

Running Head: The Autonomic Nervous System's responses to losses

Loss aversion in the eye and in the heart: The Autonomic Nervous System's responses to losses

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Abstract

The common view in psychology and neuroscience is that losses loom larger than gains, leading to a negativity bias in behavioral responses and Autonomic Nervous System (ANS) activation. However, evidence has accumulated that in decisions under risk and uncertainty individuals often impart similar weights to negative and positive outcomes. We examine the role of the ANS in decisions under uncertainty, and its consistency with the behavioral responses. In three studies, we show that losses lead to heightened autonomic responses, compared to equivalent gains (as indicated by pupil dilation and increased heart rate) even in situations where the average decision maker exhibits no loss aversion. Moreover, in the studied tasks autonomic responses were not associated with risk taking propensities. These results are interpreted by the hypothesis that losses signal the subjective importance of global outcome patterns.

Keywords: decision making, autonomic arousal, loss aversion

Introduction

In the past two decades numerous studies in diverse areas of psychology have suggested that bad is stronger than good, that is, that negative experiences have greater influence on the individual than positive experiences (see Baumeister, Bratslavsky, Finkenauer, & Vohs, 2001; Rozin & Royzman, 2001; Vaish, Grossmann, & Woodward, 2008). For example, research has shown that first impressions are more affected by unfavorable than by favorable information (Fiske, 1980) and that well being is more affected by negative than by positive social interactions (Rook, 1984). Studies of decisions under certainty similarly showed that the threat of losing a potential reward has larger effect on performance than the promise of gaining the same reward (Costantini & Hovig, 1973; Ganzach & Karshai, 1995). Additionally, researchers have recorded more physiological arousal following negative events than following positive events (Bechara, Damasio, Tranel, & Damasio, 1997; Löw, Lang, Smith, & Bradley, 2008; Satterthwaite, et al., 2007; for related findings involving brain activity, see Tom, Fox, Trepel, & Poldrack, 2007). For example, Satterthwaite et al. (2007) administered a task where the participants guessed which of two cards would turn up higher, and received positive or negative feedback according to their success. The results showed that pupil diameter (PD), an index of autonomic activation (Andreassi, 2000), became larger following negative feedback. These findings are assumed to denote a negativity bias, since autonomic nervous system (ANS) arousal, which accompanies emotional or cognitive responses to psychological stimuli (Andreassi, 2000; Annoni, Ptak, Caldara-Schnetzer, Khateb, & Pollermann, 2003; Cacioppo, Tassinary, & Berntson, 2007), has been shown to serve as a physiological correlate for behavioral responses to incentives (Heitz, Schrock, Payne, & Engle, 2008; Sokol-Hessner et al., 2009).

However, examinations of behavioral response to losses in decision making under risk and uncertainty have failed to replicate the negativity bias (Ert & Erev, 2008; Erev, Ert, & Yechiam, 2008; Erev et al., in press; Kermer, Driver-Linn, Wilson, & Gilbert, 2006; Koritzky & Yechiam, in press; Rozin & Royzman, 2001; Yechiam & Ert, 2007; 2009). These studies have demonstrated that increased sensitivity to negative outcomes is not exhibited in the classic laboratory decision making paradigms. Specifically, Kahneman and Tversky (1979) argued that because losses loom larger than gains most people would not accept gambles with mixed symmetric losses (i.e., gaining or losing an amount with the same likelihood). In reality, people tend to be indifferent, on average, between these gambles and their certainty equivalents.

On top of the recent accumulated evidence showing that individuals do not exhibit increased behavioral sensitivity to negative outcomes, due to several methodological considerations, it could be argued that the physiological results in support for a negativity bias in decisions under risk and uncertainty are equivocal. In several of these studies, gains and losses were not symmetrical in magnitude (e.g., Bechara et al., 1997; Sokol-Hessner et al., 2009; Tom et al., 2007), or frequency (e.g., Bechara et al., 1997), so firmest conclusions are not permitted (Baumeister et al., 2001). For instance, in Tom et al. (2007), losses were always smaller than their equivalent gains. Accordingly, the observed negativity bias in this study could be confounded by diminishing sensitivity to large outcomes (Kahneman & Tversky, 1979), which affected (large) gains more than (small) losses.¹ Similarly, these studies did not include a control condition which incorporates no losses. Thus, their results cannot differentiate increased sensitivity to negative outcomes from increased sensitivity to performance failure (i.e., error versus success, see e.g., Critchley, Tang,

Glaser, Butterworth, & Dolan, 2005), consistent with the error related negativity phenomenon (e.g., Frank, Woroch & Curran, 2005), or from increased sensitivity to risk in general, consistent with affect-based decision models (e.g., Clore, Schwarz, & Conway, 1994; Damasio, 1994; Loewenstein, Weber, Hsee, & Welch, 2001).

In the current study we aimed to disentangle the role of losses in decision making, by examining the behavioral response to losses and its physiological correlates in decisions under uncertainty with symmetric gains and losses. In addition, we included an appropriate control condition to differentiate the effect of absolute losses from that of relative losses, in order to compare an assertion of arousal following losses to arousal following errors.

To do so, we evaluated three contrasting hypotheses. The first hypothesis builds on the suggestion of Erev et al. (2008) that decisions under uncertainty represent a distinct context in which people have no special sensitivity to losses, as opposed to riskless decisions (see also Ert & Erev, 2008). This is explained by the argument that because in decisions under uncertainty (and risk) the same alternative produces both gains and losses, people's tendency to maintain some level of risk (and avoid boredom and monotonicity) implies no discounting of small to moderate losses compared to equivalent gains (Yechiam & Ert, 2007). Assuming that autonomic arousal also reflects the subjective indifference to losses in such decisions, then both behavior and ANS arousal should not exhibit the negativity bias.

