



Target value and prevalence influence visual foraging in younger and older age

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ABSTRACT

The prevalence and reward-value of targets have an influence on visual search. The strength of the effect of an item's reward-value on attentional selection varies substantially between individuals and is potentially sensitive to aging. We investigated individual and age differences in a hybrid foraging task, in which the prevalence and value of multiple target types was varied. Using optimal foraging theory measures, foraging was more efficient overall in younger than older observers. However, the influence of prevalence and value on target selections was similar across age groups, suggesting that the underlying cognitive mechanisms are preserved in older age. When prevalence was varied but target value was balanced, younger and older observers preferably selected the most frequent target type and were biased to select another instance of the previously selected target type. When value was varied, younger and older observers showed a tendency to select high-value targets, but preferences were more diverse between individuals. When value and prevalence were inversely related, some observers showed particularly strong preferences for high-valued target types, while others showed a preference for high-prevalent, albeit low-value, target types. In younger adults, individual differences in the selection choices correlated with a personality index, suggesting that avoiding selections of low-value targets may be related to reward-seeking behaviour.

1. Introduction

Visual information processing is influenced by the perceptual characteristics of the visual scene as well as the learned values, or rewards, associated with specific visual stimuli (Anderson, Laurent, & Yantis, 2011; Anderson, 2013; Marschner et al., 2005; Della Libera & Chelazzi, 2006; Serences, 2008). This adjustment of cognitive processing according to properties of the environment and internal representations or goals enables adaptive behavior, especially in complex tasks. However, individuals differ both in their capabilities and/or in the strategic preferences that drive behavioral adaptations (LePine, Colquitt, & Erez, 2000; Locke & Braver, 2008) and individual adaptability further changes with aging (Ridderinkhof, Band, & Logan, 1999). More specifically, it has been hypothesized that with adult aging, individuals increasingly rely on environmental information and less on internal representations to guide behavior (Lindenberger & Mayr, 2014). This age-related shift towards environmental control is assumed to result

from changes in internally-guiding representations or difficulties in maintaining those representations. One important example is an age-related decline in learning stimulus-value associations and how they impact task performance (Mell et al., 2005; Mata, Schooler, & Rieskamp, 2007). By contrast, stimulus-driven influences on behavior, like processing facilitation by perceptual saliency or priming, are typically preserved, or even increased, in older compared to younger adults (Madden et al., 2004; Wiegand et al., 2013).

1.1. Individual and age differences in the influence of target value on visual selections

Over the past years, evidence has accumulated that value and reward influence already relatively early visual perceptual and attentional processes (see Failing & Theeuwes, 2018, for a recent review). Specifically, the deployment of visual attention is biased towards stimulus features associated with greater reward (e.g., Della Libera & Chelazzi,

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2006; Munneke, Hoppenbrouwers, & Theeuwes, 2015; Navalpakkam, Koch, Rangel, & Perona, 2010; Serences, 2008). It has been suggested that reward-value adds to the relative salience of stimuli, which would give highly-valued stimuli a selection advantage over less-valued stimuli (Hickey, Chelazzi, & Theeuwes, 2010a). This line of research has also demonstrated that reward-related effects on attentional selection vary between individuals. The individual responsiveness to reward manipulation, i.e. the strength of the selection advantage of highly-valued items in visual search, has been linked to a personality index of reward-seeking behavior (Hickey, Chelazzi, and Theeuwes, 2010b; Hickey & Peelen, 2015), measured by the *Behavioral Inhibition System (BIS)/Behavioral Approach System (BAS) scale* (Carver & White, 1994). The scale was developed based on the neurobiological model of Gray (1990), which postulates that cognitive and affective processes are influenced by activity in two basic, distinct brain systems. The BIS is thought to drive avoidance behaviors, like inhibition and control, in order to prevent loss, punishment, fear and novelty (Carver & White, 1994). The BAS is thought to drive approach behaviors, is associated with impulsivity, and fundamentally involved in novelty- and reward-seeking behavior (Gray, 1990). The studies of Hickey and colleagues (2010b); Hickey and Peelen (2015) showed that individuals with higher BAS scores showed a larger effect of reward on attentional selection, suggesting that the system exerts an influence on early attentional processes.

Störmer, Eppinger, and Li (2014) investigated age differences in the responsiveness to varying target values in visual search. They found facilitated selection of targets associated with high reward-values across younger and older age groups, but that younger adults were more sensitive to the reward manipulation than older adults (Störmer et al., 2014). The authors attributed the reduced effect of target value in older adults to age-related dysfunctions in the reward system, particularly dopaminergic structures. Age-related changes in dopaminergic functions were suggested to underlie decreased sensitivity to reward information and reduced ability to use reward information for adapting behavior also in other cognitive tasks (Betts et al., 2020; Eppinger, Hämmerer, & Li, 2011; Hämmerer & Eppinger, 2012; Marschner et al., 2005; Mohr, Li, & Heekeren, 2010). Of the two systems proposed by Gray, the BAS is thought to comprise dopaminergic structures (Gray, 1990). Large-sample demographic studies showed that BAS (and also BIS) scores are negatively related to age (Jorm et al., 1998; Knyazev, Slobodskaya, & Wilson, 2004; Windsor, Pearson, & Butterworth, 2012), which would be in accordance with a decreased responsiveness of the BAS in older age.

1.2. Value and prevalence in hybrid foraging

The prior research, described above, employed simple visual selection and visual search paradigms, in which one target object per trial had to be identified. Recently, researchers have extended these classic single-target paradigms to more complex search tasks, in which multiple targets must be selected on a given trial (Cain, Vul, Clark, Mitroff, 2012; Ort & Olivers, 2020; Kristjánsson, Jóhannesson, & Thornton, 2014; Kristjánsson, Thornton, Chetverikov, & Kristjánsson, 2020; Wolfe, 2013). Search for multiple instances of targets falls in the category of foraging tasks. Such tasks have long been studied in animals, for example, to understand how animals forage for food (Pyke, Pulliam, & Charnov, 1977; Stephens & Krebs, 1986). Foraging researchers have argued for the relevance of the animal foraging literature to human decision making, noting that many of the heuristics that are part of our cognitive toolkit must have developed under the same evolutionary pressures that shape animal foraging behavior (Todd, Hills & Robbins, 2012; Wilke & Barrett, 2009; Wilke & Todd, 2010). So, for example, Wilke and Todd (2010) point out that resources like food are typically clumped (aggregated) in the environment. Apples are concentrated in apple trees, not uniformly distributed in the world. Thus, it may not be surprising that humans behave as though resources are clumped, even when the researcher has distributed them randomly (e.g. Hutchinson,

Wilke, & Todd, 2008).

Many search tasks humans perform in everyday life also involve a series of visual selections, like shopping in a store, searching the internet for information, or collecting coins after you accidentally dropped your wallet on the street. In foraging tasks, where the number of targets is unknown and the forager is free to move to a new “patch” at will, it is of interest to determine when the forager chooses to leave the current patch to “travel” to the next (Bond, 1980; Pyke et al., 1977). In a laboratory foraging experiment, the “patch” would be a trial display and “traveling” involves the initiation of a new trial display to continue the foraging task (Cain et al., 2012; Wolfe, 2013). The behavior of young adult human foragers in such an experiment, just like that of animals, follows Charnov’s (1976) marginal value theorem (MVT), at least on average for basic foraging tasks (Wolfe, 2013). MVT predicts that the optimal forager, in order to maximize gain per time, will leave a patch when the “instantaneous rate of return” from the current patch (i.e. the current display) drops below the average rate of return over all patches (i.e. an experimental block in the laboratory task).

In order to achieve optimality in terms of MVT, the forager must infer or learn the average and instantaneous rates of return. The properties of the environment influence the patch-leaving decisions in foraging. For example, if there is a long travel time between patches, the time cost of switching between patches needs to be taken into account by the forager and balanced against the quality of the resource within a patch (Wilke & Barrett, 2009; Wolfe, 2013).

In this paper, we will report on the results of foraging tasks in which observers search for multiple instances of several different types of target, e.g. quarters, dimes, and pennies. A search for any of several possible target types involves search through both our memories and the visual displays presented to us and is called a *hybrid* search task (Schneider & Shiffrin, 1977; Wolfe, 2012). Hence, a task where multiple instances of multiple target types have to be collected is called a *hybrid* foraging task (Kristjánsson et al., 2014; Wolfe, Aizenmann, Boettcher, & Cain, 2016; Wolfe, Cain, & Aizenmann, 2019). Understanding choices in a hybrid foraging task is akin to making predictions about which species should be included in an animal’s diet (as a bear, should I collect berries or insects or, perhaps, travel down to the human campground and look for trash?) (MacArthur & Pianka, 1966; Schoener, 1971; Pulliam, 1974). With multiple target types, according to the diet-breadth model (MacArthur & Pianka, 1966), maximizing gain per time can be accomplished by ranking value of the “prey” targets and pursuing the most profitable target types as long as the encounter rate of this target in the environment is sufficiently high (Levi, Lu, Douglas, & Mangel, 2011).

In a hybrid foraging task, apart from the decision when to move on to a new a patch, observers also have to make the decision which of the multiple target type to pick (first) within each patch. In the standard laboratory hybrid foraging task, all target types appear with a similar frequency at the onset of the patch and observers “gain” the same number of points for each collected target type. Under these conditions, which target type is selected depends mainly on the previous selection. Typically, observers do not pick randomly among available targets. Instead, observers collect items in “runs” of picking instances of the same target type (Kristjánsson et al., 2014; Wolfe et al., 2016, 2019). Searching again for the same item is faster than switching to search for another target type. This behavior is likely an effect of priming (Kristjánsson, & Campana, 2010; or selection history effects; Awh, Belopolsky, & Theeuwes, 2012; Theeuwes, 2018). Selection of one item facilitates the selection of items with the same features and identity (Neely, 1977; Posner & Snyder, 1975; Sperber, McCauley, Ragain, & Weil, 1979), while selecting a different item takes longer, imposing a type of switch cost (Monsell, 2003).

