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Dopaminergic and Prefrontal Contributions to Reward-Based Learning and Outcome Monitoring During Child Development and Aging

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In many instances, children and older adults show similar difficulties in reward-based learning and outcome monitoring. These impairments are most pronounced in situations in which reward is uncertain (e.g., probabilistic reward schedules) and if outcome information is ambiguous (e.g., the relative value of outcomes has to be learned). Furthermore, whereas children show a greater sensitivity to external outcome information, older adults focus less on a rapid differentiation of rewarding outcomes. In this article, we review evidence for the idea that these phenomenologically similar impairments in learning and outcome monitoring in children and older adults can be attributed to deficits in different underlying neurophysiological mechanisms. We propose that in older adults learning impairments are the result of reduced dopaminergic projections to the ventromedial prefrontal cortex, which lead to less differentiated representations of reward value. In contrast, in children, impairments in learning can be primarily attributed to deficits in executive control, which may be due to a protracted development of the dorsal medial and lateral prefrontal cortices. We think that this framework maps well onto recent neurophysiological models of reward processing and is plausible from a broader developmental perspective.

Keywords: life span development, reinforcement learning, decision making, valence bias, dopamine

Rewarding and punishing outcomes drive the acquisition of goal-directed behavior. However, in order to approach sources of reward or to avoid unpleasant outcomes, individuals have to constantly monitor and flexibly adjust their actions. Children, as well as older adults, show impairments in reward-based learning in situations in which demands on updating and monitoring of outcomes are high. These developmental differences in reward-based learning and outcome monitoring may reflect maturational changes in prefrontal areas (in the case of children) as well as age differences in the impact of projections from the midbrain dopamine system and associated striatal areas to the ventromedial prefrontal cortex (in the case of older adults). In this article, we review the current literature on life span developmental differences in reward-based learning and outcome monitoring. We try to integrate these findings into a neurophysiologically plausible framework that captures age-specific difficulties across the life span.

For the purpose of this article, we focused on the developmental periods of childhood (until about 12 years of age) and adulthood to old age. We deliberately excluded the adolescent age range that is already comparatively well documented (see Fareri, Martin, & Delgado, 2008; Somerville & Casey, 2010; Spear, 2000, for reviews).

Reward-based learning and outcome monitoring involve a dynamic interplay of reward and executive control processes. We conceptualize reward-related processes as mechanisms that allow the formation and updating of value representations (Grabenhorst & Rolls, 2011; Rangel, Camerer, & Montague, 2008). We think of executive control in terms of processes involved in the monitoring of actions and outcomes (see Botvinick, Braver, Barch, Carter, & Cohen, 2001; Miller & Cohen, 2001). For the purpose of this article, we primarily focused on reward-based learning as a way of acquiring goal-directed behavior. Of course, goal-directed behavior is acquired and represented in multiple ways, including more explicit mechanisms such as the encoding of episodic information by medial temporal lobe and lateral prefrontal structures (Polyn & Kahana, 2008; Simons & Spiers, 2003).

The salience of reward information as well as the ability to monitor and control behavior changes across the life span (cf. Mohr, Li, & Heekeren, 2010). Whereas children seem to react more strongly to reward information and may be less focused on self-control, older adults seem to value rewarding cues less and focus more on the control of rewarded actions (Crone, Jennings, & Van der Molen, 2004; Eppinger, Kray, Mock, & Mecklinger, 2008; Eppinger, Mock, & Kray, 2009; Hämmerer, Li, Müller, & Lindenberger, 2011; Mell et al., 2009; Paxton, Barch, Racine, & Braver, 2008). These changes in the relative impact of reward valuation and executive control across the life span may be due to maturational changes in the prefrontal cortex as well as age differences in the function of neuromodulatory systems (such as the midbrain dopamine system) and their projections to striatal and prefrontal areas (Bäckman, Lindenberger, Li, & Nyberg, 2010; Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006; Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002; Casey, Tottenham, Liston, & Durston, 2005; Craik & Bialystok, 2006; Samanez-Larkin, Kuhnen, Yoo, & Knutson, 2010; Volkow et al., 2000).

In this article, we propose that in many instances children and older adults show similar performance impairments in reward-

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based learning and outcome monitoring. However, we think that these deficits may be due to different underlying neurophysiological mechanisms. In children, impairments in learning seem to primarily reflect deficits in executive control processes. These impairments in action monitoring have been attributed to less developed prefrontal circuits. In contrast, in older adults, impairments in learning seem to be associated with deficits in the integration and updating of reward information. These deficits may reflect reduced dopaminergic input from the midbrain via the ventral striatum to the ventromedial prefrontal cortex.

In the following sections, we will first provide a brief overview of the reward and executive control loops involved in reward-based learning and outcome monitoring. We will then review the literature on age-related structural and neuromodulatory changes in these networks. In the main part of the article, we will review the current literature on developmental and adult age differences in reward-based learning and outcome monitoring. We conclude by integrating these findings into a neurophysiologically plausible framework that may explain age-related deficits in reward-based learning and outcome monitoring across the life span.

Neuroanatomical Considerations: Cortical and Subcortical Loops Involved in Reward-Based Learning and Outcome Monitoring

The brain structures involved in reward-based learning can be located at three neuroanatomical levels (see Figure 1). These are (a) dopaminergic neurons in the substantia nigra and ventral tegmental area (SN/VTA), (b) the basal ganglia (most important, the ventral and dorsal striatum), and (c) parts of the frontal cortex: the medial orbitofrontal cortex (mOFC)/ventromedial prefrontal cortex (vmPFC), the dorsal anterior cingulate cortex (dACC), and the dorsolateral prefrontal cortex (dlPFC).

Specifically, the midbrain dopaminergic neurons are thought to contribute the motivational drive to acquire behavior (see Wise, 2002, for a review). Findings from electrophysiological work in monkeys show that midbrain dopaminergic neurons respond with phasic bursts of activity to unexpected rewarding outcomes (Schultz, 1998). With learning, this phasic response shifts from the unconditioned reward to the reward predicting cue, suggesting that the dopaminergic neurons respond to the motivational significance of an event rather than to reward delivery per se (Schultz, 1998, 2000, 2002, 2007; Waelti, Dickinson, & Schultz, 2001). Furthermore, the magnitude of phasic dopaminergic activity in the midbrain co-varies with the expected values of reward, with magnitude, delay, and probability of expected reward taken into account (Fiorillo, Tobler, & Schultz, 2003; Roesch, Calu, & Schoenbaum, 2007; Tobler, Fiorillo, & Schultz, 2005). These observations suggest that phasic changes in the activity of midbrain dopaminergic neurons reflect the biological correlate of reward prediction errors as conceptualized in temporal difference learning models of reward-based learning (see Montague, Hyman, & Cohen, 2004, for a review). How these prediction errors are computed and whether they are transmitted to the midbrain from other parts of the brain is still unclear (Niv & Schoenbaum, 2008).