The second hypothesis, which is referred to as the individual differences hypothesis, builds on findings of individual differences in the subjective weighting of losses and gains (Busemeyer & Stout, 2002; Sokol-Hessner et al., 2009; Worthy, Maddox, & Markman, 2007). Specifically, these studies have demonstrated that some individuals give more weight to losses, and others to gains. If the autonomic arousal

generated by losses (compared to gains) is consistent with their subjective impact (as suggested by affect-based models), then a positive correlation is expected between arousal following losses and risk aversion with symmetric gains and losses, though similar to behavioral responses, there should be no negativity bias in ANS responses, on average.

The third and final hypothesis suggests that losses signal a potential threat in the environment and hence lead to increased arousal (see Critchley, Mathias, & Dolan, 2002). However, they affect the subjective significance of *whole* outcome patterns and not only the loss component. Accordingly, losses increase the perceived risk associated with choice alternatives (Yechiam, 2009). Since people are differentially affected by the perceived risk level (i.e., some people are risk averse and stay away from low to moderately risky situations while others are risk seeking and prefer them over their certainty equivalents; e.g., Holt & Laury, 2002), the increased arousal should not be associated with the individual's tendency to take risk. We shall refer to this last account as the Loss signals Risk (LSR) hypothesis. Findings consistent with this hypothesis were reported by Coombs and Lehner (1981, 1984) who showed that for a lottery where individuals have an equal chance of winning or losing \$10, adding \$10 to the loss increased perceived risk more than adding the same amount to the gain.²

It should be noted that since autonomic arousal is assumed to represent the impact of emotional responses to negative and positive outcomes (Sokol-Hessner et al., 2009), the LSR hypothesis departs from some affect-based decision-models (e.g., the *risk-as-feelings* hypothesis by Loewenstein et al., 2001; the *somatic-marker* hypothesis by Damasio, 1994), which argue that affect experienced at the moment of decision making is used to evaluate the level of risk, and to then direct behavior, even

in the face of divergent cognitive information. The LSR hypothesis is different because it suggests that the affective signal induced by losses is integrated in the more global evaluation concerning risk level (thus predicting no direct linkage between affect following losses, indexed by arousal, and subsequent choices).

To test these hypotheses, we conducted three studies. The first two studies measured the change in PD following gains compared to losses. PD was used since it is considered an immediate and direct index of autonomic activation, which is directly related to cognitive and emotional processes (Andreassi, 2000; Bradley, Miccoli, Escrig, & Lang, 2008; Granholm & Steinhauer, 2004). In addition, PD has been found to be relatively sensitive to monetary incentives used in decision making tasks (Heitz et al., 2008). Finally, it has been suggested that the parasympathetic branch of the ANS might be particularly sensitive to threatening environmental stimuli (L ow et al., 2008) and we thus chose to use a measure such as the PD which is affected by both the sympathetic and parasympathetic branches (Andreassi, 2000; Hutchins & Corbett, 1997) rather than using measures that tap only the sympathetic branch activation (such as skin conductance). Study 3 examined the same hypotheses using Heart-Rate (HR), a more commonly studied ANS measure (Andreassi, 2000; Malik, 1996).

Together, the three studies indicate that autonomic indices display a negativity bias even when behavior is not negatively biased. Moreover, the results are consistent with the LSR hypothesis, showing no association between autonomic responses to losses and behavioral tendencies to avoid them.

Study 1: Effects of gains and losses on pupil diameter

In this study, the participants were administered decision tasks involving absolute or relative monetary losses. In addition to examining their behavioral choices, we also

recorded their autonomic activity, as indexed by the effect of losses (and gains) on their pupil dilation. The participants played for points with a conversion rate of 1 New Israeli Shekel (NIS) per 10 points earned. In the first (within-subject) condition, referred to as the Mixed Condition, one choice alternative resulted in a 50/50 chance of gaining or losing 2 points and the other resulted in a 50/50 chance of gaining or losing 1 point. The second condition, labeled All-Gains, offered a similar dilemma, with the exception that a fixed value of 3 points was added to all payoffs (i.e., one alternative produced 1 or 5 points and the other produced either 2 or 4 points, with equal probability). This All-Gains condition was created to preserve the risk level while eliminating the possibility of incurring losses.

Method

Participants

Twenty-five healthy undergraduates from the Technion – Israel Institute of Technology (13 females; mean age, 23.8 years, SD = 1.9) participated in the experiment. All participants were free of neurological and psychiatric history and had normal or corrected 20/20 vision. Participants were given a show-up fee of NIS 20 and were additionally paid according to the amount earned in the experimental task.

Procedure

Participants were presented with a computerized “money machine”, which consisted of two unmarked buttons, an obtained payoff counter, and an accumulated payoff counter (see Appendix). Each selection of one of the buttons was followed by a presentation of the obtained payoff, (e.g., -2 or +2 in the risky option under the Mixed condition) on the selected button and on the obtained payoff counter for two seconds,

and an updating of the accumulated payoff counter which was presented constantly. The minimal inter-trial interval was 2 seconds, and the number of trials in each condition was 60.

The participants were instructed to repeatedly select a button in order to maximize their earning, while their PD was recorded. Participants were also informed that they would earn NIS 1 for every 10 points won in the experiment. The payoffs were contingent on the participants' choices, as indicated above. In addition, in order to make the incentive structure less obvious, a constant of 0.1-0.5 (in 0.1 intervals) was randomly added or subtracted from the sampled payoff in every trial.

