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Article (Accepted Version)

Williams, Ryan S, Biel, Anna Lena, Dyson, Benjamin J and Spaniol, Julia (2017) Age differences in gain- and loss-motivated attention. Brain and Cognition, 111. pp. 171-181. ISSN 0278-2626

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Age differences in gain- and loss-motivated attention

Ryan S. Williams[a1], Anna Lena Biel[a2], Benjamin J. Dyson[a3], & Julia Spaniol[a]

[a]Ryerson University,

350 Victoria St, Toronto, ON M5B 2K3, Canada

Corresponding Author: Julia Spaniol

Telephone: (001) 416-979-5000 x2268

E-mail: jspaniol@psych.ryerson.ca

[1] Present Address: University of Toronto, Toronto ON M5S 3G3, Canada
[2] Present Address: Ludwig-Maximilians-Universität, Professor-Huber Square 2, 80539 Munich, Germany
[3] Present Address: University of Sussex, Brighton BN1 9RH, United Kingdom

Abstract

Adaptive gain theory (Aston-Jones & Cohen, 2005) suggests that the phasic release of norepinephrine (NE) to cortical areas reflects changes in the utility of ongoing tasks. In the context of aging, this theory raises interesting questions, given that the motivations of older adults differ from those of younger adults. According to socioemotional selectivity theory (Carstensen, Isaacowitz, & Charles, 1999), aging is associated with greater emphasis on emotion-regulation goals, leading older adults to prioritize positive over negative information. This suggests that the phasic release of NE in response to threatening stimuli may be diminished in older adults. In the present study, younger adults (aged 18–34 years) and older adults (60–82 years) completed the Attention Network Test (ANT), modified to include an incentive manipulation. A behavioral index of attentional alerting served as a marker of phasic arousal. For younger adults, this marker correlated with the effect of both gain and loss incentives on performance. For older adults, in contrast, the correlation between phasic arousal and incentive sensitivity held for gain incentives only. These findings suggest that the enlistment of phasic NE activity may be specific to approach-oriented motivation in older adults.

Keywords: Aging, incentives, phasic arousal, alerting, Attention Network Test

1. Introduction

In our day-to-day lives, we are constantly bombarded with sensory information that competes for our limited attentional capacities. Despite this sensory overload, we tend to navigate our environments successfully. The ability to identify meaningful cues in the environment to guide selective attention towards high-priority information is critical in this regard. This capacity emerges early in human development, as even infants show an attentional bias for objects cued as threatening by fearful adult gazes (Hoehl et al., 2008; Hoehl, Wiese, & Striano, 2008; LoBue & DeLoache, 2010). In the current study, the objective was to examine motivational effects on attention in healthy younger and older adults.

Motivated attention and aging

In recent years, the goal-directed nature of attention has received considerable investigation within the domain of aging. Notably, numerous studies have reported an age-related positivity effect, with healthy older adults showing preference for positive over negative or neutral stimuli (for a recent meta-analysis, see Reed, Chan, & Mikels, 2014). In fact, older adults may actively avoid the processing of negative or aversive information, suppressing amygdala activity in the presence of such stimuli (Ochsner et al., 2004; Mather & Carstensen, 2005; Sakaki, Nga, & Mather, 2013; St. Jacques, Dolcos, & Cabeza, 2010). Such observations are in line with socioemotional selectivity theory, which holds that in later adulthood individuals prioritize emotion regulation goals aimed towards the attainment of meaningful, positive experiences and improved well-being (Carstensen, 1992; Carstensen, 2006; Carstensen, Isaacowitz, & Charles, 1999).

When examining the influence of motivation on attention in the laboratory, it is common to offer opportunities to gain, or in some cases lose, monetary incentives within cognitive tasks (e.g., Ashare, Hawk, & Mazzullo, 2007; Della Libera & Chelazzi, 2006; Engelmann & Pessoa, 2007). Such designs are valuable as they allow for comparisons of behavioral performance when such incentives are present versus when they are absent, with differences presumably attributable to goal-based modulations of attention. When applied to older adults, there have been findings of an age-related reduction in loss sensitivity, but preserved sensitivity to gains, consistent with a “positivity effect” (e.g. Bagurdes et al., 2008; Mikels & Reed, 2009; Samanez-Larkin et al., 2007). However this decreased responsiveness to losses is not always exhibited by this population (e.g., Ebner, Freund, & Baltes, 2006; Eppinger et al., 2013; Spaniol et al., 2011; Spaniol et al., 2015). Generally, differences involving responsiveness to monetary incentives are attributed to an age-related reduction of dopamine (DA) transmission in the brain’s reward circuit (e.g., Chowdhury et al., 2013; Eppinger, Nystrom, & Cohen, 2012; Mell et al., 2009). However, it may also be useful to consider contributions from other neural sources.

1.1 Adaptive gain theory

One promising candidate that may help clarify age-related differences in attentional sensitivity to gains and losses is the neurotransmitter norepinephrine (NE), which has long been hypothesized to influence attention through its association with wakefulness and arousal (e.g., Aston-Jones & Bloom, 1981; Foote et al., 1991; Squire, Bunsey, & Strupp, 1995). The principal source of this neurotransmitter in the brain is the locus coeruleus (LC), a small nucleus located in the brainstem, which projects to a number of cortical and subcortical regions, collectively referred to as the LC-NE system (Schwarz & Luo, 2015). Current understanding of this network distinguishes two primary modes of activation, which differentially affect attentional processes: (a) a phasic firing mode, and (b) a tonic firing mode (Aston-Jones et al., 1994; Aston-Jones, Rajkowski, & Cohen, 1999; Rajkowski, Kubiak, & Aston-Jones, 1994, Usher et al., 1999). The phasic firing mode is associated with moderate levels of global NE, in combination with bursts of activity occurring shortly after the presentation of task-relevant stimuli, or just before a behavioral response is made. The tonic firing mode, on the other hand, maintains high levels of global NE, but shows a marked reduction, if not absence, in the bursts of activity observed in the phasic mode. Enhanced task performance is observed in the phasic mode, possibly due to an increased signal-to-noise ratio for high-priority stimuli (Mather et al., in press). In contrast, the tonic firing mode of the LC is associated with increased distractibility and task disengagement.

Research on the role of the LC-NE system in goal-directed attention in older adults is currently lacking. Yet, there is reason to expect age differences in LC-NE system modulation of the attentional system. According to adaptive gain theory (Aston-Jones & Cohen, 2005), the firing mode of the LC-NE system is directly influenced by motivational states. This theory draws on the exploration-exploitation tradeoff described by reinforcement learning models, in which organisms balance between persisting at a behavior with a known set of outcomes (exploitation), and seeking alternative behaviors that may produce greater value (exploration) as they attempt to maximize utility (See Cohen, McClure, & Yu, 2007, for review). The phasic mode of LC activation promotes exploitation by directing attentional resources towards a specific task, optimizing performance and task outcomes. In contrast, the task disengagement and distractibility that characterize the tonic firing mode of the LC is well suited for exploration behavior.

