition, and this is supported by developmental studies and research on neural function (e.g., Johnstone et al., 2007; Schachar et al., 2007). The latency to inhibit a response was faster when a response needed to be cancelled, which suggests support for the idea that IC is not a unitary construct. Although the cancellation and restraint stop signal tasks are methodologically comparable inhibition tasks, the way in which the latency of IC is calculated biases faster SSRT in the cancellation relative to the restraint task (i.e., since the restraint task has a delay period of zero between presentation of the go and stop signals; Schachar et al., 2007). Thus by definition the SSRT *should* be faster in cancellation given that stop signal delays vary according to performance (Logan, 1994).

Given that the tracking algorithm limits the probability of inhibition to 0.5 in the cancellation task (Logan, 1994); participants could earn more points for successful inhibition while performing the restraint task as compared to when they perform the cancellation task. Thus, it is conceivable that over the span of a task, a child may perceive a more highly rewarded task (restraint) as more rewarding or motivating than a less highly rewarding task (cancellation). Future studies are therefore needed to test whether maintaining the amount of reward that could be earned in both tasks significantly alters any of the findings reported above. For example, one might track the stimulus display time in order to degrade the stimuli so that total inhibition is approximately 0.5 in both the cancellation and restraint versions of the task.

The new information that we have added to the literature is that reward acted similarly on cancellation and restraint to facilitate SSRT. That different forms of IC can be improved using similar reward contingencies suggests a similar mechanism of action regardless of difference between processes. The implication of these findings is that the efficiency of behavioral regulation can be ameliorated with external reinforcement, which is especially relevant to those with pathologically impaired IC, such as youths with ADHD. ADHD is associated with characteristic deficits in both cancellation and restraint (see Schachar et al., 2007), as well as abnormal responses to rewards. These children have difficulty delaying receiving rewards (Sonuga-Barke, 2002), and may need higher levels of reinforcement to motivate their behaviour (e.g. Haenlein and Caul, 1987). A recent study revealed that rewards influence inhibition in children and adolescents with known inhibition deficits and reward-related sensitivities such as those with ADHD as well as those with acquired traumatic brain injuries (Sinopoli, Schachar, & Dennis, in press). These findings suggest that behavioral interventions involving rewarding stimuli may be useful at modifying maladaptive regulatory control in these clinical populations as well as in typically developing youths.

Conclusions

A number of studies have attempted to describe the relationship between reward and IC in typically developing youth (Desman et al., 2008; Huang-Pollock et al., 2007; Iaboni et al., 1995; Kohls et al., 2009; Oosterlaan & Sergeant, 1998; Scheres et al., 2001; Shanahan, et al., 2008; Slusarek et al., 2001), yet methodological shortcomings have limited our understanding of this relationship. In addition, no study to date had compared the effect of reward on different IC processes utilizing comparable tasks across both children and adolescents. By addressing the methodological shortcomings of past studies by including a neutral or non-reward condition and by preventing the confounding of rewards and punishments, we have shown that reward can positively alter inhibition processes throughout development. Although there were differences between age groups in terms of the speed and efficiency of IC, rewards facilitated both restraint and cancellation IC in typically developing children and adolescents, suggesting a powerful influence of reward on IC processes.

Future research is needed to address whether non-tangible rewards, such as social praise, can motivate and facilitate cancellation, and if so, whether this facilitation is similar to the effects on restraint. Social rewards, such as positive facial expressions, have been shown to improve restraint inhibition in a sample of boys aged 8-12 years old (Kohls et al., 2009), yet this relationship has not been studied in adolescent populations. Peer interactions become much more important during adolescence (Steinberg, 2005), and social rewards may be more powerful motivators in this age group relative to children (Csikszentmihalyi et al., 1977). There is also evidence of hyperactivation in reward circuitry when adolescents are responding to socially desirable peers (Guyer et al., 2008), suggesting that the reward system may mediate the heightened salience of social interactions.

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Figure 1.

Cancellation and restraint versions of the SST (with permission from Sinopoli et al., in press). Trials 1 and 2 represent the primary task in both versions, where a go signal (X in Trial 1, O in Trial 2) is presented for 1000 milliseconds (ms) following a 500 ms fixation point. Participants were instructed to respond to these stimuli as quickly as possible by making the appropriate button press on a handheld controller. An inhibition trial is depicted in Trial 3. In the cancellation version (left panel), the initial auditory stop signal was presented 250 ms following onset of the go signal. If a participant was able to successfully inhibit his/her response, then the delay was increased by 50 ms on the subsequent stop trial to increase the level of difficulty. If the participant was unable to inhibit his/her response, then the delay was decreased by 50 ms on the subsequent stop trial to make cancellation easier. In the restraint version (right panel), the stop signal was always presented at the same time as the go signal (the delay between the onset of the go and stop signal was zero). In both versions of the task, the feedback following the inhibition trials were identical. Failed inhibition (i.e., going instead of stopping or withholding) resulted in no feedback in the NO condition. In the LOW and HIGH conditions, failed inhibitions resulted in the failure to win points. Successful inhibition in the NO condition also resulted in no feedback. However, each successful inhibition in the LOW and HIGH conditions resulted in the receipt of 2 or 10 points, respectively.

