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ADOLESCENT SENSITIVITY TO REWARDS, RISK-TAKING, AND ADAPTIVE BEHAVIOUR: DEVELOPMENT OF THE DUAL SYSTEMS PERSPECTIVE

UWRAŻLIWIENIE NA NAGRODY, SKŁONNOŚĆ DO RYZYKA I ZACHOWANIA ADAPTACYJNE ADOLESCENTÓW – PERSPEKTYWY ROZWOJU MODELI DUALNYCH

Joanna Fryt

Chair of Psychology, Pedagogical University, Kraków, Poland

Katedra Psychologii, Uniwersytet Pedagogiczny, Kraków, Polska

Correspondence to/
Adres do korespondencji:

Joanna Fryt
Katedra Psychologii
Uniwersytet Pedagogiczny
Moszynskiego 37d
30-698 Kraków, Polska
phone: +48 12 662 62 31
e-mail: jfryt@up.krakow.pl

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Abstract

Purpose: According to current developmental neuroscience, adolescence is a period of heightened sensitivity to rewards that results in the increased tendency towards risk. This paper presents the current state of knowledge on the consequences of adolescent sensitivity to rewards and indicates directions for future research. The following sections describe how sensitivity to rewards can be directed towards risk-taking, safe or prosocial behaviour, and improved cognitive performance, depending on different task demands and various social contexts.

Views: Studies on adolescent behaviour conducted from the dual systems perspective indicate that heightened sensitivity to rewards can constitute vulnerability. The results gathered in this paper, however, demonstrate that in several situations adolescent sensitivity to rewards can be redirected from risk-taking towards safe or prosocial behaviour, or can result in the increased cognitive performance. Particularly interesting are the findings showing that individual differences in neural reward-related activity during risk and social dilemma tasks performed in a laboratory make it possible to predict risky behaviours (e.g. substance use, skipping school) and depressive symptoms, one year after the study.

Conclusions: Investigating consequences of reward sensitivity in various tasks and diverse social contexts can shed more light on the nature of adolescent behaviour and lead to the development of the dual systems perspective.

Key words: adolescence, risk-taking, reward sensitivity, adaptive behaviour, dual systems models.

Streszczenie

Cel: Zgodnie z aktualnym stanem wiedzy w badaniach neurorozwojowych (*developmental neuroscience*) adolescencja jest okresem szczególnego uwrażliwienia na nagrody, co może skutkować m.in. skłonnością do podejmowania ryzyka. Artykuł koncentruje się na różnych konsekwencjach uwrażliwienia na nagrody i wskazuje możliwe kierunki przyszłych badań. W kolejnych częściach ukazano, jak obecność nagród może oddziaływać na zachowanie adolescentów zależnie od właściwości wykonywanego zadania i kontekstu społecznego.

Poglądy: Wiele badań nad specyfiką zachowania adolescentów, podejmowanych w kontekście dominujących obecnie modeli dualnych (*dual systems models*), koncentruje się na negatywnych skutkach zdrowotnych i społecznych zwiększonego uwrażliwienia na nagrody. Badania opisane w tym artykule ukazują tymczasem szereg uwarunkowań sytuacyjnych, w których obecność nagród nie sprzyja podejmowaniu ryzyka, lecz zachowaniom bezpiecznym i prospołecznym, a także większej wydolności poznawczej. Szczególnie interesujące wydają się wyniki wskazujące, że różnice indywidualne w aktywności układu nagrody podczas wykonywania zadań skłaniających do ryzyka i działań prospołecznych w laboratorium pozwalają przewidywać występowanie zachowań ryzykownych (np. używki, wagarowanie) i objawów depresyjnych rok po badaniu.

Wnioski: Badania nad konsekwencjami uwrażliwienia na nagrody w różnych zadaniach i kontekstach społecznych pozwalają rzucić więcej światła na uwarunkowania zachowań adolescentów i przyczyniają się do rozwoju modeli dualnych.