In many foraging searches, the relative frequency of objects in the environment may not be balanced and certain objects might be regarded as being worth more than others. You might look for all types of coins on the street, but you might find it more important to recover the quarters than the pennies. However, quarters might be rarer compared to the

pennies, making them more difficult to find. How younger observers adapt their foraging behavior when target types vary in value and prevalence was recently investigated by Wolfe, Cain, and Alaoui-Soce (2018). They introduced a hybrid foraging task in which the point value and prevalence of four different target types was systematically manipulated. They showed that, if value was kept constant while prevalence varied between targets, participants consistently showed a preference for the most common targets. Their selection rate for the more prevalent targets was over and above the selection rate that would be expected if observers pick targets randomly from the display. This prevalence effect reflects that, by default, the most prevalent target type will first be picked with a higher probability by chance¹. Due to the priming effect described above, being selected makes this target type then more likely to be selected next from the display with multiple target types (Kristjánsson et al., 2014; Wolfe et al., 2016; Wolfe et al., 2019). When target types differed in value (i.e., the number of points gained per selection), observers favored more valuable targets. Notably, under the value manipulation, individual foraging strategies became more diverse, especially when target value and prevalence were inversely related. While all observers followed a behavior in line with MVT, some observers appeared to be more value-driven, selecting most valuable targets even if those were rare and hard to find. Others appeared to be more prevalence-driven in their selection choices, collecting also the frequent, albeit low-valued, targets. Foraging models that incorporate search for targets of different quality (e.g. caloric content of prey) make the prediction that the individual item choice depends on the payoff between expected search effort and gain (MacArthur & Pianka, 1966). As our data will show, when there is a tradeoff between the speed with which a target can be found and the value of that target, different observers adopt different strategies. These may reflect different subjective estimates of search effort and reward. Thus, how foragers decide for the best search policy may depend on intrinsic motivational factors or preferences. Note that we will manipulate prevalence of different targets and their relative value, following Wolfe et al. (2018). We could also alter the spatial distribution of different types of targets (berries here, insects over there), but we will leave that for another study.

1.3. The present study

First, we investigated potential age differences in the hybrid foraging task with varying target value and prevalence using the same hybrid foraging paradigm as Wolfe et al. (2018). Our previous research with younger and older adults demonstrated that, under conditions with balanced target values and prevalence, older adults are less optimal foragers than younger adults within an MVT framework (Wiegand, Seidel, & Wolfe, 2019). When assessed in terms of points collected per unit of time, older adults tend to leave the current patch later than MVT predicts; when the instantaneous rate of collection has dropped well below the average rate of collection. We expected to replicate our previous finding that older adults are less optimal foragers than younger adults (Wiegand et al., 2019) in these new conditions where value and prevalence of target types varied. Our previous results showed that, as in younger adults, the selection of the target type is strongly influenced by the previous selection in older adults (Wiegand et al., 2019). This suggests preserved priming effects on visual foraging in older age and supports the assumption that older adults rely on external environmental cues to guide behavior (Lindenberger & Mayr, 2014). Therefore, we expected that older adults would be similarly or even more

responsive to the manipulation of prevalence than younger adults. By contrast, we expected the value manipulation might have a smaller effect on foraging in older compared to younger adults. This would be in accordance with impaired learning and implementation of stimulus-value associations (Mell et al., 2005) and a reduced reliance on internal, motivational cues with increasing age (Lindenberger & Mayr, 2014).

Second, expanding on the findings of Wolfe et al. (2018), we further investigate the origin of individual differences in foraging for targets of varying prevalence and value in the present study. We expected to replicate that observers would show a tendency to pick more prevalent and highly valued items and that individuals would differ in their responsiveness to the value manipulation. In addition, in an exploratory analysis, we tested whether target selections under conditions of varying target value and prevalence would be related to individual levels of BIS and BAS activity, which are trait markers of avoidance and approach behavior, respectively (Gray, 1990). In particular, based on the previously demonstrated relationships between BAS scores and individual responsiveness to reward-values (Locke & Braver, 2008; Hickey et al., 2010b; Hickey & Peelen, 2015), we expected that high BAS levels, driving reward-seeking behavior, would be associated with a tendency to collect high-value targets while low BAS levels would be associated with a tendency to collect highly prevalent targets, despite their low value. Finally, we expected that lower BAS levels would coincide with a reduced sensitivity to the value manipulation in the older sample.

2. Methods

2.1. Participants

We collected data from 26 younger participants between the ages of 18–35 years and from 22 older participants between the ages of 65–82 years. We computed a priori power analyses (G*Power) to justify the sample size based on a power of 0.80 and alpha level of 0.5 for each of the statistical tests. To detect within-subject and within-between subject interaction effects with a medium effect size ($\eta^2 = 0.06$) in a mixed ANOVA, the analysis suggested a total sample size of 28 participants, 14 per group. To detect an effect of a medium effect size ($d = 0.5$) in dependent t-tests, a total sample size of 27 was calculated to be sufficient. A total sample size of 42, 21 per group, was calculated to detect an effect with large effect size in independent t-tests. To achieve a medium effect size in a multiple linear regression with two predictors, the power analysis suggested a total sample size of at least 43 participants.

The younger participants were recruited by clinical trial recruitment announcements from Partners Healthcare and Brigham and Women's Hospital, Harvard University. The older participants were recruited by an advertisement in the magazine *FiftyPlus Advocate*. Participants were paid \$11 or \$12 per hour for their time. They took part voluntarily and gave their informed consent before the examination. The study was conducted in accordance with the Declaration of Helsinki on ethical principles and the Partners Healthcare Corporation Institutional Review Board approved all experimental procedures.

All participants had a visual acuity of 20/25 or better (including correction through glasses), as assessed with the ETDRS Near Vision Chart (Bailey & Lovie, 1976). None were colorblind, as assessed by the Ishihara Test (Ishihara, 1980). Participants who reported diagnoses of any neurological, psychiatric, or chronic somatic disorder were excluded from the study. Two younger participants were excluded based on this criterion. All participants were further screened for the presence of mild to severe depressive symptoms using the Center for Epidemiologic Studies Depression Scale (CES-D, Radloff, 1977). No participant had CES-D scores higher than 20, indicating no symptoms of moderate or severe depression. Older participants were additionally screened with the Mini-Mental State Examination (MMSE, Folstein, Folstein, & McHugh, 1975). They all scored higher than 26 in the MMSE, indicating no symptoms of beginning dementia. One older participant was

¹ The prevalence effect in hybrid foraging task is different from that the prevalence effect in single-target visual search. In single target search, increasing the target prevalence (i.e. the probability that a target is present in a given trial) leads to higher detection rates. However, this is explained by a response bias towards “present” decisions rather than increased sensitivity for the targets features (Horowitz, 2017; Wolfe et al., 2007).

excluded for not completing the experiment. The final participant samples for analysis therefore consisted of 24 younger adults and 21 older adults.

Of the participants meeting the inclusion criteria, we further assessed demographic information (age, sex, education) with a questionnaire and applied further tests for cognitive screening. Cognitive and visuo-motor speed was assessed with the Digit-Symbol Substitution Test (DSST, Wechsler, 1958). Verbal abilities (verbal IQ) were measured with the North American Adult Reading Test (NAART, Blair & Spreen, 1989; Nelson, 1982). Subjective cognitive failures in everyday tasks were assessed with the Cognitive Failures Questionnaire (CFQ, Broadbent, Cooper, FitzGerald, & Parkes, 1982). Finally, only for the older participants, the level of cognitive reserve² was assessed with the Cognitive Reserve Index questionnaire (CRIQ, Nucci, Mapelli, & Mondini, 2012). A summary of the demographic information and screening results of both age groups can be found in Table 1.

2.2. Assessment of sensitivity to reward and punishment

The BIS/BAS scale (Carver & White, 1994) was administered to measure individual differences in reward sensitivity according to the activation of two systems that regulate behavior: The behavioral approach system (BAS) is believed to control appetitive behavior with the goal to move towards something desired and the behavioral inhibition system (BIS), believed to control aversive behavior with the goal to avoid something unpleasant. The BIS/BAS scales consisted of a 24-item questionnaire, in which participants indicated the degree to which they agree with simple statements (e.g., “When I want something I usually go all-out to get it”). Previous large-sample factor analyses have identified two primary dimensions in the results, corresponding to BIS and BAS sensitivity (Carver & White, 1994). Additionally, the BAS scale can be subdivided into three subscales, BAS Reward Responsiveness, BAS Drive, and BAS Fun Seeking. Empirical evidence for the 2-dimensional BIS/BAS structure is solid, while the subdivision of the BAS into three dimensions has not always been supported (Miller, Joseph, Tudway, 2004; Strobel, Beauducel, Debener, & Brocke, 2001). In the present

Table 1

Demographic information and scores of the screening tests for the younger and older participants who were included in the final sample. All values, excluding gender and handedness, indicate the mean and standard deviation (in parentheses) of the samples. CES-D: Center for Epidemiologic Studies Depression Scale; CFQ: Cognitive Failures Questionnaire; CRIQ: Cognitive Reserve Index questionnaire; DSST: Digit Symbol Substitution Test; MMSE: Mini-Mental State Examination; NAART (VIQ)*: North American Adult Reading Test (Verbal Intelligence Quotient).

| Sample Information | Younger Adults (n = 24) | Older Adults (n = 21) |
|--------------------|--------------------------|--------------------------|
| Age (years) | 24.58 (3.15) | 70.52 (5.04) |
| Gender | 18 female, 6 male | 11 female, 10 male |
| Handedness | 22 right, 1 left, 1 both | 18 right, 1 left, 2 both |
| CES-D | 7.39 (7.66) | 5.29 (5.73) |
| MMSE | not acquired | 28.90 (1.30) |
| DSST | 61.39 (13.34) | 47.52 (10.18) |
| CFQ | 29.46 (11.85) | 21.67 (11.42) |
| NAART (VIQ)* | 113.77 (7.32) | 118.07 (5.39) |
| CRIQ | not acquired | 140.10 (16.65) |

*NAART scores were only acquired for native English speakers (19 younger adults and 20 older adults).