Among the most important connections of the SN/VTA neurons are reciprocal links with the striatum (Condé, 1992; Haber & Knutson, 2010; Hedreen & DeLong, 1991; Selemon & Goldman-Rakic, 1990). The striatum may hence be one of the primary

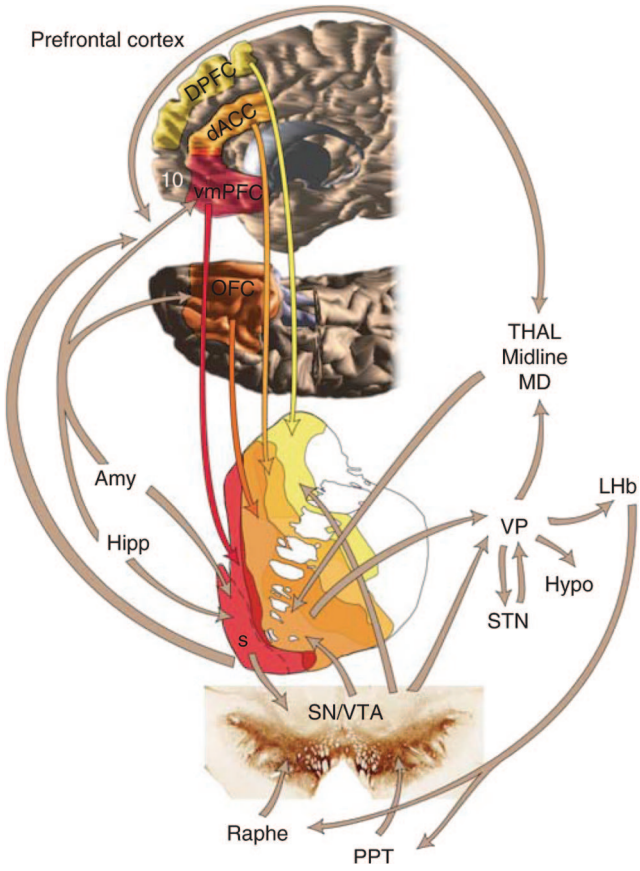

Figure 1. Schematic illustration of cortical and subcortical loops involved in reward-based learning and outcome monitoring. Amy = amygdala; dACC = dorsal anterior cingulate cortex; DPFC = dorsal prefrontal cortex; Hipp = hippocampus; Hypo = hypothalamus; LHb = lateral habenula; MD = mediodorsal nucleus of thalamus; OFC = orbital frontal cortex; PPT = pedunculopontine nucleus; S = shell, SN = substantia nigra; STN = subthalamic nucleus; THAL = thalamus; VP = ventral pallidum; VTA = ventral tegmental area; vmPFC = ventral medial prefrontal cortex. Reprinted with permission from "The Reward Circuit: Linking Primate Anatomy and Human Imaging," by S. N. Haber and B. Knutson, 2010, *Neuropsychopharmacology, 35*, p. 5. Copyright 2011 by Nature Publishing Group.

structures controlling the activity of midbrain dopaminergic neurons. The striatum itself is receiving a major part of its inputs from cortical brain structures via glutamatergic projections (discussed later). This suggests that the striatum can serve as a relay structure that is transferring inputs to midbrain dopaminergic neurons and vice versa. Interestingly, as can be seen in Figure 1, the cortico–striatal–nigral connections seem to be topographically organized: From dorsal to ventral parts of the striatum, the cortical inputs stem from regions that are decreasingly involved in reward representation and increasingly involved in action selection and executive control, such as the dACC and dlPFC (Haber, Kim, Mailly, & Calzavara, 2006; Parent & Hazrati, 1995; Smith & Bolam, 1990). This means that from the ventral shell to the dorsal striatum, the cortical inputs shift from areas that are involved in the integration and representation of different aspects of reward information (vmPFC and mOFC) to the dACC and dlPFC, areas that have been implicated in executive control. More specifically, imaging (func-

tional magnetic resonance imaging [fMRI]) findings suggest that activity in the vmPFC or mOFC reflect the subjective value of rewards by integrating factors such as reward uncertainty, expected value, relative reward magnitude, or delay (Blair et al., 2006; Kable & Glimcher, 2007; Kringelbach, 2005; Knutson, Taylor, Kaufman, Peterson, & Glover, 2005). This gradient from reward value representations to reward action contingencies is also apparent in a study comparing the response to outcomes resulting from instructed and self-chosen actions. While the vmPFC and mOFC were more responsive to outcomes from instructed actions, the dACC responded stronger to results of self-chosen actions (Rushworth, Noonan, Boorman, Walton, & Behrens, 2011; Walton, Devlin, & Rushworth, 2004). These results are in line with studies showing that the dACC is specifically responding to the reinforcement value of actions (see Rushworth & Behrens, 2008; Rushworth, Walton, Kennerley, & Bannerman, 2004, for reviews). Finally, the dlPFC is engaged when working memory or cognitive control is required for the choice between several rewarded actions and the execution of one action among competing choices (Botvinick, 2007; Kerns, 2006; Miller & Cohen, 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). A more fine-grained overview of the ventral-to-lateral gradient of prefrontal contributions to reward-based choices can be found in a recent review (Rushworth, Noonan, Boorman, Walton, & Behrens, 2011). Here vmPFC/mOFC, lateral OFC (lOFC), ACC, and anterior prefrontal cortex (aPFC) are associated with coding reward values of different choice options, linking choices to reward values, selecting actions on the basis of expected rewards, and considering a change in action on the basis of alternative outcomes, respectively. Together, these findings suggest that the cortical inputs to the striatum could be separated into two major components: (a) input from cortical areas primarily involved in multidimensional representations of reward value (vmPFC and mOFC) that target more ventral parts of the striatum and (b) input from cortical areas that are relevant for selecting and executing specific rewarded actions in light of these representations (dACC and dlPFC) that target more dorsal parts of the striatum.