Payoffs were delivered in a deterministic fashion: each task started with either a gain/relative-gain or a loss/relative-loss, and in each choice alternative (independently) the sign of the payoff was switched on each trial. This was done so as to eliminate possible surprise effects that would be non-symmetric with respect to gains and losses. In addition, the order of the two experimental conditions was controlled. Half of the participants were presented first with the Mixed condition, followed by the All-Gains condition, while for the other half this order was reversed. Similarly, half of the participants were presented with a gain/relative-gain in the first trial, followed by a loss/relative-loss in the second trial, while for the other half this order was reversed.

PD data acquisition

Eye-tracking data was collected using ViewPoint PC 60 EyeFrame system (Arrington Research, Scottsdale, Arizona). The system operates with a single tiny camera and an infrared illuminator mounted on a lightweight frame facing toward the participant's dominant eye, and supported by comfortable head straps. It records pupil data at

approximately 30 frames per second (fps). Pupil data was measured as the diameter of the pupil in response to gains and losses in the window of 0.5 seconds before the stimulus onset to 2.0 seconds after stimulus onset. Pupil data was averaged to produce a data step every 250 milliseconds. A negativity bias in this measure was expected to be manifested by an increase in the PD following losses compared to gains in the Mixed condition. The participants' heads were fixed by a head and chin rest during the whole session. New sixteen-point calibrations and validations were performed prior to the start of each session.

Results

The proportion of risky choices [P(Risky)] across all trials in Study 1 was 0.46 in the Mixed condition and 0.51 in the All-gains condition (Figure 1A). A t-test for paired samples revealed no significant difference between P(Risky) in the two conditions [$t(24) = -0.89$, $p = .38$]. In addition, both proportions were not significantly different from the 50% chance level [$t(24) = -1.25$, $p = .22$; $t(24) = 0.26$, $p = .80$, respectively]. As been shown in several recent studies of decisions under uncertainty (e.g., Erev et al., 2008; Kermer et al., 2006; Koritzky & Yechiam, in press; Yechiam & Ert, 2007), our results indicated that behaviorally, participants did not prefer outcomes with lower losses, nor exhibited more risk aversion in the Mixed condition as would be predicted if losses were overweighted.³

On the other hand, absolute losses in the Mixed condition were associated with larger average PDs compared to absolute gains approximately 625-875 ms after the outcomes were presented (Figure 1B). This was not observed for the All-Gains condition (Figure 1C). Two by two repeated measures analyses of variance (ANOVA) were conducted for each of the epochs with payment (gains versus losses; either

absolute or relative) and condition (Mixed versus All-Gains) as within subject variables. The results showed a significant interaction between payment and condition in the epoch of 625-875 ms [$F(1, 24) = 4.106, p = 0.05$].

Post-hoc paired-sample t-test analyses revealed that in the Mixed condition the increased arousal following losses was significant in the epochs of 625 ms to 1125 ms after the stimulus onset [625-875 ms: $t(24) = -2.63, p = .01$, and 875-1125 ms: $t(24) = -2.33, p = .03$, respectively]. These results were replicated for separate choice alternatives (i.e., risky versus safe) (Figure 2A and 2B), suggesting that the negativity bias is robust and does not reflect mere risk aversion. However, these findings were not observed in the All-Gains condition (i.e., *relative* losses did not lead to more arousal than relative gains) (Figure 1C). Thus, a gap appeared between the behavioral loss-indifferent choices and the autonomic negatively biased responses.⁴

We next evaluated the contrasting predictions of the individual-differences and LSR hypotheses by examining if individuals who respond to losses by increasing their arousal (compared to gains) also exhibit more loss aversion. Focusing on the Mixed condition, we calculated the correlation between the unique arousal experienced upon losses [625-1125 ms. following the onset of the outcome presentation: $PD(\text{Losses}) - PD(\text{Gains})$] and the proportion of choices from the safe alternative which produces lower magnitude losses. The results showed no significant correlation ($r = -0.06, p = .76$). This pattern of results supports the LSR hypothesis (although it should be interpreted with caution due to the small sample size), and suggests that individual differences in contingent arousal do not seem to affect the tendency to avoid losses.

Finally, we examined the intra-individual consistency between arousal following a loss and the tendency to switch choices immediately afterwards. For each

participant, the correlation between arousal in response to the large loss from the risky alternative (in time t) and the choice made following this loss (in $t+1$) was calculated (0 = no switch; 1 = switch). The result of this analysis showed that on average, the correlation was near zero (average $r = 0.025$, $SD = 0.31$, in the epochs of 625 ms to 1125 ms after the stimulus onset). A one-sample t-test analysis revealed that the average correlation was not significantly different from zero [$t(49) = 0.58$, $p = 0.57$]. These findings further support the LSR hypothesis and show that increased arousal following the losses from the risky alternative did not predict the tendency to switch to the safe alternative in the subsequent trials.

Study 2: Replication with natural numbers

The results of Study 1 could be interpreted as indicating that in decisions under uncertainty the ANS is more sensitive to losses than participants' choice behavior. However, an alternative interpretation is that the enhanced autonomic arousal was the result of the effort in processing negative numbers (Tzelgov, Ganor-Stern, & Maymon-Schreiber, 2009). Study 2 was designed to contrast these two interpretations. For this purpose the +/- signs were represented by randomly selected colors (either green or red) so that natural rather than negative numbers denoted the magnitude of penalties.