² Cognitive reserve refers to an individual’s resilience to brain damage (Stern, 2002). It describes the phenomenon where older adults with more cognitively stimulating environments (e.g. longer education, challenging occupation, leisure and social activities) show less age-related cognitive decline

study, we focused on the two dimensions of BIS and BAS. The BIS/BAS questionnaire was not completed by one older and two younger participants.

2.3. Stimuli and apparatus

The stimulus items for the hybrid foraging were drawn from the database of unique object images provided at <https://konklab.fas.harvard.edu> (Brady, Konkle, Alvarez, & Oliva, 2008). From the database of 2,400 objects, we selected 1,922. We removed images for different reasons. Some were primarily white or translucent and thus not very distinct from the background. A few were cut off and, thus, might look odd in a moving display. Some images included words, numbers, or arrows, landscapes or humans, or multiple objects. Some images were very similar to other included object images and, thus, confusable. Finally, we removed a few images that seemed potentially disturbing.

The experiment was programmed in Matlab Version 9.0.0 using the Psychtoolbox, Version 3.0.11 (Brainard, 1997). The stimuli were presented on a 24-in. screen with a refresh rate of 60 Hz, on an iMac, model A1225 (EMC 2211). Object images had a size of up to 75 × 75 pixels. At an average viewing distance of about 60 cm, images thus subtended approximately 1.8 × 1.8 degrees of visual angle. The mouse cursor subtended approximately 0.94 × 0.94 degrees of visual angle. Objects were continuously moving at a rate of 1.25°/s, following randomly defined trajectories, in order to discourage a reading strategy. They were repulsed by the edges and center of the display, as well as by other items, while overlap of objects was possible.

2.4. Experimental procedure

Observers performed a hybrid foraging task, in which they searched for multiple instances of multiple target objects among distractor objects (Wiegand et al., 2019; Wolfe et al., 2016, 2018). In the present task, observers completed three task blocks with varying value and prevalence of targets, as in the hybrid foraging task described by Wolfe and colleagues (2018). Fig. 1 shows an example display of one of these conditions. The order of blocks was counterbalanced across participants. In each of the three blocks, observers initially memorized four targets objects. Targets were randomly selected from the 1,922 available objects. Different targets were in the memory sets of the three blocks. In the memorization phase, each object was shown for three seconds, along with its associated point value (see the conditions described below). Afterwards, observers’ memory for the targets was tested in an old/new recognition test with four old and four new objects presented in random order one at a time. If participants made any errors, they repeated the memorization and recognition test sections.

After having passed the recognition test, observers moved on to the foraging task. They collected target objects from a succession of visual displays (patches). This visual set size was selected randomly for each patch. At the onset of each patch, it contained 60, 75, 90 or 105 objects. Of these, 20–30% were targets and the remaining 70–80% of objects were distractors. Participants collected items by clicking on them. Clicking on targets removed them from the patch and gave the participants points. Clicking on a distractor resulted in losing a point. A score report was displayed at the center of the screen in black font, which turned red when a point was lost. The task goal was to accumulate a certain number of points as quickly as possible. Importantly, participants were not required to collect every target from a patch. At any time, they could move on to a new patch by clicking a “Next” button, also located in the center of the screen. Between the patches, a 2-second “travel time” was added. Together with time required for computing stimuli and other programming overhead, the actual travel time between the last click in a patch and the onset of the next patch was 5 s on average.

Each of the experimental blocks was preceded by a short block of practice trials to make sure that the instructions were understood and to

Finally, we analyzed observers' individual choices of the targets collected in a patch to reveal target preferences that were expected to vary with the experimental manipulation. We used mixed ANOVAs, one-sample T-tests, and paired T-tests to test for differences between age groups and conditions. Whenever the data deviated from the normal distribution, we checked that non-parametric Friedman tests of differences among repeated measures produced the same results as the reported ANOVA.

We further analyzed whether individual differences in the responsiveness to the experimental manipulation were related to individual sensitivity to reward and punishment as measured by the BIS BAS scale. We ran multiple linear regressions with the experimental variable (collection of low-value, high-prevalence target) as dependent variable and BIS score and Age (in years) as predictors and with BAS score and Age as predictors.

For all analyses, we also report the Bayes factor (BF). In contrast to classic hypothesis testing based on p-values and effect sizes, the sample size is less critical to interpret the evidence for or against a given hypothesis based on a BF. Furthermore, the BF gives an estimate of how strongly the data support not only the presence of a hypothesized effect, but also how strongly a null effect is supported. BF01 was computed as evidence for H0/H1 and BF10 as evidence for H1/H0 (i.e. 1/BF01). Thus, BF01 > 1 indicates support for H0 (null model) and BF10 > 1 indicates support for the H1.

3. Results and discussion

3.1. Patch leaving and optimal foraging behavior

In a non-exhaustive foraging task, such as ours, observers are free to choose when to move on to a new patch and, thus, likely to leave targets in a patch behind. In fact, these missed targets can be regarded as strategic omissions to optimize foraging behavior. As Fig. 2 shows, the number of patches viewed within a block (upper panels) and the proportion of targets left behind per a patch (lower panels) varies between observers and between the conditions with varying target values and prevalence.

A mixed ANOVA with the factors Condition and Age on the number of visited patches revealed a main effect Condition [$F(2,86) = 45.57, p < .001, \eta^2 = 0.37, BF_{10} = 1.27e + 13$]. The main effect of Age [$F(1,43) = 0.03, p = .87, \eta^2 < 0.001, BF_{01} = 4.07$] and the Condition \times Age interaction [$F(1,43) = 0.15, p = .86, \eta^2 = 0.001, BF_{01} = 7.36$] were not significant. Observers searched through fewest patches in the condition with constant value and varying target prevalence and through most patches in the condition with both varying target value and prevalence. All post-hoc comparisons between conditions were significant [all $T(44) > 4.32, p < .001, d > 0.64, BF_{10} > 373.06$]. The mixed ANOVA on the proportion of targets left behind also revealed a significant main effect of Condition [$F(2,86) = 11.67, p < .001, \eta^2 = 0.10, BF_{10} = 1080.68$] and no main effect of Age [$F(1,43) = 0.03, p = .87, \eta^2 < 0.001, BF_{01} = 3.44$] or Age \times Condition interaction [$F(1,43) = 0.04, p = .96, \eta^2 < 0.001, BF_{01} = 8.01$]. The post-hoc comparisons showed that observers left

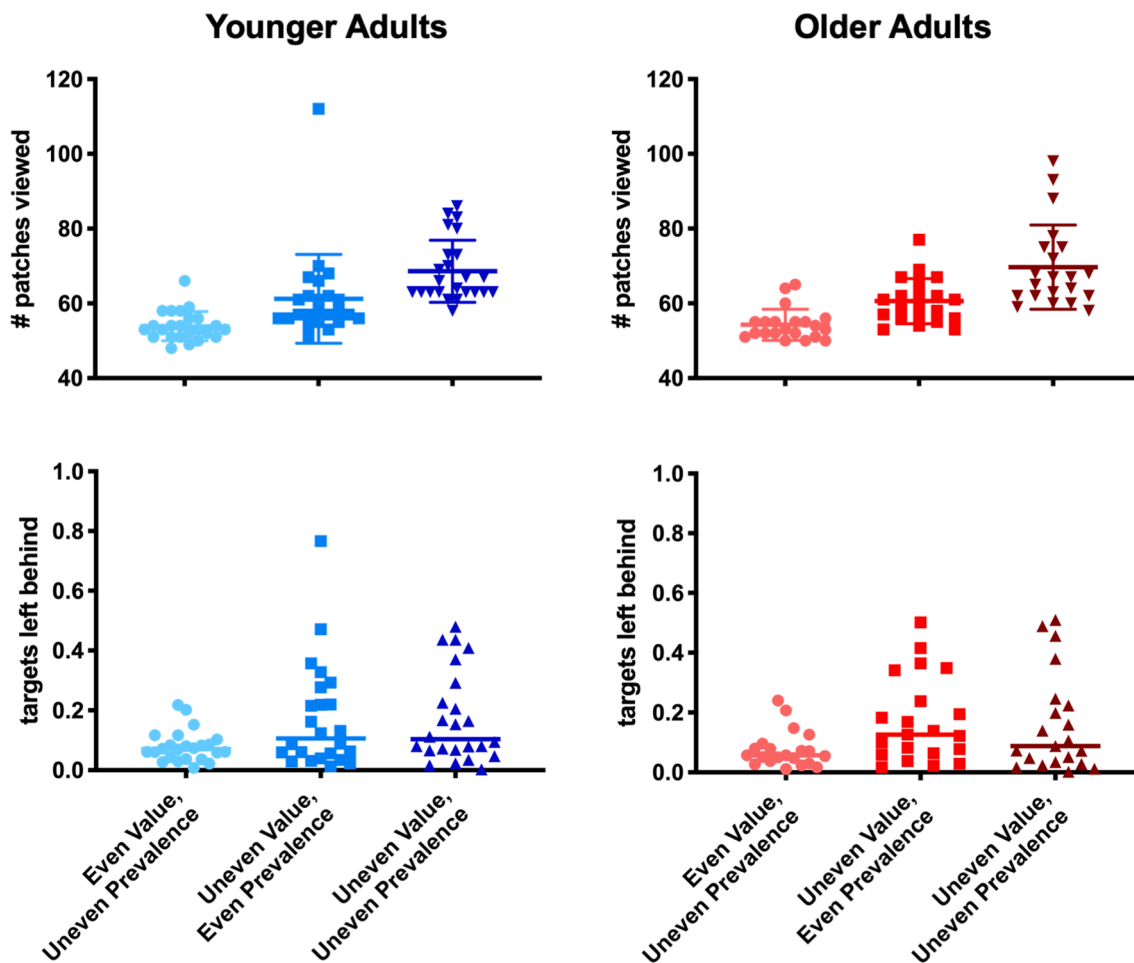


Fig. 2. Viewed patches and targets left on screen. The number of patches viewed in a block (top) and the proportion of targets left behind in a patch are shown for each condition, for younger adults (blue, left) and older adults (red, right). Each symbol denotes an individual observer. The horizontal lines indicate the mean and error bars ± 1 SD. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

more targets behind in the conditions with varying target value compared to the condition in which target value was constant [both $T(44) > 4.04$, $p < .001$, $d > 0.60$, $BF_{10} > 150.56$], while the two conditions with varying target value did not differ [$T(44) = 0.33$, $p > .99$, $d = 0.05$, $BF_{01} = 5.87$].