Aston-Jones and Cohen (2005) argue that utility-based shifts in LC-NE firing are mediated by prefrontal structures. Specifically, this role is attributed to the orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC), which have both consistently been shown to encode and represent value (for rewards and costs) during associative learning and economic decision-making (e.g. Bush et al., 2002; Gallagher, McMahan, & Schoenbaum, 1999; Kahnt et al., 2010; Kennerley et al., 2006; Kennerley, Behrens, & Wallis, 2011; O'Doherty et al., 2001). When the utility of a task is perceived as high, these evaluation structures mobilize the phasic LC firing mode, optimizing task performance. However, when the perceived utility of a task is low or diminishes, they bias the LC-NE system to fire tonically, prompting the individual to disengage from the task and search for alternative sources of utility.

1.2 Phasic alerting as a marker of NE activity

Presently, direct observations of LC-NE activity in humans are difficult to obtain non-invasively. Support for adaptive gain theory thus mostly stems from studies involving non-human species. Anatomical rodent studies, for example, have shown that electrical and chemical stimulation of medial prefrontal regions produce an excitatory influence on LC neurons, with projections from this region innervating an area nearby the LC (Jodoj, Chiang, & Aston-Jones, 1998; Shipley et al., 1996). Similarly, the central nucleus of the amygdala has been shown to innervate and activate the LC (Bouret et al., 2003; Cedarbaum, & Aghajanian, 1978; Wallace, Magnuson, & Gray, 1992). Along with its well-known role in processing emotional stimuli, the amygdala is also involved in encoding and representing value, and may thus play an analogous role to that of the OFC and ACC (Blair et al., 2005; Gottfried, O'Doherty, & Dolan, 2003; Schoenbaum, Chiba, & Gallagher, 1998; Patton et al., 2006). Lastly, rhesus monkeys exhibit phasic bursts of LC-NE activity, preceded by OFC activity, in response to reward-signaling cues, with this activity being greater for high-reward cues than low reward cues, but diminishing with increased satiation (Bouret & Richmond, 2010, 2015).

While direct measures of LC-NE activity are difficult to obtain in humans, non-invasive observations are possible through indirect physiological indices such as pupil dilation (Gilzenrat, Nieuwenhuis, & Jepma, 2010; Jepma & Nieuwenhuis, 2011; Joshi et al., 2016; Murphy et al., 2014; Phillips, Szabadi, & Bradshaw, 2000). Potential behavioral indices are also available. In their model of attention, Posner and Peterson (1990; Peterson & Posner, 2012) describe three distinct attention networks: alerting, orienting, and executive control. Particularly noteworthy here is the alerting network, which the authors implicate in maintaining vigilance. The orienting and executive control networks, in contrast, are involved in directing attention to spatial locations and conflict monitoring processes, respectively. Preparatory cues signaling target onset activate a phasic alerting response which facilitates faster responding relative to when no cue is presented (Fernandez-Duque & Posner, 1997; Thiel, Zilles, & Fink, 2004). This phasic alerting response likely corresponds to phasic activation of the LC-NE system, as administration of clonidine, an α2-adrenoceptor agonist which works to inhibit the release of NE, selectively diminishes alerting, but not orienting effects (Coull, Nobre, & Frith, 2001; Witte & Marrocco, 1997). As such, a behavioral measure of phasic alerting may be indicative of the extent to which the phasic LC firing mode is engaged during a task.

The Attention Network Test (ANT; Fan et al., 2002) is ideal for obtaining a behavioral measure of phasic alerting, as it purports to capture network scores for the three attention networks outlined by Posner and Peterson (1990). It combines an attentional-cueing paradigm (Posner, 1980) with the Eriksen-flanker task (Eriksen & Eriksen, 1974). The network score for alerting is measured by comparing responses to targets cued by a non-spatial warning cue to responses to non-cued targets, consistent with the studies described above.

1.3 Rationale and hypotheses

In the present study, we sought to examine the extent to which younger and older adults optimize task performance in the presence of gain or loss avoidance incentives. To this end, we modified the ANT to include gain and loss incentives. In the gain version, a subset of trials provided the opportunity to gain money, whereas in the loss version, a subset of trials involved the potential of losing money. Based on the observation of an age-related positivity effect, we sought to test two hypotheses. The first hypothesis was that gains and losses would differentially affect attention networks in younger and older adults, such that the impact of gains (relative to losses) would increase for older adults. Based on adaptive gain theory (Aston-Jones & Cohen, 2005), and on evidence of a link between alerting and the LC-NE system (Coull et al., 2001; Witte & Marrocco, 1997), we expected that the alerting network would be particularly likely to show an age-related positivity effect. The second hypothesis (not mutually exclusive with the first) was that younger and older adults would differentially engage the alerting network in the service of motivated attention. According to this view, the extent to which individuals benefit from incentives should relate to the magnitude of their alerting response, with larger incentive effects being associated with larger alerting scores. An age-related positivity effect could then be expressed in the relative strength of the alerting-incentive link for gains and losses.

2. Method

2.1 Participants

All study procedures were approved by the Research Ethics Board of Ryerson University. Younger adults were recruited through flyers posted around the Ryerson University campus in Toronto, as well as through online postings. Older adults were recruited from the Ryerson Senior Participant Pool. Fifty younger adults (25 gain version; 25 loss version) and 50 older adults (25 gain version; 25 loss version) participated in the study. All participants were screened using the Mini Mental State Exam (MMSE; Folstein, Folstein, & McHugh, 1975) to screen for possible dementia-related impairment. A cut-off score of 26 or below out of a possible 30 points was used to exclude participants, which was the case for one older adults who scored 25. All other participants scored at least 27 on the measure. However, additional participants (3 younger adults; 1 older adult) were later excluded for the following reasons: failure to follow task instructions, a technical error in the computer program, and a pre-existing hand injury. The remaining participants reported being free of neurological or psychiatric disorders, normal (or corrected-to-normal) vision, and being in overall good health. Demographic, cognitive, and affective information for the final sample are presented in Table 1. Written informed consent was obtained at the beginning of the experiment for each participant, and all participants received $18 in addition to a bonus obtained during the experimental task.