Method

Participants

Nineteen healthy undergraduates from the Technion (13 females; mean age, 24.1 years, $SD = 2.6$) who did not take part in Study 1 participated in the experiment. All participants were free of neurological and psychiatric history and had normal or

corrected 20/20 vision. Participants were given a show-up fee of NIS 30 and were additionally paid according to the amount earned in the experimental task.

Procedure

The procedure was identical to that of Study 1 (Mixed condition). However, the +/- signs were represented by randomly selected colors (either green or red). Specifically, participants were randomly assigned to one of two conditions. In the first condition ($n = 10$) negative outcomes were represented by red colored buttons and positive outcomes were represented by green colored buttons. In the second condition the colors were reversed. Participants were instructed about the meaning of the two colors. A manipulation check conducted after task completion revealed that all participants associated the color with its correct meaning (reward or penalty). Additionally, the accumulated payoff was also presented graphically, and its color matched the color assigned to positive or negative outcomes, depending on the sign of the accumulated sum. Finally, to ensure that the effect is not limited to small nominal magnitudes (Harinck et al., 2007), nominal payoff values were multiplied by 10.

PD data acquisition

Recordings of physiological data were conducted as in Study 1.

Results

Virtually the same pattern of results was found as in Study 1. The aggregated proportion of P(Risky) across all trials was 0.48 (Figure 3A), and not below chance level [$t(18) = -0.68$, $p = .50$]. At the same time, losses were associated with significantly larger PDs on average, in the epochs of 375-625 ms [$t(18) = -1.74$, $p =$

.09] and 625-875 ms [$t(18) = -4.44, p < .001$] after the stimulus onset (Figure 3B).

This pattern remained when choices were held constant (Figure 4).

We next calculated the correlation between the unique arousal experienced upon losses in the Mixed condition [375-875 ms. following the stimulus onset: $PD(\text{Losses}) - PD(\text{Gains})$] and the proportion of choices from the safe alternative which produces lower magnitude losses. The results show no significant correlation ($r = 0.31, p = .19$), again suggesting that loss sensitivity is relatively independent from the individual's arousal level following losses, as predicted by the LSR hypothesis.

Finally, as in Study 1, the correlation between arousal in response to the larger loss (from the risky alternative) and the decision to switch to the safe alternative afterwards was calculated separately for each participant. The result of this analysis showed that on average, the correlation was close to zero (average $r = 0.04, SD = 0.33$, in the epochs of 375 ms to 875 ms after the stimulus onset). A one-sample t-test analysis revealed that this correlation is indeed not significantly different from zero [$t(36) = 0.806, p = 0.425$]. Thus, consistent with the LSR hypothesis, increased arousal in response to the losses from the risky alternative did not predict the tendency to switch choices afterwards.

Study 3: Effects of gains and losses on Heart Rate

In this study we sought to examine the generality of the current results for other measures of autonomic arousal. While properly created control conditions can ensure that autonomic indices are not driven by baseline physiological characteristics (such as the tonic pupil size), an assessment using multiple autonomic indices serves to validate this further. We chose HR, a common measure of cognitively-related ANS activity. Like the PD, HR is affected by both the sympathetic and parasympathetic

branches of the ANS and thus represents the general response of this system (Andreassi, 2000). In this final study participants were administered the same task as in Study 1, while their autonomic activity, as indexed by HR, was monitored.

Method

Participants

Twenty-two healthy undergraduates from the Technion (8 females; mean age, 23.7 years, SD = 1.5) who did not take part in Studies 1 and 2 participated in the experiment. All participants were free of neurological and psychiatric history. Participants were given a fixed rate fee of NIS 20 and were additionally paid according to the amount earned in the experimental task.

Procedure

The procedure was identical to that of study 1 except for the minimal inter-trial interval, which was set to 15 seconds to minimize residual effects of prior outcomes.

HR data acquisition

HR data was obtained using the SitePAT-200 (Itamar Medical Ltd., Keisaria, Israel), a photo-cell sensor plethysmograph, shaped as a finger cup, which is placed at the end of the first finger of the non-dominant hand (see e.g., Karasik et al., 2002). The participants' non-dominant hand was fixed on a hand rest during the whole session. The rate of data acquisition was 100 Hz, averaged to about 1 sample per second. HR data is presented as the number of beats of the heart in a minute. HR was measured in the window of 2 seconds before the stimulus onset to 5 seconds after stimulus onset.

Results

The proportion of risky choices across all trials in Study 3 was 0.5 in the Mixed condition and 0.49 in the All-gain condition (Figure 5A). A t-test for paired samples revealed no significant difference between P(Risky) in the two conditions [$t(21) = 0.107$, $p = 0.92$]. In addition, both proportions were not significantly different from the 50% chance level [$t(21) = 0.034$, $p = 0.97$; $t(21) = -0.10$, $p = 0.92$, respectively]. Thus, similar to Studies 1 and 2, our results indicated that participants did not exhibit any increased sensitivity to negative outcomes in their behavioral choices.

On the other hand, absolute losses in the Mixed condition were associated with higher average HR compared to absolute gains (Figure 5B). A two by two repeated measures ANOVA (conducted as in Study 1) revealed a significant interaction between payment and condition in the epoch of 1-2 seconds following the outcome presentation [$F(1,21) = 4.121$, $p = 0.05$]. Consistent with the results of Study 1, this interaction suggests that the increased sensitivity of the autonomic activation index to negative outcomes was the result of a unique response to absolute losses.

