

Effect of aging on stimulus-reward association learning

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Abstract

The flexible learning of stimulus-reward associations when required by situational context is essential for everyday behavior. Older adults experience a progressive decline in several cognitive functions and show deficiencies in neuropsychological tasks requiring flexible adaptation to external feedback, which could be related to impairments in reward association learning. To study the effect of aging on stimulus-reward association learning 20 young and 20 older adults performed a probabilistic object reversal task (pORT) along with a battery of tests assessing executive functions and general intellectual abilities. The pORT requires learning and reversing associations between actions and their outcomes. Older participants collected fewer points, needed more trials to reach the learning criterion, and completed less blocks successfully compared to young adults. This difference remained statistically significant after correcting for the age effect of other tests assessing executive functions. This suggests that there is an age-related difference in reward association learning as measured using the pORT, which is not closely related to other executive functions with respect to the age effect. In human aging, structural alterations of reward detecting structures and functional changes of the dopaminergic as well as the serotonergic system might contribute to the deficit in reward association learning observed in this study.

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1. Introduction

Rewards play a crucial role in organizing and controlling goal-directed behavior. They induce subjective feelings of pleasure, act as positive reinforcers and may cause an increase of frequency and effort of behavior. The efficient control of goal-directed behavior requires the detection of rewards and their prediction on the basis of stored associations between actions and their outcomes formed by past experiences. The ability to learn and to flexibly relearn stimulus-reward associations when required by situational context is essential

for everyday behavior. Older adults experience a progressive decline in several cognitive functions (Craig & Jennings, 1992). Particularly, they show deficiencies in neuropsychological tasks requiring adaptation to external feedback of right or wrong, shifting set, or task-switching paradigms (Albert, 1994; Kramer, Humphrey, Larish, Logan & Strayer, 1994; Kray & Lindenberger, 2000; Parkin & Lawrence, 1994). The loss of behavioral flexibility could be related to impairments in learning stimulus-reinforcement associations and adapting existing ones to new situations. However, it is still unknown how aging affects stimulus-reward association learning in humans.

In animal studies, reversal learning tasks have been used to investigate this process. In these experiments, animals typically receive a primary positive reinforcer such as food or a

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pleasant liquid. Animals have to detect and predict rewards by choosing a certain stimulus and have to shift to another problem solving strategy as reward contingencies continue to change (Schultz, 2000). Animals with focal lesions in the prefrontal cortex (PFC) fail to shift their behavior after stimulus-reward associations are no longer valid (Jones & Mishkin, 1972; Schoenbaum, Nugent, Saddoris & Gallagher, 2002). In the context of aging, studies using reversal learning tasks in non-human primates, dogs, and rats reported controversial results (Bartus, Dean & Fleming, 1979; Herndon, Moss, Rosene & Killiany, 1997; Lai, Moss, Killiany, Rosene & Herndon, 1995; Rapp, 1990; Tapp et al., 2003; Voytko, 1999). Bartus and colleagues (1979) described severe deficits in reversal learning in a group of old primates compared to younger ones, especially in the second block, after the first reversal occurred. Rapp (1990) observed no differences between young and old primates in a reversal learning task, but found that old primates required more training to learn an initial pattern discrimination. Herndon et al. (1997) reported an age effect in an object reversal learning test. However, this effect was less significant than in a spatial reversal task and other tasks measuring executive functions. In contrast, Voytko (1999) showed an age effect only in the object reversal test version, but not in the spatial version. Furthermore, the impairment in learning object discrimination in aged monkeys was characterized by a prolonged period of chance performance. Schoenbaum and colleagues (2002) tested rats in an odor reversal learning task. Aged rats showed no difference in acquiring the initial odor discrimination problem but needed significantly more trials to reach criterion again after reversal. Finally, beagles tested by Tapp et al. (2003) showed impaired performance in both initial discrimination learning and reversal learning tasks. Old dogs needed longer to learn the correct stimulus-reward contingencies, whereas even older dogs displayed increased perseverative responding. Taken together, it is still controversial, whether there is an age effect on reversal learning. Furthermore, different results about the nature of the errors in older animals are reported. Some authors showed that older animals tend to perseverate on old task sets (Bartus et al., 1979; Tapp et al., 2003; Voytko, 1999). Others propose failure in learning new stimulus-reward associations as revealed in learning stage analyses (Jones & Mishkin, 1972; Lai et al., 1995; Tapp et al., 2003; Voytko, 1999).