An important route of efferent connections from the striatum to the cortex is via the pallidum and subthalamic nucleus to the thalamus, which is reciprocally linked to the frontal cortices (via the mediodorsal nucleus) and to the motor cortices (via the ventral anterior nucleus) (Haber & Knutson, 2010; Haber, Lynd, Klein, & Groenewegen, 1990; Hedreen & DeLong, 1991; Joel & Weiner, 1997; Parent & Hazrati, 1995). The striatum also projects to the nucleus basalis in the forebrain, which projects via cholinergic fibers to the cortex and might hence provide a more direct route of the ventral striatum to the PFC (Zaborszky & Cullinan, 1992). Moreover, as with the inputs from the cortex to the striatum, there is evidence for a ventral-to-dorsal gradient of the reciprocal connections of the striatum and the SN/VTA: While the ventral striatum is receiving the least midbrain inputs, it is targeting the most extensive parts of the SN/VTA (Hedreen & DeLong, 1991; Lynd-Balta & Haber, 1994b). In contrast, the SN/VTA is projecting most prominently to the dorsal striatum, which is in turn targeting the SN/VTA less than the ventral striatum (Haber & Knutson, 2010; Lynd-Balta & Haber, 1994a; Parent, 1990).

Taken together, it appears that the input from vmPFC and mOFC, reflecting reward value representations is linked via the ventral striatum and SN/VTA to the dorsal striatum and dACC and dlPFC, areas that are important for action selection and action control. This loop across cortical, striatal, and midbrain regions seems to play an integral role in linking motivation to action selection (cf. O'Doherty et al., 2004; Smith & Bolam, 1990). In support of this hypothesis, a transfer from classical to instrumental learning has been shown to be interrupted if the striato–midbrain–striatal loop is interrupted (Belin & Everitt, 2008). It should be noted, however, that other limbic structures, such as the amygdala, are also critically involved in integrating reward and affective information into value representations. Consistent with this view, the amygdala has reciprocal connections with the (ventral) striatum as well as the vmPFC and mOFC (Baxter & Murray, 2002; cf. Figure 1). Current findings suggest that the amygdala contributes more general affective information about valence that is relevant for forming value representations in the OFC (Murray, 2007). It is important to note that lesions of the amygdala do not impair reversal learning and have only transient effects on win–stay/lose–shift behavior (Izquierdo & Murray, 2007). Hence, it seems that the amygdala rather responds to the arousing properties of unexpected valenced events (Dolan, 2007; Haber & Knutson, 2010). The implication of the amygdala in affective reactions but not in reward-based learning points to a necessary separation of "a) emotional processes reflecting the goal-directed "wanting" of valenced events and (b) affective processes of "liking" valenced events. For instance, apart from the dopaminergically mediated wanting of action outcomes during learning, opioid projections onto GABAergic neurons in the ventral striatum are supposed to support a liking sensation that is insensitive to a change in dopaminergic modulation (Berridge & Robinson, 2003; Wyvell & Berridge, 2001). In the present review, we focused on motivational processes related to goal-directed wanting.

Evidence for Life Span Age Differences in the Dopaminergic Modulation of Cortical and Subcortical Loops

In older adults, there is evidence for a widespread decline of dopaminergic neuromodulation in cortical as well as subcortical brain structures involved in reward-based learning and outcome monitoring (see Bäckman, et al., 2010; Bäckman, et al., 2006, for reviews). For example, the number of dopaminergic neurons in the SN decreases by 7% per decade (Bannon & Whitty, 1997; Reeves, Bench, & Howard, 2002). In the striatum, D1 and D2 receptors decrease with age (Rinne, Lonnberg, & Marjamaki, 1990; Seeman et al., 1987; see also Severson, Marcusson, Winblad, & Finch, 1982). Likewise, in frontal, cingulate, temporal, parietal and occipital cortices, D2 receptor binding is reduced in older age (Inoue et al., 2001; Kaasinen et al., 2000). Moreover, age-related decrease in striatal D2 receptor density has been shown to be related to a decrease in glucose metabolism in frontal and anterior cingulate cortices. These results indicate a link between dopaminergic neuromodulation in the striatum and activity in medial and lateral prefrontal cortex in older age (Volkow et al., 2000). Consistent with this view, recent findings by Dreher, Meyer-Lindenberg, Kohn, and Berman (2008) pointed to age-related changes in the association between midbrain dopamine synthesis and prefrontal blood-oxygen-level-dependent (BOLD) activity.

To summarize, current findings point to an age-related decline of pre- and postsynaptic markers of the dopamine (DA) system in

several brain areas relevant for reward-based learning and decision-making. The reduction of SN neurons may lead to weaker phasic responses of the midbrain to motivationally salient events in the elderly. The decrease of dopamine transporters (DAT) and dopaminergic receptors in the striatum might weaken the link between reward and action and dampen the transmission of dopaminergic signals to cortical areas that control goal-directed behavior. Finally, the cortical areas relevant for representing action values and controlling the execution of rewarded actions appear to be less dopaminergically innervated. This might result in less precise reward representations and a weaker control of rewarded actions.

There is very little evidence on the development of the dopaminergic system and its cortical target areas during childhood. A postmortem study reported increasing DA and DAT levels in the dorsal striatum until the age of 9 years, by which time adult levels are reached (Haycock et al., 2003). Likewise, Seeman et al. (1987) reported adult levels in striatal D1 and D2 receptors at the age of 10 years. Also, they observed a rise in striatal D1 and D2 receptors above adult levels until the age of 3 years. Taken together, these findings suggest that subcortical DA levels appear to reach adult levels when children are approximately 9 years old. In contrast to the relatively early maturation of the subcortical dopaminergic system, indirect evidence for lower prefrontal dopaminergic levels comes from a genomic behavioral study in which superior action control was observed in children with a polymorphism that is associated with reduced DA degradation in the prefrontal cortex (Diamond, Briand, Fossella, & Gehlbach, 2004). Findings from structural MRI studies point to a protracted development of prefrontal areas involved in executive control (Gogtay et al., 2004; Sowell et al., 2003). Also, white matter development from childhood to adulthood appears to follow a posterior to anterior gradient, with frontal areas maturing latest (e.g. Colby, Van Horn, & Sowell, 2011). Hence, it seems reasonable to assume that developmental differences in learning and outcome monitoring might be the result of not yet fully developed prefrontal areas involved in the integration of reward information into action control. In contrast, dopaminergic subcortical and midbrain structures responsible for providing reinforcement learning signals may be fully developed before adolescence. Such an imbalance in reward-processing and action control systems may result in the frequently observed inconsequent goal-directed behavior in children (discussed later).