Post-hoc paired-sample t-test analyses revealed that in the Mixed condition, the difference was significant in the epochs of 0-1 and 1-2 seconds after the stimulus onset [$t(21) = -2.137$, $p < .05$, and $t(21) = -2.607$, $p < .02$, respectively]. However, these findings were not observed in the All-Gains condition (i.e., *relative* losses did not lead to more arousal than relative gains) (Figure 5C). Thus, as in Studies 1 and 2, a gap appeared between the behavioral loss-indifferent choices and the autonomic negatively biased responses. The same pattern of results was observed for separate choice alternatives (i.e., risky versus safe) but for conciseness this examination is not presented.

As in the previous studies, we next evaluated the contrasting predictions of the individual-differences and LSR hypotheses by examining if individuals who respond to losses by increasing their arousal also exhibit more loss aversion. Focusing on the Mixed condition, we calculated the correlation between the unique arousal experienced upon losses [0-2 seconds after the stimulus onset: $HR(\text{Losses}) - HR(\text{Gains})$] and the proportion of choices from the safe alternative which produces lower magnitude losses. The results showed no significant correlation ($r = -0.09$, $p = .68$). Thus, in support of the LSR hypothesis, individual differences in contingent arousal did not correlate with the tendency to avoid losses.

Finally, for each participant, the correlation between arousal in response to the loss from the risky alternative and the decision to switch to the safe alternative in the next trial was calculated. The results of this analysis showed that the average correlation was close to zero (average $r = -0.03$, $SD = 0.33$, in the epochs of 0-2 seconds after the stimulus onset). A one-sample t-test analysis revealed that this correlation was not significantly different from zero [$t(43) = 0.607$, $p = 0.55$]. Thus, these findings correspond to the PD findings, and provide converging support for the LSR hypothesis, suggesting that for the majority of the participants, increased arousal in response to the losses from the risky alternative did not affect the tendency to avoid this alternative; even though there was, on average, increased HR following losses than following equivalent gains.

General discussion

The present studies replicate recent findings indicating no behavioral sensitivity to negative outcomes in decisions under uncertainty (Erev et al., 2008; Kermer et al., 2006), but at the same time show that this pattern of behavior is accompanied by a

negativity bias in autonomic arousal. Additionally, the current studies show no correlation between autonomic arousal following losses (pupil size changes, heart rate) and the loss sensitivity of individual decision makers. Although there were some deviations across the three studies, overall, the correlations between arousal following losses compared to gains and risk avoidance with losses were near zero and none was significant. These results reject the individual-differences hypothesis suggesting that some individuals are sensitive to losses in their autonomic responses as well as their behavioral choices. Rather, the findings support the LSR hypothesis which argues that losses are a signal of threat, and result in an increased subjective significance of whole outcome patterns (i.e., both gains and losses).

The LSR hypothesis appears to tie together the findings in decisions under certainty and uncertainty. In decisions under certainty where outcome patterns are either all gains or all losses and no risk is involved, the subjective significance of losses is larger than that of gains because the global effect of losses is not diffused to other outcomes (since all outcomes are losses). Consequently, people show loss aversion in these tasks (e.g., Costantini & Hovig, 1973). However, in decisions under uncertainty with mixed outcomes losses are assumed to lead to an increase in the subjective effect of all outcomes, thus when the outcomes are balanced (i.e., when gains and losses are symmetric) they are assumed to increase the subjective risk level. Nevertheless, the increase in autonomic activity following losses is not translated into a tendency to avoid such mixed outcomes, even for individuals with very high arousal following losses. Some of these individuals do avoid the risky outcomes signaled by losses, but others approach them.

Additionally, the current findings also go beyond error-based explanations of the negativity bias. It has been shown that error processing (i.e., performance failure)

activates the ANS (Critchley et al., 2005). However, in the current context, this error-based explanation would suggest a similar pattern of results in the Mixed and the All-gains conditions, since both conditions contain the same degree of performance failure (relative to the reference point). The current results, showing that ANS activation was only larger following absolute losses suggests that negative outcomes trigger a distinct autonomic response, even compared to errors.

One major implication of the current results is that they suggest a boundary condition for affect based theories (e.g., the risk as feeling hypothesis by Loewenstein et al., 2001; the affect heuristic by Slovic, Finucane, Peters, & MacGregor, 2002). Specifically, affect-based models posit that risk preferences are determined predominantly by emotional responses (and that autonomic reactions are correlated with these responses). Under this logic, and consistent with the autonomic level negativity bias, we should have observed loss-averse behavioral patterns.

These results suggest that at least when risk levels are not high the link between autonomic/affective reactions is less direct and specific and involves computations which take into account assessments concerning the global situation (i.e., the effect of both gains and losses). Future studies in this direction may look into similar effects in more complex emotions. For example, in negotiations, anger is known to lead to negative feelings towards the anger expresser (Allred, Mallozzi, Matsui, & Raia, 1997), but it may also have a global effect of signaling the extremity of people's attitudes (Abelson, 1995; Friedman et al., 2004).

Additionally, the current findings have some implications to the study of individual differences in risk taking. In particular, it has been suggested that sensitivity to risk level consistently modulates risk taking behavior, which implies that individual differences in risk taking should be consistent across situations or domains

(e.g., Bromiley & Curley, 1992; Streufert, 2006). However, experimental studies have documented inconsistencies in individuals' behavioral patterns of risk taking in different contexts (Hanoch, Johnson, & Wilke, 2006; Schoemaker, 1990; Weber, Blais, & Betz, 2002) and even in different administrations of the same task (Kindlon, Mezzacappa, & Earls, 1994). This apparent contradiction could be resolved under the LSR hypothesis framework. Specifically, the LSR hypothesis proposes that when losses are available, risk is signaled, and the subjective attitude towards risk has a larger impact. It therefore suggests that losses increase behavioral consistency in risk taking behavior, and that without losses this consistency may be broken. Preliminary support for this assertion has been found in a recent longitudinal study of decisions under uncertainty (Yechiam, 2009). In this study participants performed a battery of decision tasks in two separate occasions with about 50 days difference between them. Temporal consistency in risk taking across sessions was significant only for decision tasks involving losses, suggesting that losses increase behavioral consistency.