2.2 Design and apparatus

The ANT consists of the within-subjects factors of cue (no, double, center, spatial) and flanker (congruent, incongruent, neutral). A mixed-factorial design was applied to this task consisting of two between-subject factors, age (younger adults, older adults), and version (gain, loss), as well as one within-subjects factor, incentive (absent, present). The modified ANT was administered using E-Prime 2.0 Professional (Psychology Software Tools, Inc.; Sharpsburg, PA) with participants seated approximately 50 cm from a 23-in computer monitor. All stimuli were presented against a black background.

To start each trial, a fixation cross subtending a visual angle of .50° vertically x .50° horizontally was presented in the center of the screen for a random duration between 400–1600 ms. This fixation cross was either white or pink, depending on whether or not the trial was associated with an incentive (with pink cues indicative of incentive trials). One of four cue conditions (no, double, center, or spatial) was then presented for 100 ms. For the no cue condition, the fixation cross was maintained without any other stimuli appearing. The double cue condition consisted of two asterisks presented (each .50° x .50°) respectively at equal distances (2.94°) above and below the central fixation. Both the center cue and spatial cue involved a single asterisk. In the center cue condition, this asterisk was superimposed over the fixation cross, whereas in the spatial cue condition, the asterisk appeared either above or below the cross (indicating where the target would later appear).

Following the 100 ms cue period, all cue stimuli were removed, leaving only the central fixation for the next 400 ms. The target stimulus then appeared 2.95° either above or below the fixation cross. The target was a white arrow pointing either to the left or right, presented centrally among four flankers (i.e. two flankers on either side). In some cases, the flankers were arrows that either matched the orientation of the target (congruent condition), or faced the opposite direction of the target (incongruent condition), while in other cases the flankers were horizontal lines which indicated no direction (neutral condition). The target arrow subtended a visual angle of .65° horizontally, while the target arrow with the four flankers subtended a total visual angle of 3.27° horizontally in each of the different flanker conditions.

At the time of the target, participants were given a maximum of 1700 ms to respond. Once a response was recorded, or the time limit was reached, target stimuli were removed from display, and the trial ended once a total trial duration of 4000 ms was reached. A schematic illustration of both an incentive and a non-incentive trial is presented in Figure 1.

2.3 Procedure

Prior to each experimental session, participants were randomly assigned to either the loss or gain version of the task. Participants were told by the experimenter that they would need to make a left/right judgment in response to a central arrow flanked by two arrows on either side. At this point, participants were not told that they would earn a monetary bonus during the task.

Participants then completed a practice block of the task not involving incentive trials, consisting of 24 trials balanced across the various cue and target conditions.

After completing the practice block, participants were informed that incentives would be at stake during the computer task. Those in the gain version of the task were told that on some trials they would be able to gain $0.10, which would go towards a running balance starting at $0, whereas those in the loss version were told that they could lose $0.10 from a balance that started at $30. All participants were notified that the fixation cross would periodically change from white to pink, and that this would signal that an incentive was at stake. Whether a specific trial resulted in a gain or non-loss was contingent on the participant's response. Specifically, responses that were accurate and faster than the participant's mean reaction time (RT) on all previous correct experimental trials (including both incentive and non-incentive trials) resulted in a gain or non-loss. In contrast, incorrect responses, or responses that were slower than the participant's mean RT on all previous correct experimental trials, resulted in a non-gain or loss. This payoff scheme was used to ensure that overall payoffs were similar for all participants.

Participants received the following information about the payoff scheme: "If you respond accurately and quickly, you will [gain]/[avoid losing] $0.10. The computer will track your speed throughout the study, and will [add the $.10 to your balance]/[let you keep the $0.10] if you response is accurate AND faster than your fastest reaction time in the practice block. The difficulty increases by 10% in each block."

This minor deception was used so that participants would not purposely slow down on non-incentive trials, thereby increasing their mean RT and making the incentives more readily attainable. Under the stated payoff scheme, this strategy would not have been effective, since the criterion was ostensibly linked to performance on practice trials, which had occurred before participants were aware that a performance bonus would be offered. To further discourage strategic trial-by-trial adjustments, there was no end-of-trial feedback (although there was end-of-block feedback, as detailed below). Pilot testing was conducted to establish the effectiveness of the instructions, and confirmed that participants believed the stated payout rule. Participants were able to practice again, now with both non-incentive and incentive trials. This practice block also included 24 trials, balanced across conditions.

The participant then moved on to the experimental blocks. Each block consisted of 96 trials, with non-incentive and incentive trials randomly intermixed. Each combination of cue, target, and incentive was presented with equal frequency. There were 6 blocks, resulting in a total of 576 trials. At the end of each block, participants were presented with feedback. In the gain condition, participants learned how much they money they had earned over the course of the previous block, and in the loss condition, participants learned how much they had avoided losing over the course of the previous block. Once all 6 blocks were completed, participants learned their overall final balance.

Following the experimental task, the researcher administered a battery of neuropsychological measures to assess general cognitive status, approach and avoidance motivation, and mood and affect. Participants were then fully debriefed, compensated for their time, and given the bonus earned during the task (M = \$16.65, SD = 2.37; not significantly different for younger and older adults, $t(93) = -.92$, $p = .360$).

2.4 Data analysis

Each participant's data obtained during the ANT were subjected to data cleaning prior to statistical analysis. This process involved identifying and excluding trials in which participants failed to respond to target stimuli altogether. If a participant missed 10% of trials or more in a given block, the block was excluded from all subsequent analyses, which was the case for 3 younger adults (1 gain version; 2 loss version), and 1 older adult (loss version). No participant missed more than 10% of trials in multiple blocks. The remaining data were used to calculate accuracy for each cue x flanker x incentive condition. Mean RT for correct responses was calculated for these conditions as well.

Typically in speeded tasks, older adults tend to adopt conservative response strategies that favor accuracy, whereas younger adults show a greater willingness to commit errors to decrease RTs (Forstmann et al., 2011; Rabbit, 1979; Starns & Ratcliff, 2010). It was therefore necessary to use a measure that would account for age differences in speed-accuracy tradeoff. Inverse efficiency (IE) scores were used for this purpose (Townsend & Ashby, 1983). IE scores have previously been used for an Erikson-flanker task similar to the one used in the ANT (Lange-Malecki, & Treue, 2012). IE scores were calculated by dividing RT by accuracy for each cue x flanker x incentive condition. Lower IE scores thus indicate greater efficiency.