Słowa kluczowe: adolescencja, skłonność do ryzyka, uwrażliwienie na nagrody, zachowania adaptacyjne, modele dualne.

PURPOSE

According to the dual-systems models that are prominent in current developmental neuroscience, adolescence is a period of imbalance between the hyperactive mesolimbic reward system and the still maturing cognitive control system, which is associated with the prefrontal cortex [1-3]. In both human and animal adolescents, we observe heightened dopaminergic activity in frontostriatal circuits (in particular ventral striatum and nucleus accumbens) in response to reward-related stimuli [4-6]. The adolescent peak in dopaminergic activity is associated with behavioural shifts towards pleasure, sensation and novelty seeking, greater sensitivity to positive feedback, and the rewarding effects of social interactions. The prevalence of various signs of reward sensitivity in adolescence indicates its adaptive nature during the transition to adulthood; it may foster tendencies towards independence, peer networks, and novel experiences [4, 6].

One of the most studied consequences of adolescent sensitivity to rewards is risk-taking, conceptualized as a tendency towards actions with 'the highest outcome variability' [7]; this means a preference for actions leading to a low probability big gain over actions leading to a high probability small gain. Many neuroimaging studies show that heightened frontostriatal activity is related to risky choices in gambling tasks, susceptibility to peer influence, and rule-breaking behaviours [7-9]. The results collected in this area contribute to the image of adolescence as a period of great vulnerability to social valuation and decision making, which may be suboptimal or even life-threatening. However, from the dual systems perspective, sensitivity to rewards can pose a threat to adolescent health and well-being as well as serve adaptive purposes [10, 11]. Therefore, one of the most interesting directions in the development of the dual systems models is research showing that heightened sensitivity to rewards in adolescents can lead to risk-taking or can be directed towards safe or prosocial behaviour and improved cognitive performance [8, 9]. Thanks to clever task designs that place risk in various social contexts, such studies emphasize the importance of a still unresolved question, Is tendency towards risk a hallmark of adolescence or rather a personal trait limited to a subset of adolescents [12]? In addition, they shed more light on the nature and relations between reward sensitivity and risk-taking. How can we measure these two constructs separately [13]? Are adolescents those who show the strongest response to rewards also those who take the most risks [14]? In what contexts do reward sensitivity and risk-taking become 'good' or 'bad' for adolescents?

The aim of this paper is to present the current state of knowledge about the consequences of adolescent sensitivity to rewards and to indicate directions for future research. The following sections describe how sensitivity to rewards can be directed towards risk-taking, safe or prosocial behaviour and improved cognitive performance, depending on different task demands and various social contexts. Subsequently, several issues that could expand the knowledge about adolescent decision-making and develop the dual systems perspective are discussed.

REWARD SENSITIVITY AND RISK-TAKING IN DIFFERENT SOCIAL CONTEXTS

Many studies focusing on age differences in risk-taking show that adolescents manifest stronger tendency than adults do towards risk, but only under specific task demands or in specific social contexts. A meta-analysis by Defoe *et al.* [7] shows that in studies using probabilistic gambling tasks (e.g. Iowa Gambling Task, Columbia Card Task, Balloon Analogue Risk Task) adolescent participants take more risks than adults when they are informed about their gains or losses immediately after each decision. In studies using fast-paced driving tasks (e.g. Stoplight Task, driving simulators), it is usually the peer observer that encourages an adolescent to take risks, even if he or she does not say anything to the participant or is not physically present [15-19]. We can see that in both types of studies (using gambling tasks and driving tasks performed alone vs. with a peer observer), adolescent risk-taking increases in highly arousing, incentivized conditions (when immediate outcome feedback, financial reward or a peer observer is present). According to the fMRI data, risky decisions in such conditions are usually combined with heightened frontostriatal activity, indicating that they are highly rewarding. A good example is the results obtained by Chein *et al.* [16], showing that presence of peers during fast-paced driving task promotes risk-taking in adolescents (but not in adults) by sensitizing brain regions associated with the anticipation to rewards. Taken together, studies in this area focus on situations when adolescent sensitivity to rewards leads to risky behaviour.