Potential limitations

Potential limitations of the current study include the fact that the LSR hypothesis predictions included an interaction effect (of arousal following losses compared to gains, and not following relative losses) but also a null correlation between arousal and behavioral choices. Though inconsistent with studies showing that autonomic arousal is highly implicated in decision processes (e.g., Bechara et al., 1997; Critchley et al., 2001; Gerdes, 2006), this null correlation can be interpreted as denoting complete breakup between autonomic arousal and decision processes involving risk taking. In contrast, under the LSR hypothesis the ANS serves to infer the level of environmental risk and alert the organism so that it could tailor its risk attitude

accordingly, yet this does not have a linear effect on behavior (some individuals take risk and others avoid it). Future studies should further validate the argument of the LSR hypothesis concerning the relation between autonomic arousal and actual behavior. For example, the LSR hypothesis implies that in *very high* levels of risk, the arousal following losses would be correlated with the tendency to avoid risk for most individuals.⁵

Another possible limitation is that the absence of loss aversion in the current studies could have been due to the specific conditions of the task, specifically the fact that it included unavoidable losses (i.e., a decision maker could lower the magnitude of the loss but not its frequency). Although recent studies have shown that in decisions under uncertainty where losses are avoidable there is no behavioral loss aversion (e.g., Yechiam & Ert, 2007 Erev et al., 2008), it would be important to examine if the gap between autonomic responses to losses and behavioral choices appears in these tasks as well. Examining this with affective reactions (e.g., ratings of feelings) would also enable drawing stronger conclusions with respect to the type of tasks where the predictions of affect based model hold, and where they do not.

Finally, another open question concerns the temporal dynamics of the autonomic responses. It is interesting to note that the differences in PD responses to gains and losses occurred at about 600-1000 milliseconds after the presentation of the outcome. Previous findings using PD have shown differences in a similar timeframe of approximately 1 second in the response to stimuli of different subjective significance such as in the response to relevant versus irrelevant text words (e.g., Oliveira, Aula, & Russell, 2009), and to positively or negatively marked words (Bierman, 2004). However, the significance of this time period is yet unclear.

Conclusions

The present findings show that in decisions under uncertainty, the response of the ANS is negatively biased. However, the simple interpretation of this bias as an indicator of the subjective significance of losses is inconsistent with the data. Even at the individual level, those showing high arousal did not tend to avoid losses to a greater extent. These results suggest a special role of losses in signaling the risk levels of global situations or environments, which has the ecological benefit of allowing individuals to tailor their behavioral choices to their preferred risk level (Yechiam, 2009). The current study represents the first psychophysiological test of this hypothesis, and clearly more research is needed to validate it.

Appendix

A screenshot of the experimental task (the Risky and Safe alternatives were randomly assigned to buttons A and B for each participant).

	A		B
	-2.4		-2.4
You got:	-2.4		
Total:	-1.9		

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Figure 1: Study 1 results. (A) Proportion of participants selecting the risky option in the two experimental conditions. Trials are presented in blocks of 15. (B) Average pupil diameter in the Mixed condition as a function of the event type (gain versus loss). Time zero denotes the outcome presentation onset. Significant differences are marked by black dotted lines. (C) Average pupil diameter in the All-Gains condition as a function of the event type (relative gain versus relative loss).