Figure 2 provides a schematic illustration of the reward and executive control loops relevant for reward-based learning and outcome monitoring. Whereas the reward loop is thought to be most affected during aging, the immaturity of the executive control loop, which is relevant for outcome monitoring and action selection, might be most defining for the child development of reward-based learning. It should be noted, however, that the number of studies that combine an investigation of age differences in reward-

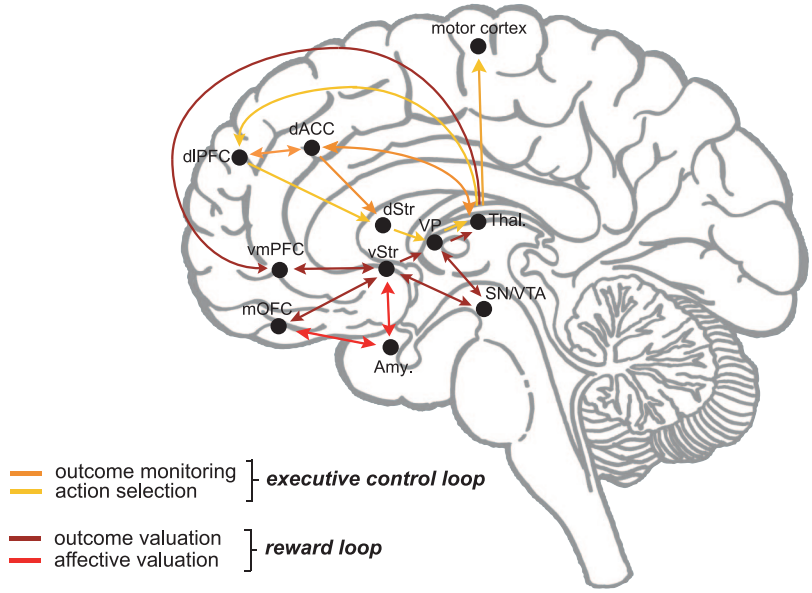

Figure 2. Simplified schematic illustration of brain structures involved in the reward loop and executive control loop. Orange arrows in the executive control loop connect structures contributing to outcome monitoring, and yellow arrows connect structures relevant for action selection. In the reward loop, dark red arrows connect structures relevant for outcome valuation, and bright red arrows connect structures relevant for affective valuation. We assume that child developmental differences in reward-based learning and decision making are due to premature prefrontal structures involved in executive control (see executive control loop). In contrast, age-related impairments in learning may be due to reduced dopaminergic projections from the midbrain to ventral striatum (vSTR) and ventral medial prefrontal cortex (vmPFC; see reward loop). Amy = amygdala; dACC = dorsal anterior cingulate cortex; dlPFC = dorsolateral prefrontal cortex; dStr = dorsal striatum; mOFC = medial orbitofrontal cortex; VP = ventral pallidum; Thal = thalamus; SN = substantia nigra; VTA = ventral tegmental area; Amy. = amygdala. Please note that the projection from the vSTR to the vmPFC goes through the nucleus basalis meynert, which is not shown in the figure due to space limitations.

based learning with research on age differences in neuroanatomical and neurochemical substrates is very limited. Hence, it is too early to be certain about which specific parts of the reward loop or executive control loop are relevant for the observed age differences in behavior. There is considerable evidence for the idea that aging-related decline in dopaminergic neuromodulation affects processing in cortical areas involved in reward-based learning and outcome monitoring. Studies of the link between midbrain and striatal dopaminergic structures on the one hand and prefrontal structures on the other hand suggest that especially the transfer of dopaminergic inputs to frontal areas involved in forming reward value representations is reduced in older adults. In children, the existing evidence suggests adult levels in dopaminergic neuromodulation of the subcortical structures are reached by the age of 9. The development of the prefrontal target areas however, extends into adulthood. These findings indicate that rewarding cues may have a similar impact in children as in young adults, whereas structures that are involved in the monitoring and control of the rewarded actions are yet to mature (cf. Figure 2).

Having outlined developmental differences in the neurobiological substrates during childhood and aging, we will now take a closer look at behavioral and functional imaging (electroencephalographic [EEG] and fMRI) evidence that characterizes developmental differences in reward-based learning and outcome monitoring.

Reward Uncertainty Affects Life Span Age Differences in the Acquisition of Goal-Directed Behavior

One of the factors that affect age differences in reward-based learning is reward uncertainty. Recent findings suggest that children and older adults are as able to learn from reward information as young adults are if the outcomes are deterministic, that is, if one stimulus or action is rewarded reliably. In contrast, both age groups are impaired in learning if reward is delivered probabilistically and outcomes are uncertain (Eppinger et al., 2008, 2009; Hämmerer et al., 2011). Consistent with these behavioral findings, children and older adults show an error-related negativity (ERN, the event-related potential [ERP] response to errors) similar in size to that of young adults' ERN if reward information is deterministic. However, if reward is probabilistic, both age groups show a reduced sensitivity to errors (a smaller ERN) during learning than young adults. This indicates that they perceive less of a mismatch between performance errors and their internal representation of the correct response. Hence, these findings suggest that children as well as older adults have problems in building up representations of task-appropriate behavior if reward information is partially inconsistent.

The electrophysiological findings are consistent with results from an fMRI study on age differences in reward-based learning (Schott et al., 2007). Schott and colleagues (2007) found that age differences in reward prediction are associated with reduced ventral striatal activations for reward-predicting cues, whereas no age differences were observed for the actual outcomes (see also Cox, Aizenstein, & Fiez, 2008; Dreher et al., 2008; Samanez-Larkin et al., 2007; 2010). Similar to the previously mentioned studies, the outcomes in this study were probabilistic (80% gains, 20% losses); that is, participants had to learn the expected value of the outcomes in order to be able to accurately predict them.

Moreover, these results line up nicely with findings from recent fMRI studies on adult age differences in decision making that suggest that older adults show preserved decision-making capacity if explicit information about the contingencies of the decision outcomes is available (Hosseini et al., 2010; Samanez-Larkin, Wagner, & Knutson, 2011). In contrast, in the absence of such explicit cues, older adults seem to be impaired in decision making, especially if they have to constantly update value representations. These impairments in the updating of representations may be mediated by increased variability in hemodynamic activity in the ventral striatum (Samanez-Larkin et al., 2010).