Initial analyses examined overall main effects and interactions of the experimental factors on ANT performance. We consider IE to be most informative measure of performance in the current context, but for consistency with the literature, we also summarize the results of analyses performed on accuracy and RT. For each measure, a mixed-model ANOVA was carried out involving the between subject-factors age (younger adults, older adults) and version (gain, loss) and the within-subject factors cue (no, double, center, spatial), flanker (congruent, incongruent, neutral), and incentive (absent, present). In cases where Mauchly's sphericity test was significant, the Huynh-Feldt correction method was used to adjust the degrees of freedom. Significant main effects on factors with three or more levels (i.e., cue and flanker conditions) were followed up using Bonferroni-adjusted comparisons among the cue and flanker conditions typically used to assess the three attention networks. Significant interactions involving the within-subjects cue factor were followed up with a mixed-model ANOVA including only the no-cue and double-cue conditions to examine alerting effects, or center-cue and spatial-cue conditions to assess orienting effects. Similarly, in the case of interactions involving the within-subjects factor of flanker, the mixed-model ANOVA was run again using only congruent and incongruent flanker conditions to investigate interference effects. Analyses of network interactions (e.g., orienting effects on executive control) were not reported, as they were not central to the research questions motivating the current study, and showed no modulation by incentives.

The critical analyses involved testing associations between incentive effects and alerting effects on performance, as indexed by IE scores. We calculated alerting effects by subtracting IE for the double cue condition from the no cue condition, but only for incentive absent trials. This was done to ensure that the alerting measure was not confounded with incentive effects. Similarly, the effect of incentives was calculated by subtracting IE for incentive-present trials from incentive-absent trials, but only for trials in the no-cue condition. This was similarly done to ensure that the incentive measure was not confounded with alerting effects. Two-tailed bivariate correlations of the two difference scores were then calculated for each combination of age group and task version (gain, loss).

3. Results

3.1 Accuracy and RT

Descriptive statistics and details of inferential statistics for accuracy and RT measures are presented in Tables 2-4. Overall, accuracy was higher for older adults than for younger adults. Alerting decreased accuracy; orienting increased accuracy; and incongruent flankers decreased accuracy. Each of these ANT effects was greater for younger adults, with older adults showing near-ceiling accuracy for every condition. Incentives affected accuracy in terms of executive control only, with greater interference when incentives were present. This effect of incentives was more pronounced for younger adults than for older adults. Incentive type (i.e., gain vs. loss) did not significantly contribute to differences in accuracy for either group.

With respect to RT (Table 4), younger adults were faster overall in comparison to older adults. Typical effects of alerting, orienting, and executive control were observed, with shorter RT for double and spatial cues relative to no and center cue conditions respectively, and longer RT for the incongruent versus the congruent flanker condition. The effect of alerting was greater for younger adults, whereas the orienting and interference effects were larger for older adults. Incentives reduced overall RT, especially for younger adults, but did not reduce flanker interference effects. Lastly, incentives reduced alerting effects on RT, due to a greater benefit for the no cue versus double cue condition.

3.2 Inverse efficiency

Descriptive statistics are presented in Table 2. Overall, lower IE scores were observed for younger adults compared to older adults, $F(1, 91) = 122.16$, $p < .001$, $\eta_p^2 = .57$, suggesting that younger adults were more efficient than older adults. As was the case for the previously described measures, the effect of version was not significant, $F(1, 91) < .01$, $p = .962$, $\eta_p^2 < .01$, nor was there an Age x Version interaction, $F(1, 91) = .96$, $p = .330$, $\eta_p^2 = .01$. Those in the gain version of the task were thus as efficient as those in the loss version, for both younger and older adults.

With respect to network effects, both main effects of cue, $F(2.39, 217.50) = 234.22$, $p < .001$, $\eta_p^2 = .72$, and flanker, $F(1.16, 105.89) = 345.94$, $p < .001$, $\eta_p^2 = .79$, were present. The follow-up comparison of no and double cue conditions revealed that IE was significantly lower in the double cue condition than the no cue condition, $t(93) = 8.22$, $p < .001$. In other words, alerting increased response efficiency. The follow-up comparison of center and spatial cue conditions was also significant, $t(93) = 17.27$, $p < .001$. IE in the spatial cue condition was reduced relative to the center cue condition, consistent with an orienting effect on task performance. Lastly, the contrast concerned with executive control (i.e. congruent versus incongruent flanker conditions) was also significant, $t(93) = -18.85$, $p < .001$. In this case, IE was higher for the incongruent condition than the congruent condition, suggesting poorer efficiency in the presence of incongruent flankers.

In contrast to what we observed for accuracy and RT, the interaction of Cue x Age was not significant for IE, $F(2.39, 217.50) = .89$, $p = .426$, $\eta_p^2 = .01$, nor was the interaction of Flanker x Age, $F(1.16, 105.89) = 2.72$, $p =.097$, $\eta_p^2 = .03$. Thus, when accuracy and RT were considered together as a single measure of IE, younger and older adults did not differ in terms of alerting, orienting, or interference cost (i.e. executive control).

Lastly, with respect to the influence of rewards and losses on IE, there was a main effect of incentive, $F(1, 91) =31.58$, $p < .001$, $\eta_p^2 = .26$. The effect was such that IE was lower when incentives were present relative to when they were absent, with more efficient performance under incentive conditions. This effect of incentive did not interact with age, $F(1, 91) = .01$, $p = .919$, $\eta_p^2 < .01$. The magnitude of alerting and orienting were not influenced by the presence of incentives as the Cue x Incentive interaction was not significant, $F(2.84, 258.79) = 1.37$, $p = .254$, $\eta_p^2 = .02$. There was, however, a significant Flanker x Incentive interaction, $F(1.63, 148.72) = 3.43$, $p = .044$, $\eta_p^2 = .04$, with interference cost being greater in the incentive-present condition than the incentive-absent condition.

In summary, younger adults exhibited smaller IE scores (i.e., greater efficiency) relative to older adults. Both alerting and orienting increased efficiency. The incongruent flanker interference cost was also significant, with reduced efficiency for the incongruent versus congruent flanker condition. These main effects did not vary by age. Incentives also affected IE, with higher efficiency when incentives were present relative to when they were absent. Despite this incentive-based enhancement, interference for incongruent flankers relative to congruent flankers was greater when incentives were present. Incentive type (gain vs. loss) did not influence any of these effects or interactions.

3.3 Correlational analyses

Scatterplots illustrating the correlations between the alerting and incentive effects on IE are presented in Figure 2. For younger adults, the correlation was significant in both the gain version of the task, $r = +.69$, $p < .001$, and in the loss version, $r = +.62$, $p < .001$. For older adults, however, the correlation was significant in the gain version of the task, $r = +.81$, $p < .001$, but not in the loss version, $r = +.03$, $p = .880$.