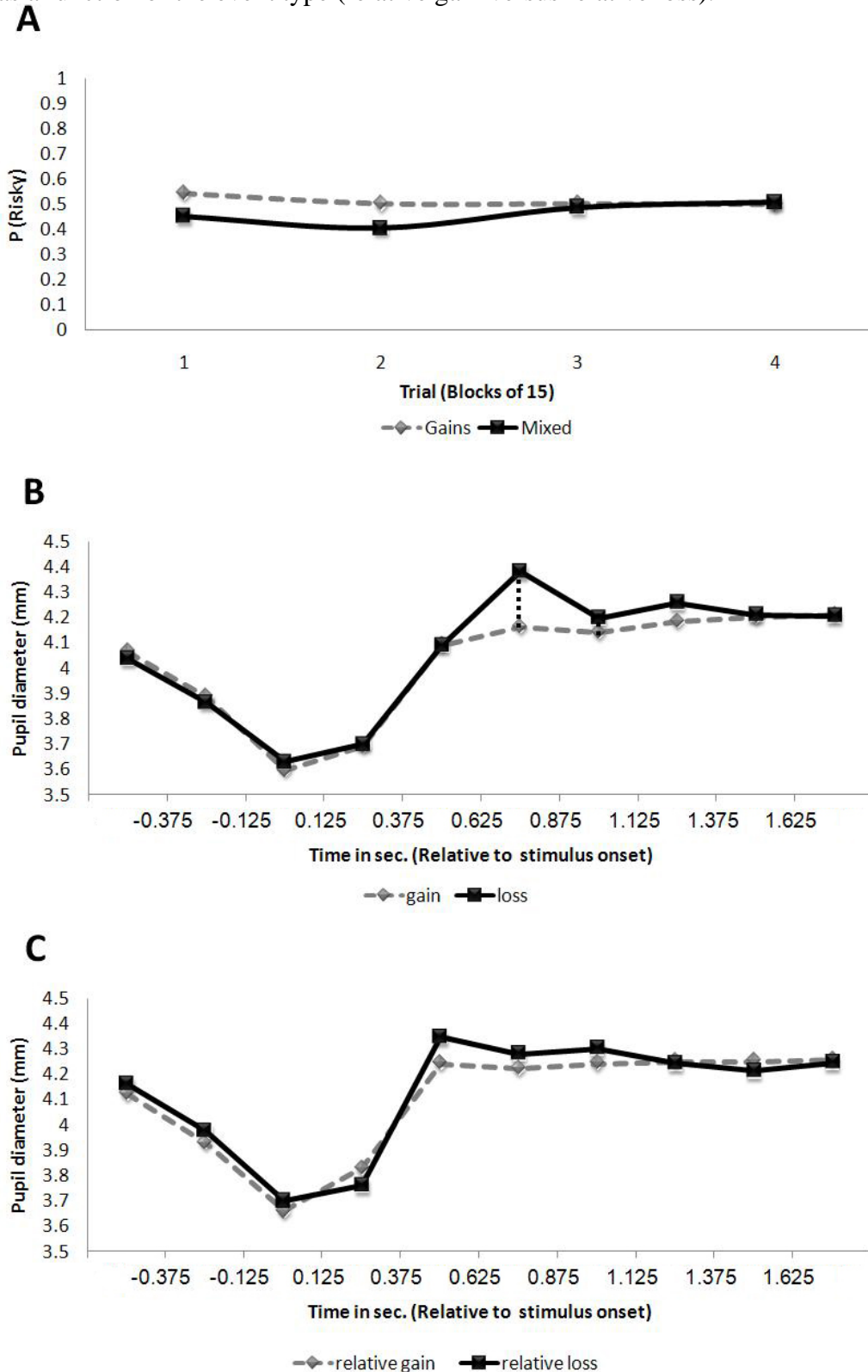


Figure 2: Detailed pupil diameter results for the Mixed condition of Study 1. (A)

Average pupil diameter as a function of the event type (gain versus loss) for the safe choices only. Time zero denotes the outcome presentation onset. Significant differences are marked by black dotted lines. The results indicate that in the epoch of 625-875 ms, pupil diameters were significantly larger following negative than following positive outcomes ($p < .01$). (B) Average pupil diameter as a function of the event type (gain versus loss) for the risky choices only. The results indicate that in the epochs of 625-1375 ms pupil diameters were significantly larger following negative outcomes ($p < .05$).