To summarize, the present findings suggest that reward uncertainty leads to learning impairments in children as well as older adults. These impairments may reflect deficits in the ability to form and update value (outcome) representations. The source of these deficits is unclear. One speculative idea regarding the deficits in older adults would be to assume that reduced dopaminergic input to the vmPFC, leads to less differentiated representations of outcomes in older adults. This would be consistent with findings by Dreher et al. (2008) that point to age-related changes in the association between midbrain dopamine synthesis and prefrontal BOLD activity. Furthermore, such a view would be in line with findings from Volkow and colleagues (2000) that showed that age-related decline of D2 receptors availability in the striatum is associated with reduced metabolism in lateral and medial PFC.

With respect to developmental differences in learning, the current data indicate that children are more driven by external rewarding cues but less able to integrate external reward information into goal-directed action plans (Eppinger et al., 2009; Hämmerer et al., 2011). These findings are consistent with developmental data on heart rate variability that suggest that younger children (8–12 years old) respond strongly to both informative and uninformative negative feedback during learning (Crone et al., 2004; Crone, Somsen, Zanolie, & Van der Molen, 2006). In line with that, in comparison to more mature age groups, children show stronger activations to action outcomes in the mOFC and lOFC, areas involved in the processing of outcomes unrelated to an individual's own actions (Galvan et al., 2006; van Leijenhorst, Crone, & Bunge, 2006; Walton, Devlin, & Rushworth, 2004). This might suggest that children perceive outcomes less as a consequence of their actions. It remains an open question whether a decreased sense of agency in children is related to the protracted development of prefrontal control structures. However, such an argument would be quite consistent with our framework, as well as with findings that point to a link between theory of mind development and maturation of the medial and lateral PFC (Frith & Frith, 2003). The topic of perceived agency and its relation to outcome monitoring during childhood development seems an important and comparatively unaddressed question.

Life Span Age Differences in the Acquisition of Relative Reward Value

Another variable that seems to affect age differences in learning is ambiguity on the outcome level. That is, older adults seem to be impaired in learning when they have to process outcomes in relation to alternative outcomes that could have been obtained. In a recent ERP study by Eppinger & Kray (2011), participants had to learn to disambiguate neutral outcomes (neither gain nor loss)

depending on whether they were better or worse than the alternative outcome (either gain or loss). The behavioral results showed pronounced age-related impairments in learning. The ERP data showed that young adults were able to differentiate correct from incorrect responses, irrespective of the ambiguity of outcomes. In contrast, older adults showed an ERN component only to unambiguous outcomes (gains and losses) but not to ambiguous (neutral) outcomes.

Again, similar findings have been obtained in studies on age-related changes in decision making using the Iowa Gambling Task (IGT). Results from Zamarian, Sinz, Bonatti, Gamboz, and Delazer (2008) suggest that older adults make more disadvantageous decisions (decisions that favor short-term over long-term benefits) when outcome information is ambiguous and has to be learned. In contrast, in unambiguous decision contexts, older adults perform as well as young adults (see also Denburg, Tranel, & Bechara, 2005; Fein, McGillivray, & Finn, 2007). It is interesting to note that young (6–9 years old) children show a deficit similar to that in older adults, that is, a preference for disadvantageous immediate outcomes in the IGT (Crone & Van der Molen, 2004; Kerr & Zelazo, 2004). Over the course of development the ability to integrate information about the probability of future outcomes increases. Multivariate analyses of developmental differences in IGT behavior suggest that these changes may reflect a shift from one-dimensional to multidimensional proportional reasoning (Huizinga et al., 2007).

Taken together, these findings point to more general difficulties of children and older adults in learning relational outcome representations in order to disambiguate the value of rewards. These impairments show some similarities to learning and decision-making deficits of patients with lesions in the vmPFC (Bechara, Tranel, & Damasio, 2000; Camille et al., 2004; Fellows, 2006). One prominent deficit of these patients is that they are impaired in determining the relative value of reward options. As a consequence they rely on simpler decision strategies and, similar to younger children and older adults, show a tendency to decide for the disadvantageous options in the IGT (Bechara et al., 2000; Denburg et al., 2005; Fellows, 2006). Whether the impairments of younger children and older adults in the ability to form multidimensional value representations reflects a similar underlying neurophysiological deficit is an open question. The current literature indicates that in older adults impairments in learning and decision making in ambiguous contexts may reflect deficits in the integration of dopaminergic reward signals into relational representations of reward value (Eppinger & Kray, 2011; Samanez-Larkin et al., 2010). In contrast, in children, developmental changes in decision making may reflect maturational processes in the medial PFC rather than a deficient use of reward value signals (Crone & van der Molen, 2004; Kerr & Zelazo, 2004).

Life Span Age Differences in Outcome Monitoring

In order to optimize performance, we have to constantly monitor outcomes and adjust subsequent behavior in case of expectancy violations. A large body of evidence suggests that the feedback-related negativity (FRN) may serve as an early electrophysiological indicator of outcome monitoring (Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Miltner, Braun, & Coles, 1997). Specifically, the FRN reflects a dichotomous evaluation of outcomes along a predefined good–bad dimension (Holroyd, Hajcak, & Larsen, 2006; Nieuwenhuis, Yeung, Holroyd, Schurger, & Cohen, 2004; Philiastides, Biele, Vavatzanidis, Kazzer, & Heekeren, 2010). For instance, larger FRN amplitudes have been observed to the worst and intermediate negative outcomes and smaller FRN to the best possible outcome, irrespective of the actual outcome value (Holroyd et al., 2006; Holroyd, Larsen, & Cohen, 2004). These findings suggest that the feedback negativity reflects a context-dependent outcome representation. That is, the FRN reflects the classification of events, according to whether those events are favorable for achieving the task-specific goals in question (Holroyd et al., 2006). Recent work on adult age differences in outcome monitoring indicates that the FRN is reduced in older adults (Eppinger et al., 2008; Hämmerer, et al., 2011; Mathewson, Dywan, Snyder, Tays, & Segalowitz, 2008). Moreover, compared with young adults, older adults differentiate less between positive and negative outcomes and show no evidence for an increase of the FRN with the degree of expectancy violation or the salience of the good–bad dimension (Eppinger et al., 2008; Hämmerer, et al., 2011; Herbert, Eppinger, & Kray, 2011; Mathewson et al., 2008). This suggests that older adults have difficulties in evaluating external inputs in relation to their reward representations.