To test formally whether the relationship between alerting and incentive effects was diminished in the old-loss group, we created a set of dummy variables coding for group membership (young-gain, young-loss, old-gain, old-loss), with old-loss as the reference category. We then estimated a regression model in which the incentive effect was the outcome regressed on the alerting effect, the dummy variables representing the groups, and interactions between alerting and the dummy variables (Cohen, Cohen, West, & Aiken, 2003). We next examined the regression slope coefficients to determine for which groups the slopes differed significantly from the slope for the old-loss group (i.e., the reference category). The difference was significant for the old-gain group and the young-gain group, both $p < .001$; it narrowly missed significance for the young-loss group, $p = .051$. Finally, visual inspection of the scatterplots suggests the presence of outliers in the young-gain and old-gain groups. However, Cook's distance (Cook, 1977), which measures the influence of each case of the regression model, yielded values between 0.0 and 0.3, well below the conventional guideline of 1.0 that would indicate the presence of problematic outliers in this regression analysis.

A possible explanation for the observed correlations is that some individuals are more effective than others at using contextual cues to enhance performance. In this case, those who rely on double cues for alerting may also be better at using incentive information to enhance performance. To test whether the observed correlations were in fact attributable to the effect of alerting rather than a general ability to use contextual information, we also calculated correlations between the incentive effect and the orienting effect on IE (incentive-absent center cue condition – incentive-absent spatial cue condition), separately for each of the four groups. These analyses yielded no significant correlations (r = -.04 – +.29, p = .188 – .977), suggesting that the correlations with the alerting measure are unlikely to be an artifact of individual differences in reliance on cues in general.

4. Discussion

The present study examined how attentional processing responds to gain and loss incentives in younger and older adults. Consistent with previous studies that have shown motivational goals to influence attention (e.g., Ashare et al., 2007; Della Libera & Chelazzi, 2006; Engelmann & Pessoa, 2007), incentives led to an overall performance enhancement in both age groups. Contrary to our first hypothesis and to some other findings in the literature (e.g., Bagurdes et al., 2008; Samanez-Larkin et al., 2007), there was no evidence for greater gain-enhanced alerting than loss-enhanced alerting in older adults, nor did we observe age-related positivity effects on orienting or executive control networks. However, there was support for our second hypothesis, according to which aging alters the enlistment of LC-NE activity to support motivational modulation of attention. An analysis of the correlation between incentive effects and phasic alerting revealed a dissociation between gains and losses for older adults. Specifically, gain effects on performance were correlated with phasic arousal effects, but loss effects were not. For younger adults, both gain and loss effects were associated with phasic arousal effects. The statistical significance of this dissociation was confirmed in an analysis of regression slopes. To our knowledge, this is the first demonstration of an age-related difference in the link between phasic arousal and incentive-based motivational effects on attention.

4.1 Phasic arousal, incentives, and aging

Utilization of the alerting score obtained during the ANT to make inferences regarding the LC-NE system appears justified on the basis of previous studies. Pharmacological studies involving primates and humans, for example, have demonstrated that the use of clonidine, an α2-adrenoceptor agonist that inhibits the release of NE, diminishes the alerting response (Coull et al., 2001; Witte & Marrocco, 1997). Extending these findings, neuroimaging work involving a revised version of the ANT (i.e. ANT-R; Fan et al., 2009) showed that activation of the LC was selectively related to the alerting response (Xuan et al., 2016). Given this association between alerting and the LC-NE system, the present findings are suggestive of an arousal-mediated influence of incentives on attention, consistent with adaptive gain theory (Aston-Jones & Cohen, 2005). Specifically, those individuals who demonstrated the largest alerting effects were most effectively engaging the phasic LC-NE firing mode during the task. Since this alerting score was related to the magnitude of the incentive effect, it is likely that the two processes relied on the same mechanism. This interpretation is supported by the lack of similar correlations with the orienting response, which relies more heavily on the cholinergic neurotransmitter system (Davidson & Marrocco, 2000; Stewart, Burke, & Marrocco, 2001).

The relationship between incentives and alerting was present for older adults in the gain version of the task, but absent for those in the loss version. This asymmetry mirrors the age-related positivity effect reported in other domains (Reed et al., 2014) and is consistent with socioemotional selectivity theory (Carstensen, 1992; Carstensen, 2006; Carstensen, Isaacowitz, & Charles, 1999). Importantly, the current findings do not suggest that aging is associated with reduced alerting responses to loss or threat signals *per se* (see also Mather & Knight, 2006). Rather, aging appears to disrupt the enlistment of the alerting response in modulating attentional performance in the face of loss signals. This suggests that age differences in motivated attention are relatively subtle, and may reflect alterations in the interaction between LC-NE and dopamine systems, rather than simple decline (see next section for further discussion of this possibility).

A point that should be acknowledged is the finding that neither alerting nor the presence of incentives reduced the interference produced by incongruent flankers, which runs counter to the idea that phasic arousal should increase the signal-to-noise ratio of target stimuli (e.g., Mather et al., in press). However, the failure of alerting and the presence of incentives to reduce interference is consistent with previous studies using the ANT and the Eriksen-flanker task (e.g. Callejas et al., 2005; Fan et al., 2002; Marini, van den Berg, & Woldorff, 2015; Seifert et al., 2006). As suggested by Marini et al. (2015), this might have to do with the similarity of the target and distractor arrows used for the Eriksen-flanker. Specifically, because the target and distractors share the same visual properties, the phasic NE filtering mechanism may have been diminished by the lack of a salient property distinguishing the target from distractors, limiting more local effects of incentives on target processing.

4.2 Dual mechanisms of control framework challenge

A competing explanation that can be raised to account for the incentive-based effects is the dual mechanisms of control framework (Braver, 2012; Braver et al., 2007; Braver et al., 2009). This theory proposes that attentional control can be engaged either proactively or reactively. Proactive control involves the active maintenance of goal-relevant information in order to anticipate and prepare for an upcoming response or event, whereas reactive control is a more spontaneous mechanism that is recruited as needed, such as when interference or an unanticipated event is detected (Braver, 2012). Consequently, in this framework, it could be argued that incentive-based improvements are not related to the firing mode of the LC-NE system, but rather reflect greater employment of proactive control, which is believed to rely on the dopaminergic system (Braver & Cohen, 1999; Dreisbach et al., 2005). In this case, the lack of a relationship between incentives and the alerting response for older adults in the loss version of the task could be attributable to a failure of loss incentives to engage proactive control mechanisms in a manner consistent with the alerting response for this population.