In the context of learning and adapting stimulus-reinforcement contingencies in older human adults, several studies have used the Wisconsin Card Sorting Test (WCST; Fristoe, Salthouse & Woodard, 1997; Grant & Berg, 1948; Hartman, Bolton & Fehnel, 2001; Kramer et al., 1994; Ridderinkhof, Span & van der Molen, 2002) in which participants receive positive feedback for choosing a certain category (color, shape, or number) and have to shift response strategies as soon as stimulus-reinforcement contingencies change (Grant & Berg, 1948). Older human adults typically show performance deficits. Their tendency to perseverate on old task sets has been interpreted as an impairment in set-

shifting abilities (Ridderinkhof et al., 2002) or reduced working memory capacity (Fristoe et al., 1997; Hartman et al., 2001).

Using reversal learning tasks, stimulus-reinforcement learning can be tested. In those tasks the participant has to adapt responses to a certain stimulus-reward contingency and to inhibit previous responses. These tasks were previously used in animal models (Jones & Mishkin, 1972) but were also adopted for use in human patients suffering from Alzheimer's disease (Freedman & Oscar-Berman, 1989), Korsakoff syndrome (Oscar-Berman & Zola-Morgan, 1980), and frontal lobe lesions (Rolls, Hornak, Wade & McGrath, 1994). Recently, probabilistic versions of reversal learning paradigms have been applied. In the probabilistic versions, the feedback to the correct stimulus is degraded following a probabilistic schedule (i.e. there is a stochastic variation of the amount of reward). It has been shown that under this condition several clinical populations such as patients with organic depression (Reischies, 1999) or Huntington's disease (Lawrence, Sahakian, Rogers, Hodges & Robbins, 1999) show impaired performance in stimulus-reward association learning.

It is important to point out that there is a difference between reversal learning paradigms and the WCST. The WCST requires abstraction abilities and the ability for set-shifting. Abstraction abilities are required because one has to find out which sorting rules are critical (i.e. color, shape, number). Extra-dimensional shifts are needed to switch from one rewarded category (e.g. color) to another category (e.g. shape) after the feedback schedule has changed. These subprocesses require other cognitive abilities than basic stimulus-reward association learning (Rolls, 2000; Rolls et al., 1994). In contrast to the WCST, in reversal learning tasks, such as the probabilistic object reversal task (pORT), stimulus-reward contingencies have to be adapted within only one perceptual dimension (intra-dimensional shift).

It should be noted that other reward-related decision-making tasks such as the Iowa gambling task (Bechara, Damasio, Damasio & Anderson, 1994) or Rogers' gambling task (Rogers et al., 1999) are frequently used in neuropsychological studies of decision-making disturbances in frontal lobe damaged patients (for review see Bechara, 2001; Rahman, Sahakian, Cardinal, Rogers & Robbins, 2001). An important characteristic of these tasks is that participants have to decide between two options with different odds of success and different pay-offs (e.g. a small very likely reward or a larger less likely reward). In Rogers' task, subjects have to weigh the probability of winning a reward with the amount of possible reward or punishment, and in the Iowa gambling task, participants have to learn to avoid the disadvantageous alternatives by using feedback from previous trials. In contrast to this, in the pORT used in the present study, only one letter at a time is maximally rewarded (and never associated with a punishment) and the pORT therefore relies on reward-seeking behavior.

Taken together, studies in various species (monkeys, rats, dogs) suggest an effect of aging on stimulus-reinforcement

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