This pattern of results indicates that observers leave a patch more readily, thus, view more patches within a block, if the value of the target types in a patch varies and especially, if the value is inversely related to the prevalence of the target. They also leave more targets behind when the value of targets varies. When the value is the same, the choice of target is presumably shaped by the local prevalence of different target types. Observers should keep picking the most common item until it isn't the most common item. In the uneven cases, it may be tempting to move on as soon as the valuable item is depleted. Notably, we do not find any evidence for age differences in this basic patch leaving behavior across condition blocks. Thus, younger and older observers appear to adapt their patch leaving behavior similarly to the manipulation of target value and prevalence. But are they also equally efficient foragers? How do younger and older observers decide when it is better to move on to another patch?

MVT proposes that an optimal forager will leave the current patch when the rate of point collection at a given moment while foraging in a patch, called the instantaneous rate of collection, reaches or drops below the average rate for the whole block. Fig. 3 shows the average rate of collection (dashed line) and the instantaneous rates of collection for the three conditions (solid lines) as a function of reverse click position for the last 10 clicks in a patch. As noted above, Reverse click 1 is the final click in the patch before the observer clicks the “next” button and moves to the next patch. Reverse clicks 2, 3, and so on, count backward from

that final click. The instantaneous rate is computed as the reciprocal of the average RT multiplied by the probability that the item clicked is a target (i.e., $1 - \text{false alarm rate}$) multiplied by the point value of this target. The average rate of collection is the total number of points in a block divided by the total time spent to complete the block (the sum of time in each patch plus the travel time between the patches). Note that, in order to make the conditions comparable in terms of collected targets per time, we have rescaled the data in the Uneven Value, Even Prevalence condition. The expected point value in this condition is 7.5 points $[(2 + 4 + 8 + 16)/4]$, while the expected point value in the conditions Even Value, Uneven Prevalence and Uneven Value, Uneven Prevalence is only 4 points. Without rescaling, both the average and instantaneous rate in the Uneven Value, Even Prevalence condition would be higher. From Fig. 3, prominent age group differences in the rates of collection are visible; rates are overall higher in younger adults than in older adults. As a consequence of age-related RT slowing, older adults need more time per selection and, thus, need more time to collect the same number of targets as younger adults. On average, younger adults need $0.9 (\pm 0.8)$ seconds per collection and older adults need $1.7 (\pm 2.1)$ seconds per collection. Accordingly, a mixed ANOVA on the average rate of collection with the factors Condition and Age revealed a significant effect of Age [$F(1,43) = 128.90$, $p < .001$, $\eta^2 = 0.68$, $BF_{10} = 3.66e + 11$]. The main effect of Condition and the Age \times Condition interaction were not significant [both $F(2,86) < 2.55$, $p > .08$, $\eta^2 < 0.006$, $BF_{01} > 1.65$]. Thus, while older adults collected targets overall at a lower rate than younger adults, in neither age groups, the manipulation of target value and prevalence affected the average rate of collection.

Fig. 3 shows that the instantaneous rate falls with continuing clicks in the patch as targets become depleted. This is visible for all three

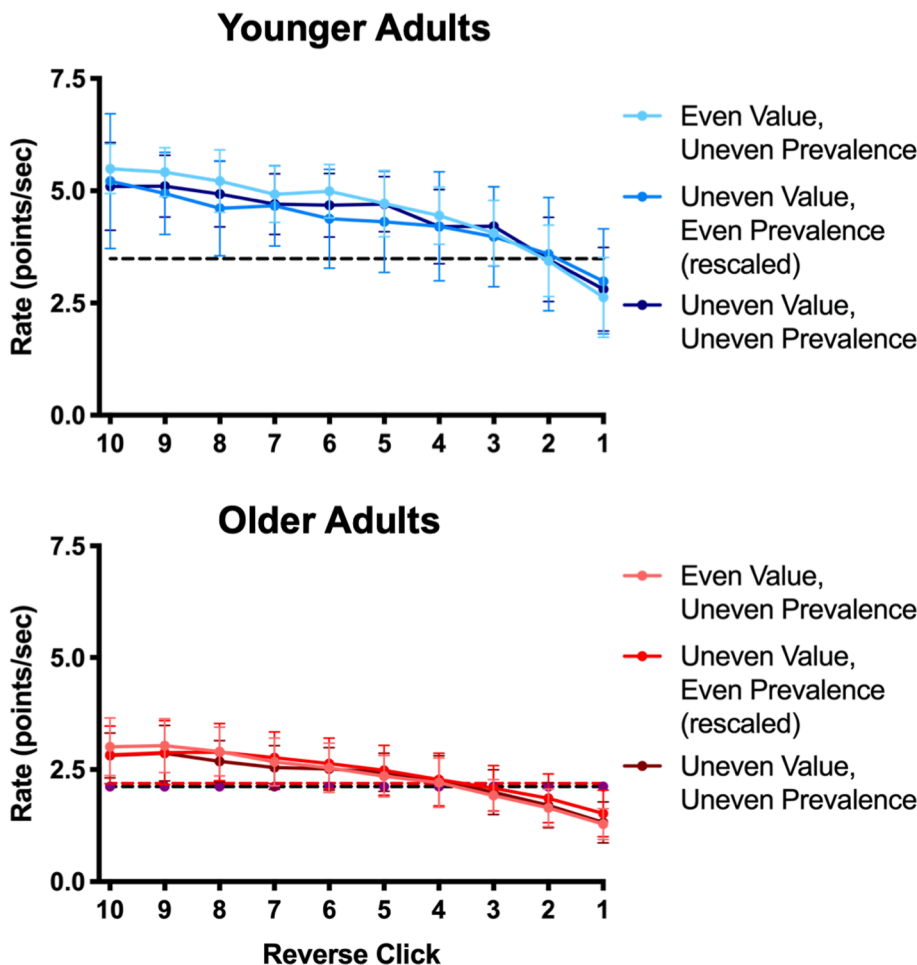


Fig. 3. Rates of collection. The instantaneous rates of collection (solid lines) of the last 10 clicks in a patch and average rate of collection (dashed lines) are plotted for each condition for younger adults (blue, top) and older adults (red, bottom). Note that the expected point value in the Uneven Value, Even Prevalence condition is 7.5 points and the expected point value in the conditions Even Value, Uneven Prevalence and Uneven Value, Uneven Prevalence is 4 points. We have rescaled the average rate and the instantaneous rate of collection in the Uneven Value, Even Prevalence condition to make the conditions comparable in terms of the rate of collection per time. Each point indicates the mean and error bars ± 1 SEM. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

conditions and both age groups. Another aspect, which is more important with regard to understanding age differences in foraging, is also visible in Fig. 3. Younger adults leave the patch right after their instantaneous rate of collection falls below their average rate of collection. This behavior is in line with predictions of optimal foraging according to MVT. Older adults, by contrast, stay for another 2–3 clicks. On average, they leave the patch only when the instantaneous rate of collection has fallen well below their average rate of collection. According to MVT, they leave the patch too late. This makes them less efficient foragers in terms of collecting points per time. Notably, the optimal point of leaving – that is, the deviation of the instantaneous rate of collection at the final click from the average rate of collection – is independent from an observer’s overall RT and thus not affected by general age-related slowing.

Fig. 4 visualizes these age differences in foraging behavior. For each of the conditions, the instantaneous rate of collection of the last three clicks in a patch is plotted against the average rate of collections. If behavior followed MVT, only the instantaneous rate of collection in the last click in a patch should be below the average rate. This is what we see, on average, in younger adults. In older adults, the instantaneous

rate of collection in the last three clicks in a patch is below the average rate. We tested this statistically by comparing the instantaneous rates of collection at reverse clicks 3–1 with the average rate of collections in each age group and each condition. In younger adults, the instantaneous rate of collection at reverse click 3 was significantly above the average rate, in all conditions [all $T(23) > 2.98$, $p < .008$, $d > 0.60$, $BF_{10} > 6.77$]. The instantaneous rate of collection at reverse click 2 did not differ from the average rate of collection, in none of the conditions [all $T(23) < 1.25$, $p > .22$, $d < 0.25$, $BF_{01} > 2.34$]. The instantaneous rate of collection at reverse click 1 was significantly below the average rate, in all conditions [all $T(23) > 4.83$, $p < .001$, $d > 0.99$, $BF_{10} > 374.25$]. In older adults, the instantaneous rate of collection was significantly below the average rate, in all conditions, at reverse click 3 [all $T(20) > 3.12$, $p < .006$, $d > 0.68$, $BF_{10} > 8.64$], at reverse click 2 [all $T(20) > 7.51$, $p < .001$, $d > 1.66$, $BF_{10} > 54074.59$], and at reverse click 1 [all $T(20) > 11.87$, $p < .001$, $d > 2.59$, $BF_{10} > 5.87e + 7$].