However, there are some conditions in which incentives, such as the presence of observers during a risk task, do not cause increased tendency towards risk and increased activity of the adolescent reward system. Firstly, as Cascio *et al.* demonstrated [20], we can lead adolescent participants to believe they are being observed in a driving simulator by a cautious peer or a peer who often takes risk and breaks rules on the road. Results have revealed that social cues change participants' behaviour: young drivers take fewer risks in a simulator when believe that a cautious peer is observing them. The fMRI data show that social clues moderate the extent to which cognitive control processes are used to inhibit risky tendencies: in the presence of a cautious peer, the influence of cognitive control on adolescent behaviour is stronger. Secondly, as Silva *et al.* showed [21], we can significantly reduce risk-taking in the Stoplight Task (a fast-paced driving game) by introducing a young adult to the group of adolescent observers. The presence of a slightly older observer reduces not only risk-taking, but also the preference for immediate rewards in a delay discounting task. Last, as was demonstrated in a clever experiment by Telzer *et al.* [22], adolescents can be encouraged to behave safely on the road by the introduction of their mothers as observers. The mother's presence during the Stoplight Task makes an adolescent drive more safely than when they perform the task alone. According to the fMRI data, the presence of a parent attenuates frontostriatal activity during risky decisions, indicating that risk-taking in such conditions becomes simply less rewarding. Furthermore, making safe decisions in the mother's presence is accompanied by increased activity of the ventrolateral prefrontal cortex (VPFC) and greater functional coupling between the cognitive control system (VPFC activity) and the reward system (ventral striatum activity). Together, the results of the presented studies indicate that rewarding aspects of risk-taking can be reduced in several social contexts (e.g. when a cautious peer, slightly older observer or a parent is present during a risky task). Furthermore, Telzer *et al.* [22] showed how adolescent sensitivity to rewards can be directed towards adaptive behaviour, such that the reward system and the cognitive control system interact to promote safe decisions on the road.

REWARD SENSITIVITY AND PROSOCIAL BEHAVIOUR

A decision to drive safely, when the social context encourages this, is not the only example that sensitivity to rewards can serve an adaptive function for adolescent health and well-being. In a series of experiments, Telzer *et al.* [8, 23, 25] demonstrated that rewarding aspects of being prosocial can protect adolescents from risky behaviour and depressive symptoms. Considering that engagement in prosocial behaviour (e.g. charity) is usually accompanied by rewarding feelings and heightened dopaminergic activity [24], Telzer *et al.* [23] used a task in which adolescents make a series of decisions about earning money for themselves or giving it to their families (e.g. 'you – 3$, family – 0$;' 'you – 1$, family – 3$). Results showed that those adolescents who manifest heightened activity of the ventral striatum when making prosocial decisions (donating their earnings to the family) display less risky behaviour (e.g. drug and alcohol use, skipping school) within the next year. In another fMRI study, Telzer *et al.* [25] used the same 'you vs. family' decision-making task as well as the Balloon Analogue Risk Task to check if reward-related neural activity can predict the occurrence of depressive symptoms in participants after a one-year follow-up. Results indicated that heightened activity of the ventral striatum during prosocial decisions predicts a decline in depressive symptoms after a year, whereas heightened activity of this area during a risk-taking task predicts an increase of symptoms. Such findings highlight that adolescent sensitivity to rewards can be both a source of risky tendencies and a protective factor for health and well-being, depending on the task and social context.