While the dual mechanisms of control framework offers a compelling alternative to adaptive gain theory, the two models do not necessarily need to be considered independent of one another. Notably, prefrontal DA and LC-NE systems may jointly contribute to goal-directed influences on attention. For example, in rodents, salience attributions for rewarding and aversive stimuli depend on NE levels in the PFC, which work to increase DA in the neural reward circuit (Ventura, Morrone, & Puglisi-Allegra, 2007; Ventura et al., 2008). Further, Chiew and Braver (2013, 2014) report that under conditions of proactive control, greater transient changes in pupil dilation are observed just prior to the presentation of a target when a reward is at stake versus when no incentive is offered within the same block (Chiew & Braver, 2013; Chiew & Braver, 2014). Given the well-established link between pupil dilation and the LC-NE system (e.g., Joshi et al., 2016; Murphy et al., 2014; Phillips et al., 2000), this finding suggests that the deployment of proactive control may involve a phasic LC-NE system response. It can thus be suggested that prefrontal control systems and the LC-NE system interact to sustain attention in a goal-directed manner to optimize task performance.

When viewed this way, we can speculate as to why older adults in the gain and loss version of the task show no meaningful performance differences, despite the lack of a relationship between alerting and the response to losses in this age group. Specifically, the alerting response and the response to gains may involve an interaction of the phasic NE response with proactive control mechanisms to sustain goal-directed attention, whereas older adults in the loss version of the task may rely more reactive mechanisms in the presence of incentives, leading to similar performance. One way to test this hypothesis would be to use target stimuli involving greater conflict, in which case compensatory reactive mechanisms may not be sufficient to improve performance for loss-incentive trials.

4.3 Attention network effects

Beyond our main findings, the present study also contributes more broadly to improving understanding of age differences in Posner and Peterson’s (1990) three attention networks. Typically, when performance in the ANT is compared between younger adults and older adults, age-adjusted RT is used as the primary outcome measure. Such studies, commonly report preserved orienting and executive control, but an age-related reduction in alerting (Gamboz, Zamarian, Cavallero, 2010; Jennings et al., 2007; Williams et al., 2016). Here, we similarly report age-preserved orienting and executive control when using IE as our dependent measure, but not a decline in alerting. Previously, we observed younger and older adults to exhibit a comparable electrophysiological response to double cues in the ANT, with differences between the two groups occurring at the time of the target (Williams et al., 2016). We thus suggested that reported age differences in alerting may not reflect a deficit per se, but rather a difference in response strategy. The lack of an age difference in the IE measure of alerting in the current study provides further evidence that RT-based measures of alerting may not tell the whole story.

4.4 Limitations and future directions

The balance of males-to-females between age groups in the current study was a potential limitation of the present study. In particular, the older adult sample was almost entirely female, while this was not the case for the younger adult sample. Work involving rodents has shown that structural differences in the LC-NE system may exist between females and males, with increased branching of this system in females, potentially leading to greater sensitivity to environmental stressors and emotional stimuli (Bangasser et al., 2011). On the other hand, a recent study using an in vivo biomarker of LC structure, neuromelanin-sensitive weighted MRI, in healthy younger and older adults found higher values of this biomarker in males than in females (Clewett, Lee, Greening, Ponzio, Margalit, & Mather, 2016). Overall, these findings suggest that sex differences may need to be taken into account when studying LC-NE function. However, within the older adult sample in the current study, a comparable number of females were assigned to the loss version of the ANT relative to those assigned to the gain version. As such, sex differences cannot account for the existence of a relationship of gain, but not loss, incentives to alerting in older adults.

Another limitation of the current study was that we did not systematically control for the time of day at which participants were tested. Prior research has shown that most older adults show peak levels of cognitive performance in the morning, whereas most younger adults show peak levels later in the day (Roenneberg, Kuehnle, Pramstaller, Ricken, Havel, & Guth, 2004). Furthermore, alerting effects have been shown to be maximal at off-peak times of day for both younger and older adults (Knight & Mather, 2013). Most participants in the current study were tested in the afternoon, but the proportion of participants tested in the morning was greater among older adults (45%) than among younger adults (23%). In future studies it would be important to hold constant, or else manipulate experimentally, the time of day (peak vs. off-peak) at which LC-NE function is studied in younger and older adults.

Lastly, the size of the trial-by-trial incentives used in the present study ($.10) is smaller than incentives that have sometimes been offered in previous studies (e.g. Engelmann, & Pessoa, 2007; Samanez-Larkin et al., 2007). Older adults may show a greater arousal response to loss prospects if the incentives are more impactful. This idea should be addressed by future research.

The present findings raise a number of other questions to be addressed in future studies. For instance, it will be important to understand at which stage of attentional processing differences are occurring for gain and loss incentives among older adults. Specifically, it should be investigated whether differences in phasic NE recruitment occur at early stages of processing (such as when the incentive-prospect is recognized) or later on (such as at the time of the target/response). For reasons described above, pupillometry methods may be useful for this purpose, as might observations of certain event-related potentials (ERPs) believed to be influenced by NE (e.g., the P3 component; Murphy et al., 2011; Nieuwenhuis, Aston-Jones, & Cohen, 2005). Such endeavors may also be useful in helping to improve understanding of the LC-NE system in relation to proactive and reactive control mechanisms. Additionally, it may also be useful to provide trial-by-trial feedback for similar studies in the future. Presumably, this should make the incentives more salient. This avenue is worth pursuing to investigate if the increased salience will enhance incentive effects for older faced with losses, or reduce such effects by increasing the influence of arousal-inhibiting mechanisms.

4.5 Conclusion

In conclusion, we report evidence of an arousal-related influence of motivational incentives on attention that is absent for older adults faced with the prospect of experiencing a loss. This finding adds to the literature on age-related positivity effects, and provides support for recent advances in affective and cognitive neuroscience that point to a role of the LC-NE system in supporting goal-directed cognition across the lifespan.

Acknowledgments

We thank Pete Wegier and Leann K. Lapp for helpful discussions during early stages of this project, with further thanks to Pete Wegier for his help with computer programming. We also thank Kathleen M. Lyons for her assistance with data collection, and David B. Flora for statistical advice. This research was supported by a grant from the Natural Sciences and Engineering Research Council (DG# 358797 to J.S.), by the Canada Research Chair program (J.S.), and by an Early Researcher Award from the Ontario Ministry of Research and Innovation (J.S.).