In contrast, children show an enhanced FRN compared with that of young adults, indicating that they may be more sensitive to reward information than young adults (Eppinger et al., 2009; Hämmerer et al., 2011). However, even though they show an overall enhanced reaction to outcomes, they differentiate less between positive and negative outcomes than adults (Hämmerer et al., 2011). Given that outcome-based learning is an adaptive process, it is difficult to disentangle whether a less differentiated monitoring of action outcomes is a consequence or a cause of reduced learning performance in children and older adults. Recent findings show that the FRN does not change with learning and is hence independent of how much is known about action outcomes (Eppinger et al., 2008, 2009; Hämmerer et al., 2012; Philiastides et al., 2010). This suggests that a differentiated monitoring reaction as reflected in the FRN is a prerequisite rather than a symptom of efficient learning from outcomes. To summarize, children appear to be more sensitive to external rewarding input, whereas older adults show weaker monitoring of outcomes along the good–bad dimension. However, in their overall stronger (in the case of children) or weaker (in the case of older adults) responsiveness to external inputs, both age groups appear to differentiate positive and negative outcomes less and hence evaluate external outcomes less in relation to their reward representations.

Life Span Age Differences in Learning From Reward and Punishment

Apart from the fact that older adults are impaired in learning in uncertain or ambiguous environments, there is also evidence indicating that older adults differ from young adults in the way they learn from rewards and punishments. Results from Frank & Kong (2008) suggest that older seniors (mean age 77 years) show a bias toward learning from negative outcomes compared with young seniors (mean age 67 years). A similar negative learning bias was previously observed in patients with Parkinson's disease, which led to the conclusion that these age-related changes in learning may be due to reduced levels of subcortical dopamine in older

adults (Frank, Seeberger, & O'Reilly, 2004). Recent electrophysiological and behavioral findings support the idea that older adults may learn better from avoiding losses than from approaching rewards (Eppinger & Kray, 2011; Hämmerer, et al., 2011). Eppinger and Kray (2011) found greater individual differences in learning biases in older than in young adults. Moreover, negative learning biases were most pronounced in older learners. However, in contrast to bias effects in young adults, this negative learning bias in older adults was not associated with a stronger sensitivity to losses as reflected in a larger error-related negativity. In contrast, these findings rather suggest that the subcortical (dopamine-related) components of learning may be relatively unaffected by age, whereas the integration and updating of these learning signals into value representation in the vmPFC may be impaired in older age.

At first sight, these findings seem inconsistent with results from an fMRI study on reward prediction in young and older adults (Samanez-Larkin et al., 2007). Results of this study suggest that older adults anticipate losses less than younger adults whereas no age differences were obtained during reward anticipation. The authors interpret their findings in the context of the socioemotional selectivity theory, which suggests that older adults are more engaged in emotion regulation and focus on positive rather than negative cues in their environment (Carstensen, 2006; see also Samanez-Larkin & Carstensen, 2011, for a discussion of the corresponding neurobiological systems). However, it should be noted that the tasks applied in the previously mentioned studies differ in many respects. In the Samanez-Larkin et al. (2007) study, participants were explicitly told what they could expect if they pressed a button within a certain time window. Outcomes in this study did not have an impact on subsequent behavior. In contrast, in the learning studies cited, the acquisition of behavior critically depended on outcome processing. That is, in a context in which the outcome does not have an impact on subsequent behavior, older adults focus less on loss-predicting cues. In contrast, in a context in which successful performance depends on outcome processing, they focus more on avoiding negative outcomes than on approaching rewards. Given that during learning, the rare loss outcomes are very salient indicators of erroneous behavior, such a strategy of focusing more on loss outcomes might even be considered adaptive in view of decreasing attentional and working memory resources in older adults. Indeed, in the context of adaptive decision making, older adults have been observed resorting to cognitively less taxing strategies (Mata, Schooler, & Rieskamp, 2007, Mata, von Helversen, & Rieskamp, 2010; Pachur, Mata, & Schooler, 2009).

Consistent with the findings by Samanez-Larkin et al. (2007), results from a study by Wood, Busemeyer, Koling, Cox, and Davis, (2005) point to a reduced negativity bias in older adults. The authors used the Iowa gambling task (IGT) and showed that in contrast to greater aversion to loss seen in young adults, older adults may show a more equal weighing of gains and losses during decision making. Similar findings are reported in a study by Denburg, Recknor, Bechara, and Tranel (2006). In this study, the IGT was applied in two groups of older adults and skin conductance responses were measured. Denburg and colleagues found that high-performing older adults showed increased anticipatory skin conductance responding to advantageous decks, which was not the case for low-performing older adults (Denburg et al., 2006). The problem with studies using the IGT, however, is that it is not possible to determine whether participants go for the smaller gain decks or avoid the larger punishment decks. Furthermore, the IGT has been criticized because the reward probability structure is (most likely) explicitly accessible. Hence, it could be that performance in the IGT reflects an intact ability (especially in high-performing older adults) to calculate the expected utility of rewards rather than adjustments in performance based on rewarding or aversive outcomes (see Dunn, Dalgleish, & Lawrence, 2006).

Nevertheless, it should be noted that the literature on valence or learning biases is far from being conclusive. This interesting question needs to be addressed in broader and more structured computational and empirical frameworks. First, the relation between emotional valence and valence in the context of reward-related processing needs to be established. Age-related biases toward positive or negative information may differ depending on how valence is defined. Second, as mentioned previously, the task context may be critical for the expression of these preferences. That is, it most likely matters whether outcomes have an impact for subsequent behavior. Third, it is unclear how explicit these biases are. In the context of probabilistic learning, biases toward rewarding or aversive outcomes are most likely implicit, whereas the recollection of emotional information in memory paradigms most likely reflects strategic operations.

In children, the evidence for a bias in the sensitivity to gains and losses is mixed as well. Findings by van Leijenhorst, Crone, and Bunge (2006) suggest that during risky decision making, children may be more sensitive to negative feedback than young adults. This is consistent with findings that point to a larger FRN to losses during learning in children than in adults (Eppinger et al., 2009; Hämmerer, et al., 2011). Furthermore, analyses of win–stay/lose–shift behavior during reward-based learning showed a reduced impact of gains compared with losses on subsequent choices (Hämmerer, et al., 2011). However, there is also evidence for a greater impact of positive outcomes on performance adjustments in children than in adolescents and adults (van Duijvenvoorde, Zanolie, Rombouts, Raijmakers, & Crone, 2008). In the study by van Duijvenvoorde et al. (2008), participants were asked to apply a stimulus–response rule following random feedback and to use the outcome information on the following (repeat) trial. In contrast to the learning task used in Hämmerer et al.'s study (2011), outcome information is not integrated across repetitions but is relevant only locally with respect to the following trial. That is, similar to the findings in older adults, the bias toward gains or losses in children seems to depend on whether the outcomes are relevant for learning or are just considered locally with respect to the trial at hand or adjustments on the following trial.