The research of Braams *et al.* [26, 27] also confirmed the supposition that adolescent risk-taking is not purely a consequence of the hypersensitivity of the reward system, but is strongly related to the social context in which it occurs. In a simple decision-making task, participants (children, adolescents, and young adults) decided who would lose or receive money won by them in a game, i.e. themselves, a chosen best friend, or an antagonist peer. According to the fMRI data, reward-related neural activity was higher among adolescents than among children and young adults, but was dependent on the beneficiary. A peak in ventral stratum activity was observed in adolescents when they decided to earn money for themselves or eventually for a chosen friend (but this was revealed only in girls who, as compared to boys, more highly evaluated the quality of their friendship with the selected peer). Winning for the antagonist peer, however, was accompanied by the highest sensitivity (among adolescents compared to younger and older participants) of the medial prefrontal cortex (mPFC), a region related to mentalizing and social processing.

Findings such as those of Telzer *et al.* [8, 23, 25] and Braams *et al.* [26, 27] highlight the crucial role of the reward system in risky or prosocial decisions made by adolescents in various social situations. These findings can be interpreted as follows: due to heightened sensitivity to incentives, adolescents may be particularly prone to choosing actions that are rewarded in the current social context. However, it is possibly not the sensitivity to rewards that is so important for adolescent decision-making, but the sensitivity to social cues. If so, we should observe a peak in neural activity in adolescents associated with processing of social cues instead of reward processing. This hypothesis was supported by a study by van Hoorn *et al.* [28], who investigated the effects of peers on prosocial behaviour and neural activity during early and mid-adolescence. Participants played online with four anonymous peers in the Public Goods Game (a social dilemma task, in which each person independently decides whether to allocate offered tokens to the common pool or keep them for themselves). A series of decisions was made in three conditions: (1) with two peer observers giving online feedback ('Like') for prosocial choices; (2) with two online observers but without feedback; (3) without observers. The results showed that donating tokens to the group increases in the presence of peer observers, and even more when peers provide prosocial feedback. Contrary to the work of Telzer *et al.* [8, 23, 25] and Braams *et al.* [26, 27], the fMRI data showed that activity of the reward system does not increase during donation choices or when receiving peer feedback. There was, however, an increase in the activity of the social brain network (medial prefrontal cortex, temporoparietal junction, and superior temporal sulcus) in such cases. In a review article, van Hoorn *et al.* [29] proposed that peer presence enhances not the activity of the reward system specifically, but the activity of task-related brain areas. More studies investigating the interplay between the reward system and the social brain are needed to confirm this hypothesis and better understand the nature of positive peer influence.

REWARD SENSITIVITY AND ENHANCED COGNITIVE PERFORMANCE

The supposition that heightened activation of the reward system can enhance cognitive performance was firstly supported in research by Geier *et al.* [30-33], who used fMRI in a rewarded vs. not rewarded antisaccade paradigm. Preliminary studies demonstrated that financial rewards improve cognitive control (precisely reaction inhibition, which is measured by the antisaccade task) and that such an improvement can be greater in adolescents than in adults [30, 31]. Further studies indicated that behavioural responses to rewards (or losses) vary individually, with some participants showing improvement, some decline, and some no change in performance in the antisaccade task [32, 33]. On the neural level, however, cognitive control efficiency, when rewarded, was related to the activity of the ventral striatum. Such results are another example that the sensitivity of the adolescent reward system may lead to adaptive behaviour.

Heightened activity of the ventral striatum can be seen as a neural representation of motivation to perform well in a task [34]. Such motivation can be extrinsic, when financial rewards are offered in the study for performance, or intrinsic, related to rewarding feelings when correctly completing a task. Satterthwaite *et al.* [34] investigated the activity of the ventral striatum (VS) during an unrewarded working memory task (the n-back) with different levels of difficulty in a group of participants aged 8-22 years. The results showed that VS activity was higher during correct than incorrect responses, and increased with task difficulty. Magnitude of the VS response peaked during mid-adolescence and correlated with task performance, indicating the role of the ventral striatum in promoting working memory efficiency. As no rewards or outcome feedback were used to enhance cognitive performance, this is an interesting study that shows an adolescent peak in intrinsic motivation signals during a standard cognitive task. In a further study, Telzer & Qu [8] examined VS activity in Chinese and American students during a prolonged go/no-go task that measured reaction inhibition. At the beginning of the task, both groups showed similar cognitive control efficiency. Over time, however, the Chinese students revealed an improvement in cognitive performance and increased VS activity, whereas the American students showed a decline in performance and low VS activity. Moreover, over the course of the task, the Chinese students manifested increasing connectivity between ventral striatum and prefrontal cortex; this connectivity was related to cognitive performance. Together, the results of the two presented studies indicate that the activity of the ventral striatum may represent an intrinsic motivation signal that enhances cognitive performance.