These results replicate our previous findings in a hybrid foraging task in which target value and prevalence were both constant (Wiegand et al., 2019). Older adults foraging is less optimal than that of younger adults, because they leave the patch too late. They show a strategic shift

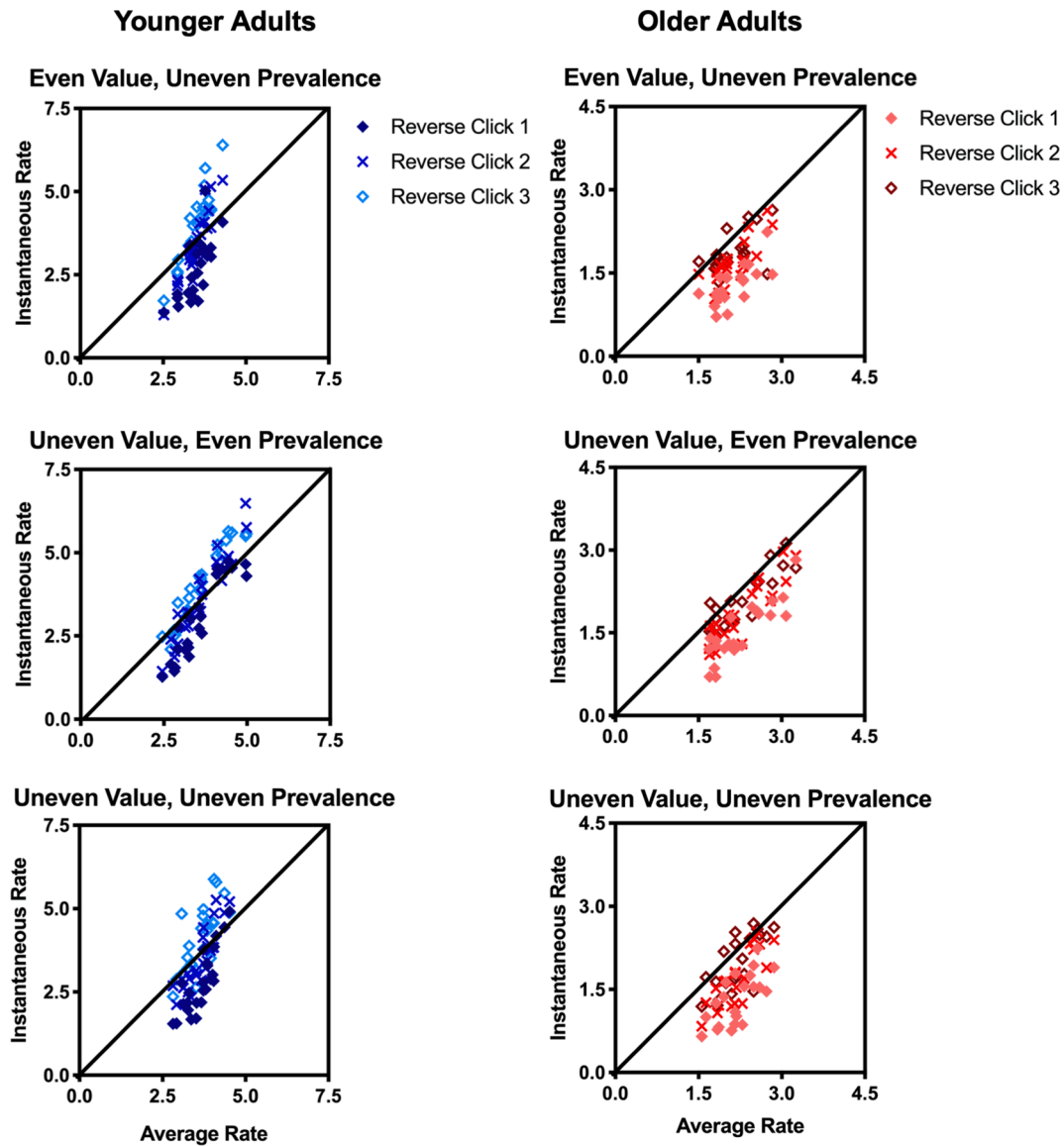


Fig. 4. Individual rates of collection. The plots show the instantaneous rate of collection for reverse click 3–1 plotted against the average rate of collection for every observer in each of the conditions, for younger adults (blue, left) and older adults (red, right). The diagonal line indicates equality between the instantaneous rate and average rate. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

towards more exploitative, or conservative, behavior, spending too much time on searching left-over targets in the patch before they move on. The criterion for patch-leaving, and age differences therein, did not differ between blocks of varying target value and prevalence. Observers left more targets behind and left a patch earlier, when the target value varied. This implies that observers followed a similar strategy according to MVT, adapting their rate of collections within the patches to the average rate of collection across all patches in a block. Note that in the computation of the rates of collections, the type of target selections is not specified. An observer who slowly collects highly-valued but rare, hard-to-find, targets, may have the same rate of collecting points as an observer who quickly picks prevalent target types of a lower value. Thus, different strategies to respond to target value and prevalence can be equally efficient in terms of MVT. In a next step, we therefore looked at how varying target value and prevalence affect which target types are picked within a patch, in younger and older observers.

3.2. What do foragers pick in a patch?

On average, observers collected 17.5 targets per patch. The number of collected targets did not differ between younger and older adults [$T(45) = 0.03, p = .98, d = 0.01, BF_{10} = 3.38$]. Note that, mirroring the different proportions of targets left behind reported above, observers of both age groups picked a few more targets, 19 on average, in the condition with constant value and varying prevalence than in the conditions with varying target values, where they picked 17 targets on average [both $T(44) > 4.14, p < .001, d > 0.61, BF_{10} > 162.88$]. How were those selections distributed among the four target types in a patch?

Fig. 5 shows the percentage of target selections (solid lines) and the percentage of targets on the screen (dotted lines) for each of the four target types as a function of forward click in a patch, from the first click

to the 15th click in the patch, averaged across younger and older observers. It is clear from the plots that observers do not pick target types randomly. If they did, the percentage of picked targets would mirror the actual percentage of available target types in the display, which is clearly not the case. For example, in the second row of the figure, the dark solid lines show that valuable targets are initially picked at a much higher rate than their presence in the display. In general, some targets are “overpicked” while other target types are “underpicked”. Overpicking is shown when the curve showing the percentage of target selections lies above the curve showing the actual prevalence of this target type and vice versa for underpicking. Which target type is preferentially picked appears to depend on both the target value and the target prevalence: In the *Even Value, Uneven Prevalence* condition, observers overpick the most common target type and underpick the rare target types. In the *Uneven Value, Even Prevalence* condition, observers respond to the value manipulation by overpicking the most valuable target type and underpicking the least valued target types. In the *Uneven Value, Uneven Prevalence* condition, observers again overpick the targets with high value and underpick the targets with low value. Comparing the two age groups visually, the effects of varying value and/or prevalence on target selections look remarkably similar in younger and older adults.

We investigated the pattern of target type collections statistically by averaging each observer’s data over the first five target selections in a patch (Forward click 1–5). We chose the first five clicks because the initial clicks reflect selection preferences most clearly and are not markedly affected by the change in overall target prevalence as collection continues (Wolfe et al., 2018). After all, you cannot continue to overpick valuable items if you have already collected all the valuable items. Individual observer data for the first five target selections are shown in Fig. 6. A mixed $3 \times 4 \times 2$ ANOVA with the factors Condition, Target Type, and Age, on the percentages of the first five selections,

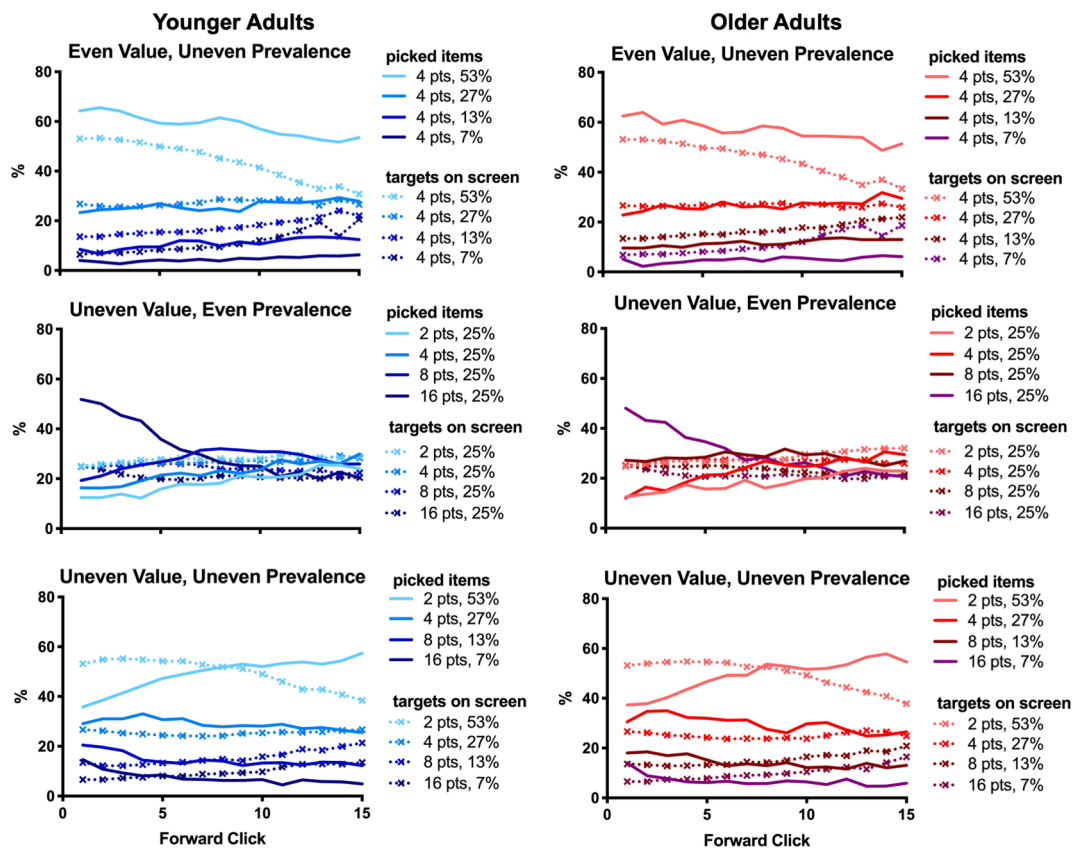


Fig. 5. Target types within a patch. The percentage of the target types selected (solid line) and target types on screen (dotted line) as a function of clicks in the patch. Shown is the average across observers and patches in each condition for the groups of younger and older adults. Note that the total number of clicks varies between patches and observers and therefore, especially at higher numbers of forward clicks, some observers may contribute to individual data points more than others.