Taken together, these findings indicate that biases toward gains or losses during learning and decision making strongly depend on whether these outcomes are relevant with respect to subsequent behavior. In situations in which the outcomes only have local relevance, factors such as general attitudes toward gains and losses may play a more prominent role for incentive processing (Samanez-Larkin et al., 2007). In contrast, in situations in which the outcomes are relevant for the subsequent acquisition or adjustment of behavior, the focus on either loss or gain outcomes might depend on the salience of the respective outcome for behavior. Clearly, more research is necessary to substantiate these conclusions and to define the conditions under which children, young

adults, or older adults learn more or less from rewarding or punishing outcomes. Furthermore, the question of whether age differences in learning biases reflect developmental changes in dopaminergic neuromodulation or whether these biases are also affected by higher-order cognitive control (strategic) mechanisms is unclear. Given the available evidence, it seems that more mechanistic analogies between age-related deficits and impairments as found in dopamine-related pathologies such as Parkinson's disease may not be sufficient to explain the complex life span developmental patterns that emerge. More generally, at this point, it seems questionable whether these biases are necessarily biologically determined (in the sense of age-related structural or neuromodulatory changes). They may rather reflect strategic context-dependent adaptations to optimize well-being and performance across the life span.

Discussion

In many instances, children and older adults show similar impairments in reward-based learning and outcome monitoring. These learning impairments are most pronounced in situations of (a) reward uncertainty (e.g. probabilistic reward schedules) and (b) reward ambiguity (e.g., the relative value of outcomes has to be learned). Furthermore, we showed that whereas children are more sensitive to external outcome information, older adults focus less on a rapid evaluation of outcomes along the good–bad dimension. Finally, we provided evidence for the idea that children and older adults differ from young adults in the way they value reward and punishment during learning. Despite the similarities in the behavioral impairments in learning and outcome monitoring, children and older adults seem to differ with respect to the neurophysiological mechanisms that underlie these deficits.

For older adults, the current literature points to reduced dopaminergic links of the ventral striatum and vmPFC during reward processing and learning (Dreher et al. 2008; Volkow et al., 2000). These age-related reductions in dopaminergic signaling may lead to less differentiated representations of reward value in older adults. Such a deficit becomes most apparent if value representations have to be constantly updated (reward uncertainty) or if an outcome has to be evaluated against a range of possible outcomes (reward ambiguity). In contrast, the available literature on developmental differences in learning suggest that children are more driven by external rewarding cues and less able to integrate reward information into goal-directed action plans. These deficits in the executive control of behavior during learning are most likely the result of less developed circuits in the dorsal medial and lateral prefrontal cortices (Diamond et al., 2004; Gogtay et al., 2004; Sowell et al., 2003).

It is interesting that these life span age differences in neurophysiological mechanisms involved in reward-based learning map well onto what is known about the cortical and subcortical loops involved in reward-based learning and outcome monitoring and their development across the life span (see Figure 2). These loops can be broadly subdivided into a reward loop that is involved in the valuation of outcomes (including the SN/VTA, ventral striatum, and vmPFC/mOFC) and an executive control loop that consists of cognitive control and motor areas involved in action selection (such as the dorsal PFC, dACC, and dorsal striatum). These two pathways are highly interconnected and include convergence zones such as the vmPFC and the dACC that allow a dynamic and task-dependent contribution of the relevant structures. In children, there is evidence for a protracted development of the medial and lateral prefrontal cortex, areas that are involved in the executive control loop previously described (Gogtay et al., 2004; Sowell et al., 2003). Evidence for developmental changes in neuromodulatory systems and the reward areas is relatively scarce, but it suggests adult levels in subcortical dopaminergic modulation by the age of 9 (Haycock et al., 2003; Seeman et al., 1987). In older adults, there is substantial evidence for a decline in dopaminergic neuromodulation (Li, Lindenberger, & Bäckman, 2010; Li, Lindenberger, & Sikström 2001). This decline is rather widespread and includes the PFC, basal ganglia, and the midbrain dopaminergic structures. The fact that this decline is so diffuse makes it difficult to relate age-associated behavioral deficits to specific aspects of the reward loop. However, in support of our hypothesis, recent multimodal imaging findings by Dreher et al. (2008) point to age-related changes in the association between midbrain dopamine synthesis and prefrontal BOLD activity. Furthermore, the decrease of D2 receptors in the striatum with age has been shown to be related to reduced metabolism in lateral and medial prefrontal brain regions (Volkow et al., 2000).

Regarding age differences in outcome monitoring, the current literature suggests that children are more sensitive to external outcome information, whereas older adults focus less on a rapid evaluation of the rewarding properties of outcomes. Moreover, both age groups show a reduced sensitivity to expectancy violations, indicating that they process outcomes less in relation to internal representations (Bellebaum, Kobza, Thiele, & Daum, in press; Eppinger et al., 2008). With respect to older adults, these deficits in outcome monitoring are consistent with the idea of less differentiated reward representations in older age. The enhanced sensitivity of children to external rewarding cues dovetails with findings that indicate that young children especially are less able to assess the informational value of outcomes and to use the feedback to optimize their actions. These results are consistent with our idea that children's deficits in reward-based-learning and outcome monitoring are primarily due to less developed prefrontal circuits involved in executive control. Whether these effects are associated with a decreased sense of agency in children is an open question. Such an interpretation would certainly fit with proposed links between the development of theory of mind and maturation of the medial and lateral PFC (Frith & Frith, 2003).

Finally, we showed evidence supporting the idea that biases toward gains or losses during learning and decision making strongly depend on whether these outcomes are relevant with respect to subsequent behavior. In situations in which the outcomes only have local relevance, factors such as general attitudes toward gains and losses may play a more prominent role for incentive processing (Samanez-Larkin et al., 2007). In contrast, in situations in which the outcomes are relevant for learning, a focus on loss or gain outcomes might depend on the motivational salience of the respective outcome. Given the limited literature on this topic, it seems unclear whether age differences in learning biases reflect developmental changes in dopaminergic neuromodulation or whether these biases are also affected by higher order cognitive control (strategic) mechanisms. On a more general level, it seems questionable whether these biases are necessarily biologically determined (in the sense of age-related structural or neuro-

modulatory changes) or whether they rather reflect strategic adaptations to the task context at hand.