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Table 1. Group Characteristics

	Younger Adults				Older Adults				Age Effects[a]		
	Gain		Loss		Gain		Loss				
	M	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*F*	*p-value*	η_p^2
N	24	-	23	-	25	-	23	-	-	-	-
N (Female)	9	-	16	-	22	-	20	-	-	-	-
Age, years	21.88	3.55	21.87	2.42	65.96	6.02	64.43	3.50	**2600.99**	**< 0.001**	**0.97**
Age Range, yrs	18-34	-	18-29	-	60-82	-	60-82	-	-	-	-
Education, yrs	15.29	2.22	15.70	1.74	17.06	3.99	16.28	2.95	**3.98**	**0.049**	**0.04**
Mill Hill Vocab.	13.88	2.91	16.65	4.04	22.72	3.29	22.43	5.69	**75.74**	**< 0.001**	**0.45**
Digit Symbol	88.88	13.06	88.22	13.92	69.76	12.84	72.26	12.45	**42.69**	**< 0.001**	**0.32**
MMSE	29.58	0.50	29.48	0.67	29.16	1.11	29.22	0.90	**4.02**	**0.048**	**0.04**
BIS/BAS[b]											
BIS	20.92	2.9	19.17	2.79	20.25	3.10	19.65	4.14	0.02	0.889	0.00
Drive	11.63	2.63	11.87	2.30	10.08	2.36	11.48	1.93	**4.07**	**0.047**	**0.04**
Fun Seek.	13.13	2.07	12.70	1.82	11.71	2.35	12.48	2.33	3.38	0.07	0.04
Reward Resp.	18.04	1.83	18.09	1.93	16.92	2.02	17.04	2.84	**5.79**	**0.018**	**0.06**
BAS Total	42.79	5.01	42.65	4.79	38.71	5.60	38.71	6.17	**6.58**	**0.012**	**0.07**
PANAS											
Pos. Affect	30.96	6.7	30.91	9.64	34.64	5.40	35.48	8.83	**6.69**	**0.011**	**0.07**
Neg. Affect	13.21	4.79	12.57	4.39	11.88	2.40	11.04	1.80	3.78	0.055	0.04
DASS-21[c]											
Depression	7.92	7.63	6.52	4.68	3.76	4.59	4.35	5.99	7.01	0.01	0.07
Anxiety	9.25	6.29	7.22	7.18	3.83	7.05	3.04	4.55	**13.35**	**< 0.001**	**0.13**
Stress	13.33	8.88	12.52	7.12	10.25	8.18	8.17	6.85	**5.31**	**0.024**	**0.06**

Note: [a]Reported statistics reflect main effects of age following 2 (age) x 2 (version) between-subjects ANOVA. There were no significant effects of version, or interactions of Age x Version. [b]One older adult was not included for not completing the measure. [c]One older adult was not included for not completing the measure. BIS/BAS = Behavioral Inhibition System and Behavioral Activation Scales; PANAS = Positive and Negative Affect Schedule; DASS-21 = Depression Anxiety Stress Scales.

Table 2. Accuracy, Reaction Time, and Inverse Efficiency Scores

				Cue Condition				**Flanker Condition**		
				No	**Double**	**Center**	**Spatial**	**Congruent**	**Incongruent**	**Neutral**
	Age	**Version**	**Incentive**	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*	*M (SD)*
Accuracy (prop. correct)	Younger Adults	Gain	Absent	.95 (.07)	.92 (.08)	.93 (.06)	.97 (.05)	.98 (.04)	.89 (.10)	.97 (.05)
			Present	.94 (.06)	.92 (.08)	.92 (.08)	.95 (.07)	.97 (.05)	.86 (.12)	.96 (.06)
		Loss	Absent	.96 (.03)	.92 (.07)	.93 (.05)	.95 (.05)	.98 (.03)	.88 (.09)	.97 (.04)
			Present	.96 (.04)	.92 (.07)	.92 (.06)	.95 (.06)	.98 (.03)	.86 (.09)	.97 (.04)
	Older Adults	Gain	Absent	.98 (.02)	.98 (.02)	.98 (.02)	.99 (.01)	1.00 (.01)	.97 (.03)	.99 (.02)
			Present	.99 (.01)	.98 (.02)	.99 (.01)	.99 (.01)	1.00 (.00)	.98 (.02)	.99 (.01)
		Loss	Absent	.99 (.02)	.98 (.03)	.99 (.02)	.99 (.01)	.99 (.01)	.97 (.04)	1.00 (.01)
			Present	.98 (.01)	.98 (.02)	.98 (.02)	.99 (.02)	1.00 (.01)	.97 (.03)	.99 (.01)
RT (*ms*)	Younger Adults	Gain	Absent	506 (47)	459 (44)	469 (48)	427 (49)	444 (43)	508 (59)	444 (41)
			Present	488 (49)	446 (53)	452 (53)	413 (49)	427 (43)	495 (69)	427 (41)
		Loss	Absent	520 (40)	469 (44)	487 (44)	445 (40)	453 (41)	536 (53)	452 (34)
			Present	499 (39)	466 (47)	468 (44)	426 (44)	439 (37)	519 (55)	437 (34)
	Older Adults	Gain	Absent	694 (83)	665 (92)	682 (98)	614 (87)	631 (85)	733 (103)	628 (84)
			Present	687 (92)	658 (94)	666 (102)	603 (86)	620 (88)	726 (107)	614 (87)
		Loss	Absent	676 (75)	646 (73)	667 (78)	599 (93)	614 (68)	718 (105)	609 (71)
			Present	668 (76)	639 (75)	657 (79)	591 (82)	608 (71)	710 (103)	598 (66)
IE Score	Younger Adults	Gain	Absent	539 (64)	508 (71)	512 (58)	444 (58)	456 (51)	585 (84)	461 (59)
			Present	528 (63)	499 (67)	504 (56)	440 (63)	441 (43)	589 (104)	448 (54)
		Loss	Absent	548 (43)	516 (50)	532 (47)	472 (39)	464 (44)	619 (64)	468 (39)
			Present	527 (43)	525 (76)	517 (46)	454 (41)	447 (37)	617 (75)	452 (35)
	Older Adults	Gain	Absent	706 (83)	677 (88)	695 (94)	622 (89)	633 (84)	754 (100)	637 (84)
			Present	693 (91)	670 (95)	673 (103)	609 (86)	622 (89)	743 (107)	619 (89)
		Loss	Absent	685 (80)	662 (82)	679 (81)	607 (96)	619 (67)	745 (129)	611 (72)
			Present	680 (76)	654 (81)	672 (83)	600 (88)	612 (71)	737 (122)	605 (67)

Table 3. Effects of Age Group and Task Conditions on Accuracy

	F	***df***		***p***	η_p^2
Omnibus ANOVA					
Age	37.14	1	91	< 0.001	0.29
Cue	22.95	2.9	264.7	< 0.001	0.20
Cue x Age	11.84	2.9	264.7	< 0.001	0.12
Flanker	109.88	1.1	102.7	< 0.001	0.55
Flanker x Age	47.73	1.1	102.7	< 0.001	0.34
Cue x Flanker	12.38	4.1	368.6	< 0.001	0.12
Cue x Flanker x Age	6.18	4.1	368.6	< 0.001	0.06
Flanker x Incentive	4.22	1.7	157.5	0.021	0.04
Flanker x Incentive x Age	5.23	1.7	157.5	0.009	0.05
Alerting					
Cue (No Cue vs. Double Cue)	29.95	1	91	< 0.001	0.25
Cue x Age	16.33	1	91	< 0.001	0.15
Orienting					
Cue (Center vs. Spatial)	29.25	1	91	< 0.001	0.24
Cue x Age	16.35	1	91	< 0.001	0.15
Executive Control					
Flanker (Congruent vs. Incongruent)	122.11	1	91	< 0.001	0.57
Flanker x Age	50.50	1	91	< 0.001	0.35
Flanker x Incentive	8.73	1	91	0.004	0.09
Flanker x Incentive x Age	8.38	1	91	0.005	0.08

Note: Only significant effects ($p < .05$) are shown.