CONCLUSIONS AND FUTURE DIRECTIONS

Studies on adolescent behaviour conducted from the dual systems perspective indicate that heightened sensitivity to rewards can constitute vulnerability. Firstly, we can observe maladaptive, unhealthy or life-threatening decisions in contexts that simply reward them (e.g. negative peer influence, when adolescents choose to drive recklessly in the presence of a risky peer, but take fewer risks when driving alone or when being observed by someone cautious). Secondly, maladaptive decisions can be associated with the weaknesses of control processes (e.g. impulsive risk-taking, when an individual cannot override risky tendencies aroused by salient incentives). The results gathered in this paper, however, demonstrate that in several situations adolescent sensitivity to rewards can be redirected from risk-taking towards safe or prosocial behaviour, or can result in increased cognitive performance. Particularly interesting are the findings showing that individual differences in neural reward-related activity during risk and social dilemma tasks performed in a laboratory make it possible to predict risky behaviours (e.g. substance use, skipping school) and depressive symptoms one year after the study. The disadvantage of the dual systems models is that they do not specify when cognitive-motivational imbalance results in adaptive behaviour or becomes a source of vulnerability. Thus, future studies should focus on internal and external factors determining different consequences of reward sensitivity.

First, an often-mentioned direction for studies on adolescent risk-taking is comparing individuals differing in cognitive control efficiency and behavioural impulsivity. According to results showing that activity of the reward system can enhance (not decline) reaction inhibition and working memory, it is possible that only a subset of adolescents can be viewed as impulsive risk-takers who cannot override risky tendencies due to weaknesses of the control processes [35]. Second, the nature of adolescent risk-taking is still not fully understood: it is not clear whether various risk tasks used in experimental research measure one or many types of risky behaviour (e.g. economic risk, driving risk). It can be expected that adolescent tendency towards risk manifests in selected areas, limited by age, availability and the extent of knowledge about the world. For example, from a practical point of view, it is interesting whether knowledge about the possible consequences of a risky choice promotes or reduces adolescent risk-taking. Moreover, adolescents may be sensitive to selected types of incentives (e.g. peer approval) and may prefer immediate over delayed rewards) [36]. It should be also determined whether sensitivity to rewards or to social cues is important for adolescent decision-making.

In order to answer the question of how adolescent risk-taking can be reduced or directed towards safe or prosocial decisions, we need more novel, experimental designs that examine reward sensitivity in diverse social contexts. Only studies that go beyond the negative context of risk (e.g. substance use, reckless driving) can determine factors enhancing adaptive behaviour in the presence of salient incentives. Another promising direction is research that examines how neural reward-related activity predicts engagement in healthy behaviour [8]. Particularly valuable are experiments that make it possible to create effective interventions (such as the study of Silva *et al.* [21], who showed that introducing a slightly older adult to the group is an effective strategy for reducing risky tendencies in late adolescents). The results gathered in this article show that due to heightened sensitivity to incentives, adolescents are particularly prone to choosing actions that are rewarded in the current social context. Thus, involving youth in activities that are not perceived by them as valuable or rewarding is not an effective strategy for behaviour change. Focusing on individual differences in reward sensitivity makes it possible to identify various responses to reward and loss (e.g. risk tendency, risk aversion, sensitivity to negative and positive peer influence) in diverse social contexts and helps develop individualized interventions for those most vulnerable.

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