The present framework does not preclude the possibility that older adults show impairments in executive control. Evidence for such deficits has been found in several previous studies using the Stroop task or task-switching and dual-task paradigms (Eppinger, Kray, Mecklinger, & John, 2007; Kray & Lindenberger, 2000; West, 2004; West & Alain, 2000; West, 1996). However, it should be noted that these deficits only occur if the demands on cognitive control are very high (e.g. infrequent Stroop trials, working memory load during task-switching) (see Verhaeghen & Cerella, 2002, and Verhaegen & De Meersman, 1998, for meta-analyses). Most of the learning and decision-making tasks that are described throughout this review are not subject to very high demands on cognitive control. Nevertheless, older adults show learning impairments under conditions of reward uncertainty or ambiguity. In our view, these impairments are due to a decline of the dopaminergic projections to the vmPFC. This is not to say that in a task context with high demands on control (such as reversal learning or more complicated hierarchical reinforcement learning tasks), older adults would not show disproportionate impairments.

We also do not want to deny the fact that there are developmental changes in reward processing, especially during adolescence. For example, recent findings by Cohen and colleagues (2010) suggest that adolescents (14–19-year-olds) show an overactive dopaminergic prediction error response compared with such response in children and adults, which may result in reward-seeking behavior. However, puberty is a very special developmental period that is characterized by fundamental changes in hormonal and neurotransmitter systems, which are not the focus of the current article.

The purpose of this review is to provide a framework to explain age differences in the relative contributions of reward-related processes and executive control mechanisms to reward-based learning and decision making. We suggest that in older adults, the contribution of dopaminergic decline to changes in reward-based learning and decision making is higher, whereas in children immature prefrontal circuits contribute to difficulties in outcome monitoring and action selection.

Limitations of This Review and Outlook for Future Studies

Given the sparse evidence on the development of goal-directed behavior, our ideas at present are forced to be speculative, and several limitations apply. The available literature is limited; this is true for both age groups but most apparent with respect to neuroimaging findings in children. Hence, many findings should be interpreted cautiously given the lack of replications and the small and heterogeneous samples. Moreover, there is a lack of studies that combine an investigation of age differences in reward-based learning with research on age differences in the relevant neural substrates and neuromodulatory systems. The present review had to rely mostly on studies that link only two of these aspects (i.e. neural substrates relevant for reward-based learning, age differences in these neural substrates, and age differences in reward-based learning). The few existing studies suggest that dopaminergic changes with aging are indeed contributing to age differences in reward-based learning. The previously mentioned study by Dreher et al. (2008) combined positron-emission tomographic (PET) and fMRI measurements in young and older adults during a slot-machine gamble and observed a changed association of ventral striatal dopamine synthesis and dlPFC activation with age. Further, self-stimulation of the medial forebrain bundle in rats, that is supposed to have a dopaminergically mediated reinforcing effect, was found to be reduced in older rats but could be enhanced by administering amphetamine (Lewis, 1981; but see also Sonnenschein & Franklin, 2008, for no age differences in baseline response level or amphetamine response). Hence, the limited existing evidence suggests a contribution of changes in dopaminergic structures with age, but is inconsistent with respect to the direction of the effects. In the case of the children, even less evidence is available. PET is, for good reasons, rarely used in healthy children, which makes statements about life span developmental changes in neuromodulatory systems difficult. With respect to structural differences, very recent findings point to an association between white matter integrity in the PFC and inhibitory control during childhood development (Madsen et al. 2010; Olson et al., 2009). Despite these first promising results, it is clear that there is a great need for studies that test how age differences in reward-based learning are related to age differences in the integrity of the reward or executive control loop.

In addition to these limitations, we have identified several important methodological considerations and open research questions that we think should be addressed:

1. One important issue that is relevant to most of the reviewed studies that use monetary rewards is whether those rewards have a similar saliency for the different age groups. It seems obvious that depending on the income level, individuals differ with respect to how they value outcomes. One way to avoid these problems could be to use primary rewards (D'Ardenne, McClure, Nystrom, & Cohen, 2008; McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007). However, it should be noted that primary rewards may be problematic for other reasons, such as age differences in gustatory processing or loss of taste receptors and so on (see Jacobson, Green & Murphy, 2010). Another factor that is relevant with respect to decision-making studies is incentive compatibility. That is, monetary transactions should be realistic and participants should be able to actually earn the money they make decisions on. In this context another important aspect is whether outcomes are actually performance-dependent. Given that older adults strongly focus on accuracy, their behavior might be different in situations in which the feedback is dichotomous (correct/incorrect) and draws their attention to the "correctness" of their outcomes and situations in which value information has to be integrated with accuracy (Starns & Ratcliff, 2010).

2. An obvious limitation in most of the current studies on age differences in reward-based learning is the fact that the subprocesses involved in learning are only loosely defined and in most cases rely on verbal theories. Future studies should focus more on the modeling of behavior and on model-based analysis approaches. That is, the present attempt to incorporate functional evidence into a neurobiologically plausible model should be followed by more systematic investigations of age differences in the different component processes of learning and outcome monitoring. For example, in future studies, reinforcement learning models, such as temporal difference learning models, could be used to derive time-varying indicators of prediction errors, reward representations, and the contingency with which reward representations are translated into actions (Montague et al., 2004; Niv & Schoenbaum, 2008). The hypothesis that older adults show reduced dopaminergic prediction error signals could be investigated by testing the fit of a model with a reduced impact of prediction errors in older

adults. Likewise, the assumed reduced distinctiveness of reward representations in older adults should be evident in less distinct reward probability estimates of the respective options. In contrast, in children, one might expect to find reduced learning rates (i.e., a reduced translation of prediction errors into action control). The use of such models may help us to better understand age differences in the subprocesses involved in reward-based learning. This also applies to the framework presented in this article. At this point, it is unclear whether impairments in the formation and updating of value representations reflect reduced dopaminergic prediction error signals from the midbrain to the ventral striatum or deficits in the formation of higher order representations in the vmPFC.

Conclusion

Taken together, we think that phenomenologically similar impairments in the acquisition and monitoring of behavior in children and older adults can be attributed to deficits in different underlying neurophysiological mechanisms. We propose that in older adults, learning impairments are the result of reduced dopaminergic connections with the vmPFC, which lead to less differentiated reward representations. In contrast, in children, impairments in learning can be primarily attributed to deficits in executive control, which are due to a protracted development of the dorsal medial and lateral prefrontal cortices. We think that this framework maps well onto recent neurophysiological models of reward processing (Haber & Knutson, 2010; Parent, 1990; Smith & Bolam, 1990) and is plausible from a broader developmental perspective.

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