Table 3. Effects of Age Group and Task Conditions on Reaction Time

	F	***df***		***p***	**η_p^2**
Omnibus ANOVA					
Age	186.61	1	91	< 0.001	0.67
Incentive	70.00	1	91	< 0.001	0.43
Incentive x Age	4.34	1	91	0.040	0.05
Cue	410.90	2.7	264.7	< 0.001	0.82
Cue x Age	13.60	2.7	264.7	< 0.001	0.13
Cue x Incentive	3.26	3	273	0.022	0.03
Flanker	385.66	1.3	113.4	< 0.001	0.81
Flanker x Age	11.92	1.3	113.4	< 0.001	0.12
Cue x Flanker	15.80	5.7	514.5	< 0.001	0.15
Cue x Flanker x Age x Version	3.12	5.7	514.5	0.006	0.03
Alerting					
Cue (No Cue vs. Double Cue)	451.05	1	91	< 0.001	0.83
Cue x Age	17.59	1	91	< 0.001	0.16
Cue x Incentive	5.61	1	91	0.020	0.06
Orienting					
Cue (Center vs. Spatial)	360.58	1	91	< 0.001	0.80
Cue x Age	19.72	1	91	< 0.001	0.18
Executive Control					
Flanker (Congruent vs. Incongruent)	407.21	1	91	< 0.001	0.82
Flanker x Age	10.72	1	91	0.001	0.10

Note: Only significant effects ($p < .05$) are shown..

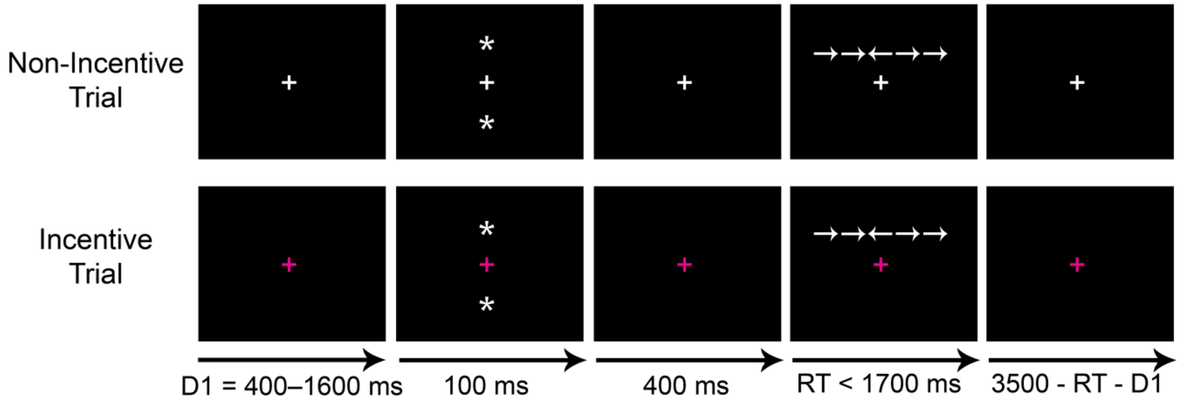

Fig.1. Example of a non-incentive (top) and incentive trial (bottom). Both trials shown demonstrate a double-cued target flanked by incongruent flankers. Stimuli are not to scale.

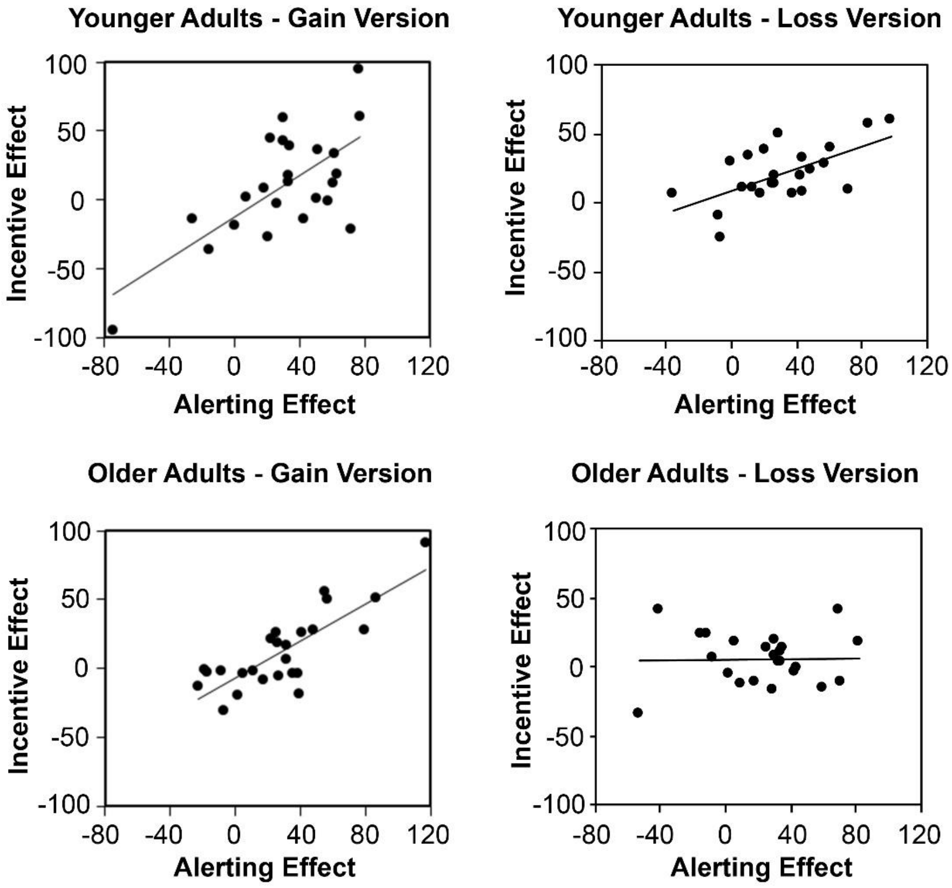

Fig. 2. Relationship between alerting and incentive effects for each participant group.