Table 1

Participant Characteristics

Group	Age (Years) *	WASI Scores *	Family SES*	Handedness (Right : Left)	Sex (Females : Males)
CHILD	9.52 (1.8)	116 (12.8)	54 (6.6)	19:3	13:9
TEEN	15.36 (1.3)	108 (7.3)	51 (5.5)	22:0	8:14

* Mean (standard deviation)

Table 2

Inhibitory Control Performance (means and standard error) on the Cancellation and Restraint Tasks

Dependent Variable	Reward Condition	Group	
		CHILD	TEEN
SSRT-C (milliseconds)	NO *	239.67 (10.0)	206.38 (18.8) [^]
	LOW	221.77 (13.5)	173.93 (13.3) [^]
	HIGH	215.91 (13.9)	162.01 (13.7) [^]
SSRT-R (milliseconds)	NO *	439.90 (17.9)	329.05 (17.7) [^]
	LOW	407.19 (16.2)	317.03 (15.9) [^]
	HIGH	385.71 (15.6)	309.12 (15.4) [^]
PI-C	NO	56.25 (1.3)	55.60 (1.3)
	LOW	53.12 (1.1)	52.28 (1.1)
	HIGH	54.37 (1.0)	50.33 (1.0)
PI-R	NO **	84.41 (3.1)	91.92 (3.1) ^{^^}
	LOW **	87.46 (2.7)	92.77 (2.6) ^{^^}
	HIGH	93.19 (1.4)	93.89 (1.4)

Legend: SSRT-C = stop signal reaction time, cancellation task; SSRT-R = stop signal reaction time, restraint task; PI-C = percent inhibition, cancellation task; PI-R = percent inhibition, restraint task; NO = no reward condition; LOW = low reward condition; HIGH = high reward condition

* SSRT was faster in the LOW and HIGH conditions relative to the NO condition in both tasks

** A greater percentage of responses were inhibited in the NO and LOW conditions relative to the HIGH condition of the restraint task

[^] The TEEN group exhibited faster inhibitory control relative to the CHILD group

^{^^} The TEEN group inhibited a greater percentage of responses on the restraint task relative to the CHILD group, especially in the NO and LOW reward conditions

Table 3

Response Execution Performance (means and standard error) on the Cancellation and Restraint Tasks

Dependent Variable	Reward Condition	Group	
		CHILD	TEEN
MRT-C (milliseconds)	NO	557.64 (22.3)	490 (22.0)*
	LOW	581.84 (22.0)	482.66 (21.7)*
	HIGH	584.42 (20.0)	478.15 (19.7)*
MRT-R (milliseconds)	NO	552.07 (17.5)	441.39 (17.3)*
	LOW	533.85 (19.9)	422.72 (19.7)*
	HIGH	535.31 (20.84)	421.15 (20.6)*
SDRT-C (milliseconds)	NO	124.79 (7.6)	107.19 (7.5)**
	LOW	136.75 (6.9)	102.75 (6.8)**
	HIGH	138.04 (7.5)	105.71 (7.4)**
SDRT-R (milliseconds)	NO	122.55 (8.3)	90.49 (8.2)**
	LOW	129.66 (9.0)	84.60 (8.9)**
	HIGH	127.55 (10.7)	87.00 (10.5)**
PCR-C	NO^	95.43 (0.7)	99.07 (0.7)^
	LOW	95.43 (0.8)	98.14 (0.8)^
	HIGH	94.93 (0.8)	98.54 (0.8)^
PCR-R	NO^	95.65 (0.6)	98.30 (0.6)^
	LOW	93.08 (1.2)	97.46 (1.2)^
	HIGH	93.52 (0.9)	97.47 (0.9)^

Legend: MRT-C = mean go reaction time, cancellation task; MRT-R = mean go reaction time, restraint task; SDRT-C = standard deviation of go reaction time, cancellation task; SDRT-R = standard deviation of go reaction time, restraint task; PCR-C = percent correct of go responses, cancellation task; PCR-R = percent correct of go responses, restraint task; NO = no reward condition; LOW = low reward condition; HIGH = high reward condition

* MRT was faster in the TEEN group compared to the CHILD group in both tasks

** TEENS exhibited less variable responding compared to the CHILD group in both tasks

^ A greater percentage of responses were inhibited in the NO conditions relative to the LOW and HIGH conditions of both tasks

^^ The TEEN group exhibited better accuracy than the CHILD group in both tasks