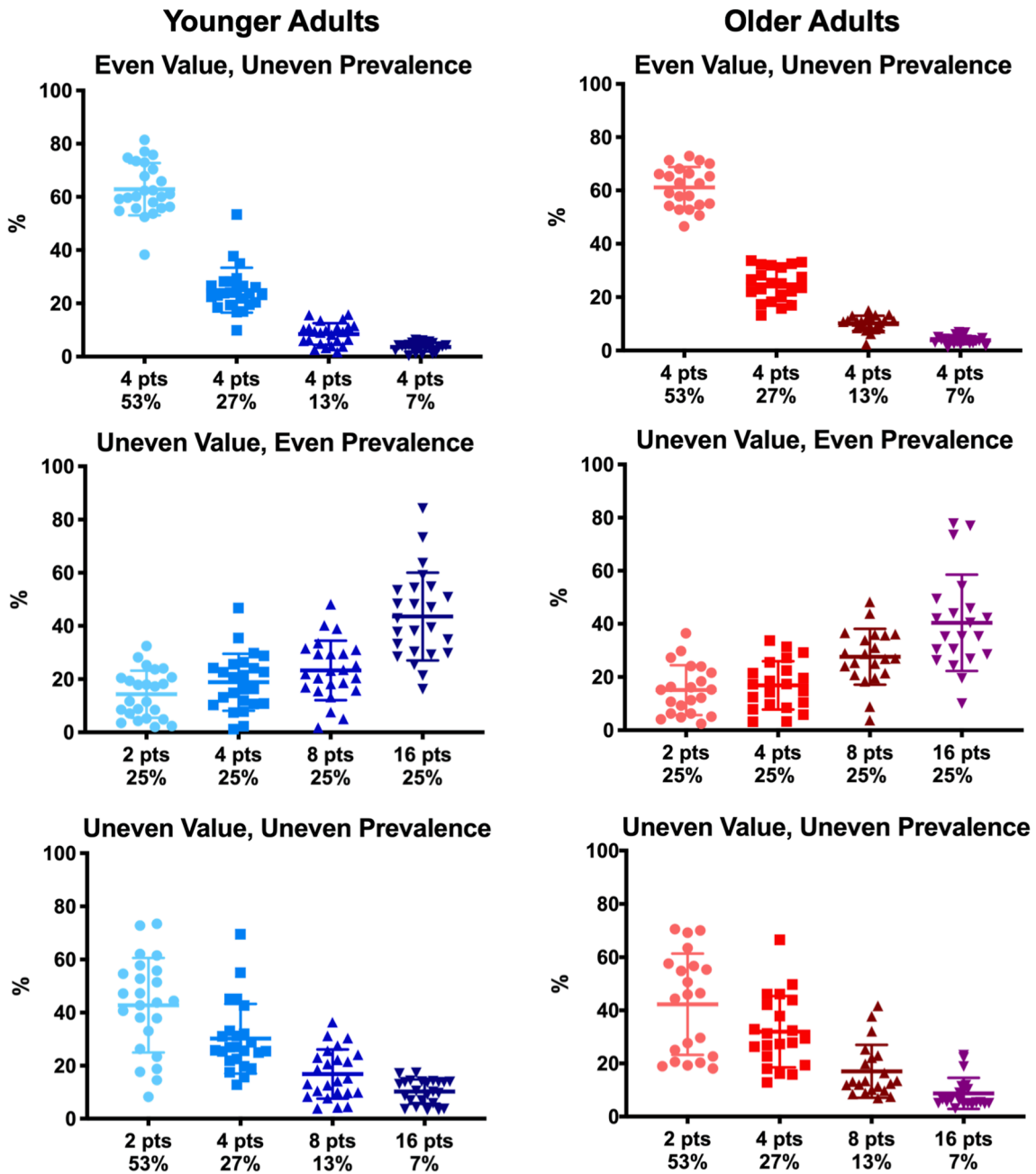


Fig. 6. Individual target type selections. Percentage of target selections in the first five clicks in a patch is plotted for each target type, condition, and age group. Each symbol denotes an individual observer. The horizontal lines indicate the mean and error bars ± 1 SD.

unsurprisingly, revealed a significant main effect of Target Type [$F(3,86) = 72.62, p < .001, \eta^2 = 0.21, BF_{10} = 7.27e + 23$] and a Target Type \times Condition interaction [$F(6,258) = 117.95, p < .001, \eta^2 = 0.49, BF_{10} = 2.04e + 103$]. Noteworthy, the main effect of Age and the interactions involving Age were not significant [all $F < 2.22, p > .14, \eta^2 < 0.002, BF_{10} > 8.28$]. This supports the observation that younger and older adults did not differ in the selections of target types in either of the conditions. This was confirmed by post-hoc independent t -test, which did not reveal significant age group differences in any of the conditions for any the target type (even before Bonferroni correction) [all $t < 1.61, p > .10, d < 0.49, BF_{10} < 0.84$].

Next, we used one-sample t -Tests to test whether the percentage of selections deviated from the percentage on the screen for a particular target type in each condition, i.e. were over- or underpicked. We tested across the entire sample group, as the initial ANOVA did not reveal any

age differences. The t -tests confirmed that in the *Even Value, Uneven Prevalence* condition, the most prevalent target was overpicked [62% vs. 53%; $T(44) = 6.87, p < .001, d = 1.02, BF_{10} = 739248.34$] and the two less frequent target types were underpicked [9% vs. 13%, $T(44) = 6.94, p < .001, d = 1.04, BF_{10} = 931386.46$; 4% vs. 7%, $T(44) = 13.59, p < .001, d = 2.03, BF_{10} = 2.40e + 14$]. This result reflects the pure effect of prevalence on target selections in hybrid foraging. The most prevalent target is, first, found more easily and picked more often by chance. Once the target type is picked, the chance of picking more items of this same target type is further increased. This was attributed to priming effects, which prompt observers to collect the same target types in “runs” (Kristjánsson et al., 2014, 2020; Wolfe et al., 2016). This “run” behavior has been observed in both younger and older adults (Wiegand et al., 2019). The individual data points, plotted in Fig. 6 show that the effect of prevalence is very consistent across individuals within and across age

groups.

In the *Uneven Value, Even Prevalence* condition, the most valued item was overpicked [42% vs. 25%, $T(44) = 6.43$, $p < .001$, $d = 0.96$, $BF_{10} = 9.24e + 6$] and the two lower valued items were underpicked [18% and 14% vs. 25%, both $T(44) > 4.83$, $p < .001$, $d > 0.72$, $BF_{10} > 1244.56$]. Here, with balanced frequencies of the four target types, we see the pure effect of target value on the choice of selections. On average, observers show a clear tendency to pick highly valued targets first. However, Fig. 6 also shows that the influence of value on target selections appears to vary more between individuals than the prevalence effect described above. Some individuals showed a stronger preference for highly-valued items than others. This inter-individual variability in overpicking the most-valued target type is observable in both age groups.

In the *Uneven Value, Uneven Prevalence* condition, the two most valued, but less prevalent targets were overpicked [17% vs. 13%, $T(44) = 2.77$, $p = .008$, $d = 0.41$, $BF_{10} = 4.68$; 10% vs. 7%, $T(44) = 3.26$, $p = .002$, $d = 0.49$, $BF_{10} = 14.75$]. The low-value, high-prevalence target was, on average, underpicked [42% vs. 53%, $T(44) = 3.86$, $p < .001$, $d = 0.58$, $BF_{10} = 71.90$]. The second-most prevalent and second-least valued target type was slightly overpicked [31% vs. 27%], however, not significantly after the Bonferroni correction and evidence from the Bayesian analysis was equivocal [$T(44) = 2.05$, $p = .05$, $d = 0.31$, $BF_{10} = 1.08$]. This condition reflects the interaction of effects of target value and prevalence on target selections. Here, on average, observers have a preference for the highly-valued target types, however, the more prevalent target types of lower value are still selected most. Also in this condition, we see considerable variability between observers, particularly in the selections of the most frequent but low-valued target type. Some observers might have been driven more by the prevalence effect in this condition, showing overpicking of the most frequent target type, despite the low gain. Others, however, were driven more by the value of target types and picked only very few of these ‘cheap’ targets. Again, the variability between individuals is of comparable size across the two age groups, suggesting no age-specific trend towards the one or the other selection strategy.

3.3. Individual differences in value- and prevalence-driven foraging behavior

The analyses of selections per target type across conditions revealed that individuals of both age groups very consistently collected the most prevalent target when all targets were of similar value. However, individuals differed quite substantially when the target values varied, and particularly when target value was inversely related to prevalence. Individual variability in the hybrid foraging task in response to the manipulation of value and prevalence was previously reported in a sample of younger adults (Wolfe et al., 2018). In this study, we wanted to explore potential sources of these individual differences further. Specifically, we tested whether target selections in the condition with both varying value and prevalence were related to individuals’ activation level of the behavioral inhibition and behavioral approach systems, as assessed by the BIS and BAS scores, respectively (Carver & White, 1994).

Younger adults scored higher than older adults on both the BIS and the BAS scale. The average scores of each age group and statistical age comparisons for the BIS and the BAS scales are shown in Table 3. The relative variability was comparable across groups, indicated by similar coefficients of variation for younger and older adults (BAS-scores: $YA_{CV} = 0.10$, $OA_{CV} = 0.09$; BIS-scores: $YA_{CV} = 0.14$, $OA_{CV} = 0.18$). To test for any relationship between BIS and BAS scores and individual foraging behavior, and potential age differences in this relationship, we conducted two moderated multiple linear regression analyses. As the independent variable, we chose the variable of foraging behavior that revealed marked individual differences in target selection choices. This was the proportion of selections of the most prevalent low-valued targets in the first five clicks in the *Uneven Value, Uneven Prevalence* condition

Table 3

BIS/BAS Scores. The average scores and standard deviations (in parentheses) of the BIS and BAS scales, and the BAS subscales, are shown for the groups of younger and older adults. Age groups’ scores were statistically compared with independent t-tests.

| | Younger Adults (n = 22) | Older Adults (n = 20) | T-test |
|-----|-------------------------|-----------------------|------------------------------------------------------------|
| BIS | 21.82 (3.05) | 19.75 (3.51) | $T(40) = 2.04$, $p = .05$, $d = 0.63$, $BF_{10} = 1.55$ |
| BAS | 42.45 (4.36) | 39.85 (3.48) | $T(40) = 2.12$, $p = .04$, $d = 0.66$, $BF_{10} = 1.76$ |

(Fig. 6, bottom panels). The scatter plots in Fig. 7 shows the relationship between BIS Scores and the proportion of target selections and BAS scores and the proportion of target selections, for the two age groups.

In the first multiple regression analyses, we inserted individual BIS scores as predictor of low-value/highly-prevalent target selections and age (in years) as a possible moderator. The regression equation with an $R^2 = 0.05$ was not significant [$F(3,38)$, $p = .59$, $BF_{01} = 7.59$]. As also visible from Fig. 7, BIS scores did not predict which target was picked [$T(39) = 1.37$, $p = .18$, $BF_{01} = 2.46$], and age did not moderate the effect [$T(39) = 1.10$, $p = .28$, $BF = 1.31$]. Thus, we find no indication of a relationship between the activation of the behavioral inhibition system and individual differences in the selection of targets. In the second regression analysis, we inserted individual BAS scores as predictor of target selections and age (in years) as a possible moderator. The regression equation, with an $R^2 = 0.15$, did not reach significance [$F(3,38) = 2.23$, $p = .10$, $BF_{10} = 0.66$]. The BAS score, however, predicted which target was picked significantly [$T(39) = 2.59$, $p = .01$], though the Bayes factor was equivocal [$BF_{10} = 0.48$]. The moderation effect (Age \times BAS interaction) was significant [$T(39) = 2.27$, $p = .03$] and supported by the Bayes factor [$BF_{10} = 3.02$]. To resolve the moderating effect, we conducted simple linear regressions with the BAS score as a single predictor of target selections for each age group separately. In younger adults, the regression equation was significant [$R^2 = 0.23$, $F(1,20) = 5.91$, $p = .025$, $BF_{10} = 2.71$]. Younger individuals who scored lower on the BAS scale were more likely to pick frequent, low-value targets than individuals with higher BAS scores. This is in accordance with our assumption that individuals with lower activity in the behavioral approach system, who are less responsive to reward and less impulsive, are more likely to pick targets of high prevalence despite their lower value. In older adults, the regression equation was not significant [$R^2 = 0.04$, $F(1,19) = 0.75$, $p = .40$, $BF_{01} = 1.93$], suggesting no systematic relationship between BAS activity and foraging behavior in the older age group.

4. General discussion

4.1. No adult age differences in the effects of target value and prevalence on hybrid foraging

As expected and in line with previous results (Wiegand et al., 2019), younger adults were more efficient foragers than older adults according to optimal foraging theory in terms of maximizing output per time (Charnov, 1976). We assume that this reflects age-related changes in balancing the exploration–exploitation trade-off (Chin, Anderson, & Chin, 2015; Mata, Wilke, & Czienskowski, 2013). Older observers appear to adopt a more conservative criterion to not “waste” targets. They tend to exploit the patch and spend time on searching the hard-to-find left-over targets instead of moving on to a new patch. This strategy is suboptimal if the goal is to maximize the rate of picking over time (see also Wiegand et al., 2019, for a detailed discussion of this effect). Notably, older adults are less efficient foragers than younger adults due to a strategic differences but not due to declined attention and/or memory functions (Wiegand et al., 2019). Whether these strategic age differences reflect actual change caused by the aging process or reflect

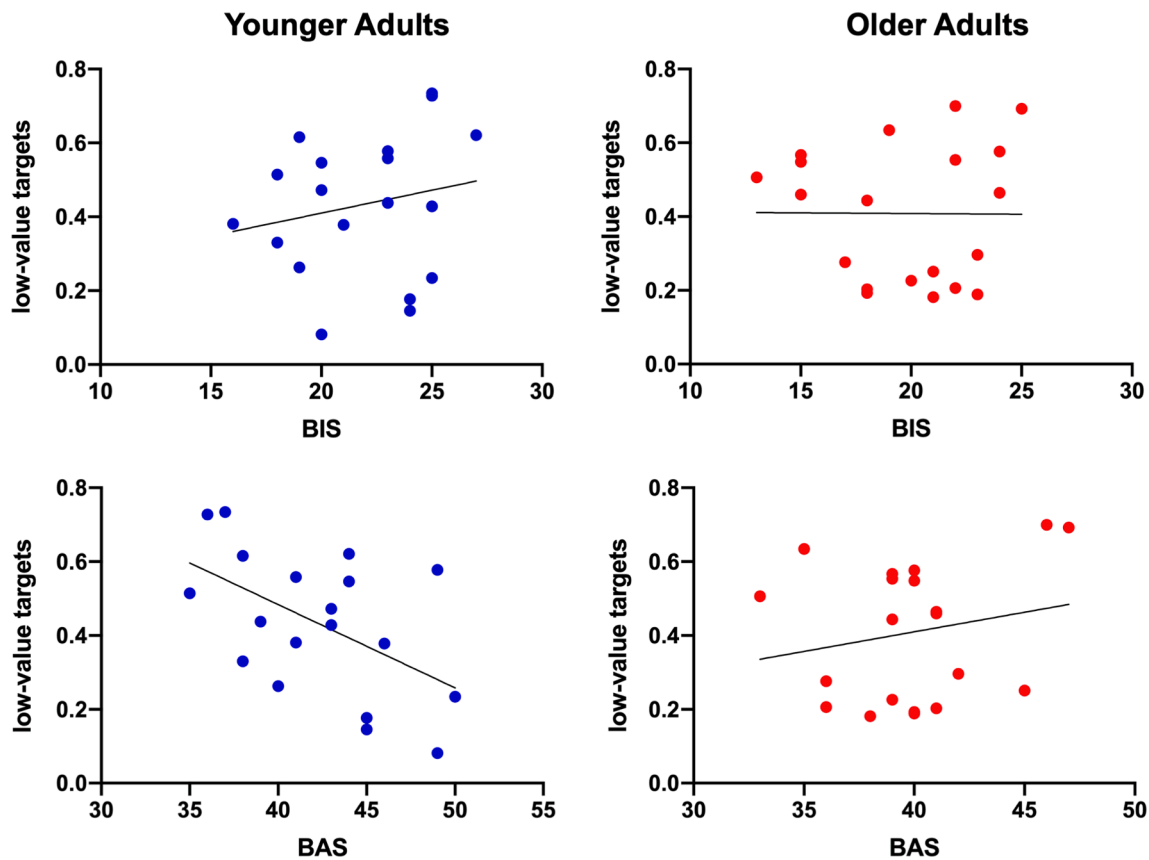


Fig. 7. BIS/BAS scores and target selections. The BIS and BAS scores are plotted against the proportion of selections of the target type with low value and high prevalence in the condition with inversely related target value and prevalence for younger adults (left, blue) and older adults (right, red). BIS scores are shown at the top and BAS scores are shown at the bottom. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

cohort effects cannot be clarified in a cross-sectional study as ours.

The age differences were prominent across the experimental conditions. Younger adults largely followed the optimality criterion according to MVT predictions also when target value and prevalence varied. This implies that observers adapted their foraging strategy quite well to the properties of the visual environment manipulated in our task.

In addition, as we anticipated, older adults change their selection preferences in foraging behavior according to the prevalence of targets. Similar to younger adults, when value was balanced, older adults consistently overpicked the most prevalent target type. We attribute this effect to preserved priming effects on visual search in older age (Madden, 2007; Madden, Whiting, Spaniol, & Bucur, 2005; Madden, Whiting, Spaniol, & Bucur, 2005; McCarley et al., 2004; Wiegand et al., 2013), which induced both older and younger observers to search in “runs” in a foraging task with multiple target types (Wiegand et al., 2019). Contrary to our hypothesis, however, we found no evidence for age differences in the effects of target value on foraging behavior. On average, the tendency to overpick highly-valued target types was as pronounced in older adults as in younger adults. Also comparable to the younger observers, we found larger interindividual variability in value-driven selections compared to the very consistent effects of prevalence on target selections also in the older observers (for a further discussion on individual differences, see below).

This finding is inconsistent with previous reports of reduced reward-sensitivity in older age (Eppinger, Kray, Mock, & Mecklinger, 2008; Eppinger, Nystrom, & Cohen, 2012; Hämmerer, Li, Müller, & Lindenberger, 2011; Störmer et al., 2014), including one study on visual search (Störmer et al., 2014). In the latter, the relative RT difference between trials with targets of high- vs. low reward-value was found to be smaller in older compared to younger adults. There are a number of differences

between the designs of the visual search tasks employed by Störmer et al. (2014) and the present hybrid foraging task that could explain the discrepancy of results. First, observers in Störmer et al.’s (2014) study performed a speeded single-target T-among-Ls search task, with RT being the main variable of interest. Reward values were associated with target colors and observers were not informed about the color-value association before the search task. Older adults generally process information and learn associations slower (Salthouse, 1996), which may have contributed to the reduced target-value effect on visual search in the older group. In the hybrid foraging task, by contrast, we focused on choices, rather than speed, of selections and the target-value association was learned prior to the search task. This may have encouraged value-based selections in older adults. Nevertheless, it is noteworthy that the RT effect of reward-value on target selections in the study by Störmer et al. (2014) was reduced, but not disrupted in older adults. Thus, that study also supports the conclusion that an influence of target-value on visual attention is preserved across the adult lifespan.

The learning requirements of the task constitute another task-related factor that was proposed to explain age differences in reward-value processing (Mata, Josef, Samanez-Larkin, & Herwig, 2011). Previous studies showed pronounced age differences mostly in the context of goal-directed reinforcement learning and decision making tasks. There was an impaired ability to learn stimulus-reward associations from performance feedback in older age (Eppinger et al., 2008; Eppinger, Heekeren, & Li, 2015; Hämmerer et al., 2011; Weiler et al., 2008). Stimulus-reward associations were often probabilistic, making learning even more difficult (Simon, Howard, & Howard, 2010). Different to such feedback-based learning paradigms, in the present task, the target-value associations were well learned before the onset of the search task and fully deterministic. Good recognition memory performance across age

groups indicates that the value information was indeed available to all observers during the foraging task. Thus, in the absence of an age-related learning deficit, we demonstrate similar sensitivity to the variation in target values in both age groups. This is in accordance with previously reported age-invariant reward-value effects on memory. Both younger and older adults are able to selectively retrieve highly-valued items and show better recognition memory for high vs. low-value items (Mather & Schoeke, 2011; Spaniol, Schain, & Bowen, 2014). Furthermore, high-value items are better recalled than their low-value counterparts (Castel, 2007), a phenomenon referred to as value-directed encoding (Castel, Benjamin, Craik, & Watkins, 2002). On a more general level, our finding supports the assumptions that older adults are as adaptive in adapting their strategy to environmental conditions and internal goals as long as the cognitive demands of the task are well manageable (Mata et al., 2007). In the realm of foraging task, it would be interesting to test whether age differences occur when other environmental factors are manipulated, for example, the spatial and/or temporal distribution of targets within and across patches (Wilke et al., 2018).

4.2. Individual differences in value-driven foraging

Replicating the findings of Wolfe et al. (2018), we found that target value and prevalence shaped behavior in the hybrid foraging task. With constant value and varying prevalence, observers preferred the most common item very consistently. This supports prior findings that show target selections to be strongly driven by priming through previous selections (Kristjánsson et al., 2014; Wolfe et al., 2019). Varying the value of target types increased the selection of the higher-valued targets.

This behavior is ecologically plausible and in line with optimal foraging according to foraging models that make predictions about how observers maximize input on the level of individual choices (MacArthur & Pianka, 1966). When value is balanced, observers preferentially pick prevalent targets. Finding the prevalent item is easier (i.e. faster). Thus, starting with the most prevalent item provides the best payoff in terms of expected gain per search time by decreasing the time spent in searching an item. When different targets have the same prevalence but different values, picking the high-value targets first provides the best payoff by increasing the gain per selected item. In line with the diet-breadth model, the most profitable target is pursued, as long as there is a sufficient encounter rate with this target within the local environment. However, in our data, the preference for high-value targets was less consistent across individuals. This was especially true when value was inversely related to prevalence. In this condition, the encounter rate and thus, expected search time, play off against the expected gain, complicating the forager's decision. Apparently, the subjectively estimated tradeoff between search effort and point value varies over individuals (Wolfe et al., 2018). Some foragers are strongly attracted by reward value and, thus, inclined to pick the most valuable targets first. For others, value is a weaker force of driving behavior. Targets associated with high reward might still be preferred, however, particularly when those targets are difficult to reach, observers may be more likely to select highly prevalent and primed targets with lower-value instead. Adding to the previous study, we show that these individual differences in target type selections are related to a trait index of reward sensitivity derived from the BIS/BAS scale. Individuals with high BAS scores, related to impulsive, novelty- and reward-seeking behavior, were less likely to pick highly-prevalent targets of low-value than individuals with lower BAS scores. This finding provides further evidence for an influence of personality traits on perceptual and attentional processes (Hickey et al., 2010b; Hickey & Peelen, 2015) and demonstrates its' relevance for behavior in a rather complex search tasks akin to real-world visual searches.

After validating the relationship between BAS scores and selections in a foraging task in a larger healthy sample group, it would be interesting to test the association between personality traits and foraging

behavior also in clinical samples. Substantial differences in the responsiveness to reward manipulations in attentional tasks have previously been observed in clinical groups. Individuals with depressive symptoms show reduced responsiveness to reward (Anderson et al., 2017), while individuals with addiction disorders show an enhanced reward-related selection bias (Anderson et al., 2013), compared to healthy control participants. The hybrid foraging task - which is sensitive enough to detect individual differences even within a healthy sample - might be well suited to detect also subtle trends in personality and pathological traits that shape behavior in important real-world cognitive tasks.

Notably, BAS scores correlated with individual selection choices in the foraging task rather than patch-leaving decisions according to MVT. Whether individual and age differences in patch-leaving criteria are also related to other personality aspects would be another interesting question to explore.

Other than for the BAS scores, we found no relationship between individual BIS scores and target selections. Activity of the BIS is related to anxiety and behavioral inhibition to avoid negative outcomes. None of the possible target selections in the present task was associated with a loss. With each target selection, something would be gained, just the amount of gain differed between the target types. There was a small "punishment" for clicking on distractor items; however, this happened rarely and, importantly, did not differ between the conditions with varying target value and prevalence. Thus, there was no need to avoid losses or inhibit actions to prevent negative consequences. This could explain why individual differences in BIS activity were irrelevant in the present foraging task. In a different foraging task with a task manipulation that involves positive and negative valences, BIS activity might well influence which foraging strategy is adopted. That would be an interesting future experiment, which could further be applied to test the impact of high vs. low trait anxiety on visual foraging.

We observed the relationship between individual BAS scores and responsiveness to the value manipulation in the foraging task only in the younger, but not in the older, sample group. Overall, older adults had lower BIS scores and BAS scores than younger adults, which is accordance with previous reports from larger-sample studies (Jorm et al., 1998; Müller et al., 2013). This finding indicates that the responsiveness of both systems is reduced in older age. It implies that both approaching behavior to seek rewards and inhibiting behavior to avoid negative consequences are less pronounced in older age. Reduced activity in the BIS and BAS could result from age-related changes in the physiology of the autonomic nervous system and the brain mechanisms regulating arousal in general (Lau, Edelstein, & Larkin, 2001; Lee, et al., 2018; Robertson, 2014; Wiegand, Petersen, Bundesen, & Habekost, 2017; Wiegand & Sander, 2019; Williams et al., 2016). Correspondingly, changes in arousal have been proposed to affect the influence of value and reward on cognitive selectivity in older adults (Swirsky & Spaniol, 2019; Williams, Biel, Dyson, & Spaniol, 2017). Furthermore, response patterns in questionnaires, particularly those including complex and situational item types, have been suggested to be affected by age-related cohort effects unrelated to age-dependent changes in personality or arousal per se (Hofer, Flaherty, & Hoffman, 2006; Olaru, Schroeders, Wilhelm, & Ostendorf, 2019). For example, survey-responses might be biased by age group differences in the vocabulary used or social desirability (Dijkstra, Smit, & Comijs, 2001). These non-specific effects of aging on the BIS and BAS scores, which presumably vary between individuals, too, may have disrupted the relationship between individual BAS scores and target selections in the older age group.

4.3. Limitations

The primary limitation of this study may be its use of targets that are roughly evenly distributed in the foraging space. Unless you are a sheep, grazing in a uniform meadow, resources are usually arranged in a more patchy manner. Moreover, as Wilke and Todd (2010) suggest, our foraging behaviors may have been shaped by an evolutionary history

that involved hunting for the right clumps of targets. The result could be that the behaviors, seen in uniform fields, are not optimal because observers are behaving as if there were patches. This would be an interesting direction for future research.

4.4. Conclusions

We demonstrate that older adults are less efficient foragers than younger adults, however, the responsiveness to varying target-value and prevalence, was strikingly similar across age groups. We assume that task dependent factors determine whether age differences in value processing alter performance. Specifically, in previous work, difficulties in learning the association between visual stimuli and reward-values may have caused reduced reward effects in older age, rather than a reduced impact of reward on visual processing per se. The absence of age differences in the effects of target value and prevalence in the present hybrid foraging task add to our accumulating evidence of preserved attention and memory processes in perceptually and conceptually rich, engaging search tasks that resemble real-world searches (Wiegand & Wolfe, 2020; Wiegand et al., 2019). Age-related impairments may occur also in hybrid foraging, if the search task taps into other age-sensitive cognitive processes, like incidental associative learning (Wiegand, Westenberg, & Wolfe, in press). In younger adults only, individual differences in adapting foraging behavior according to the target-value and -prevalence were related to a personality index linked to reward-seeking behavior. This demonstrates an association between personality traits and visual foraging behavior, at least in younger age.

5. Data statement

The study was pre-registered at the Open Science Framework: <https://osf.io/qcjkj>. The experimental data and sample information are available at <https://osf.io/c8jv2/> (DOI 10.17605/OSF.IO/C8JV2).

CRedit authorship contribution statement

Iris Wiegand: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Funding acquisition, Project administration. **Jeremy M. Wolfe:** Conceptualization, Methodology, Writing - review & editing, Resources, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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