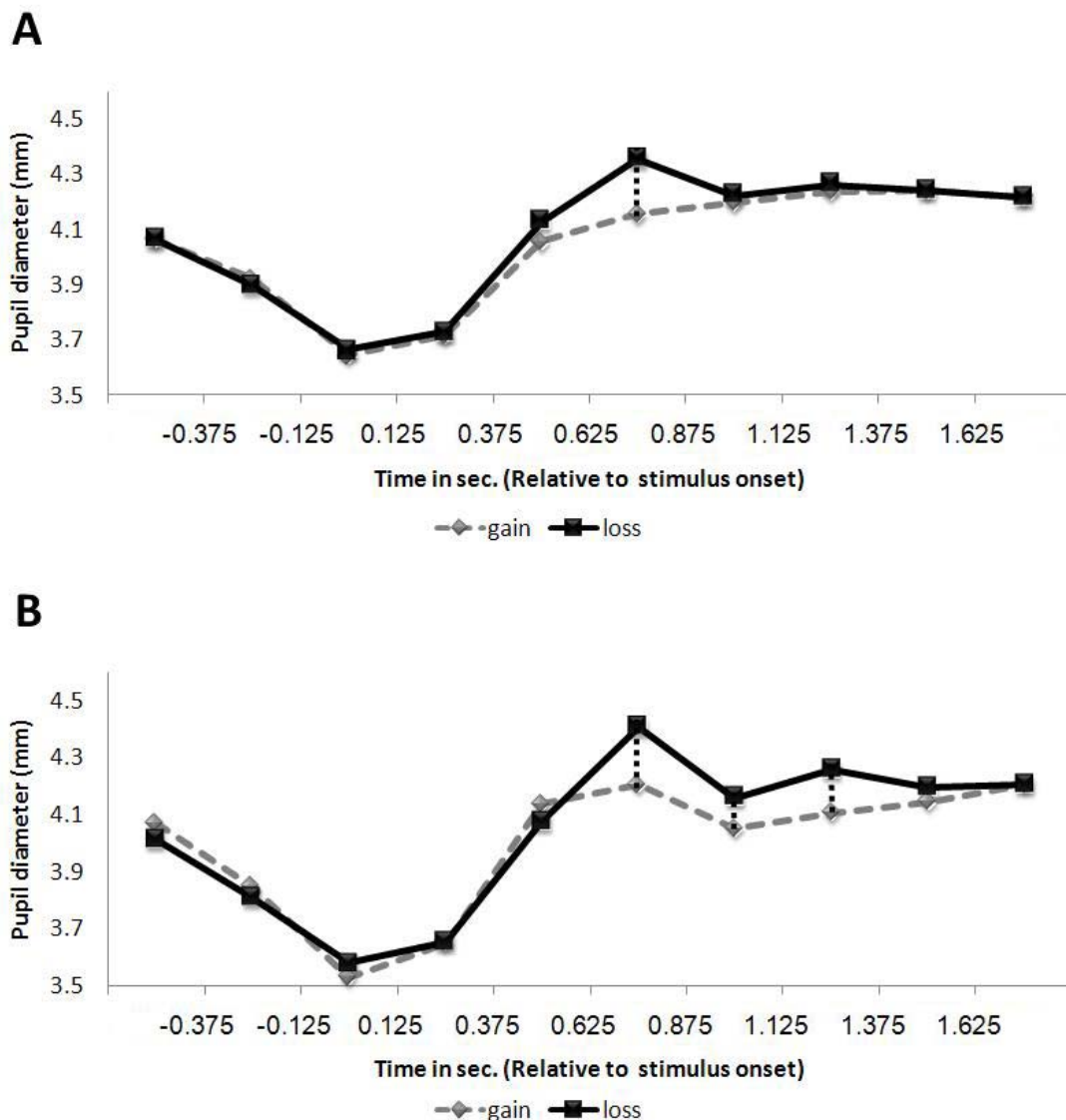


Figure 3: Study 2 (color version) results. (A) Proportion of participants selecting the risky option. Trials are presented in blocks of 15. (B) Average pupil diameter as a function of the event type (gain versus loss). Time zero denotes the outcome presentation onset. Significant differences are marked by black dotted lines.

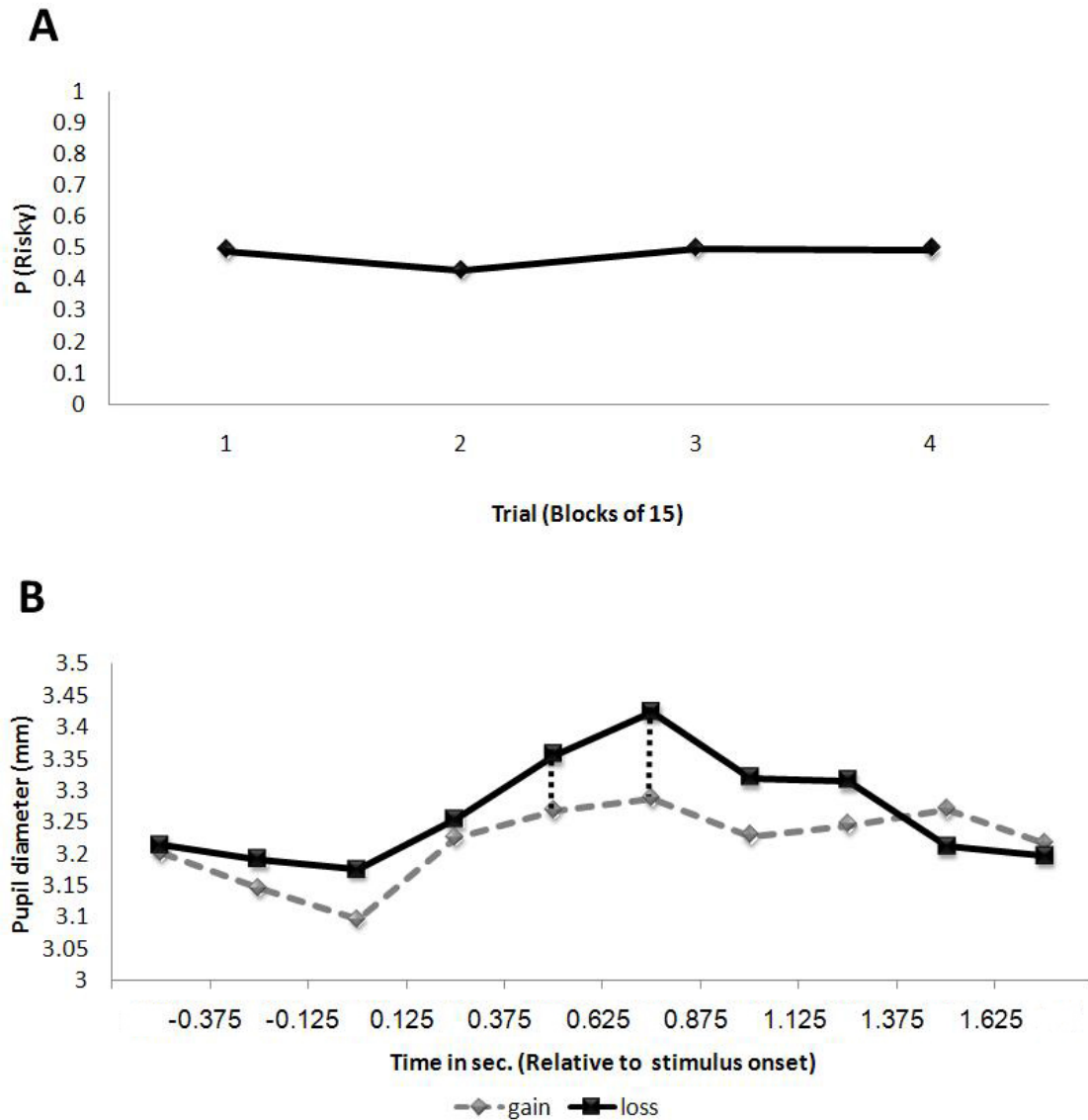


Figure 4: Detailed pupil diameter results for Study 2. (A) Average pupil diameter as a function of the event type (gain versus loss) for the safe choices only. Time zero denotes the outcome presentation onset. Significant differences are marked by black dotted lines. The results indicate that in the epochs of 625-1375 ms pupil diameters were significantly larger following negative than following positive outcomes ($p < .05$). (B) Average pupil diameter as a function of the event type (gain versus loss) for the risky choices only. The results indicate that in the epoch of 626-875 ms, pupil diameters were significantly larger following negative than following positive outcomes ($p < .05$).

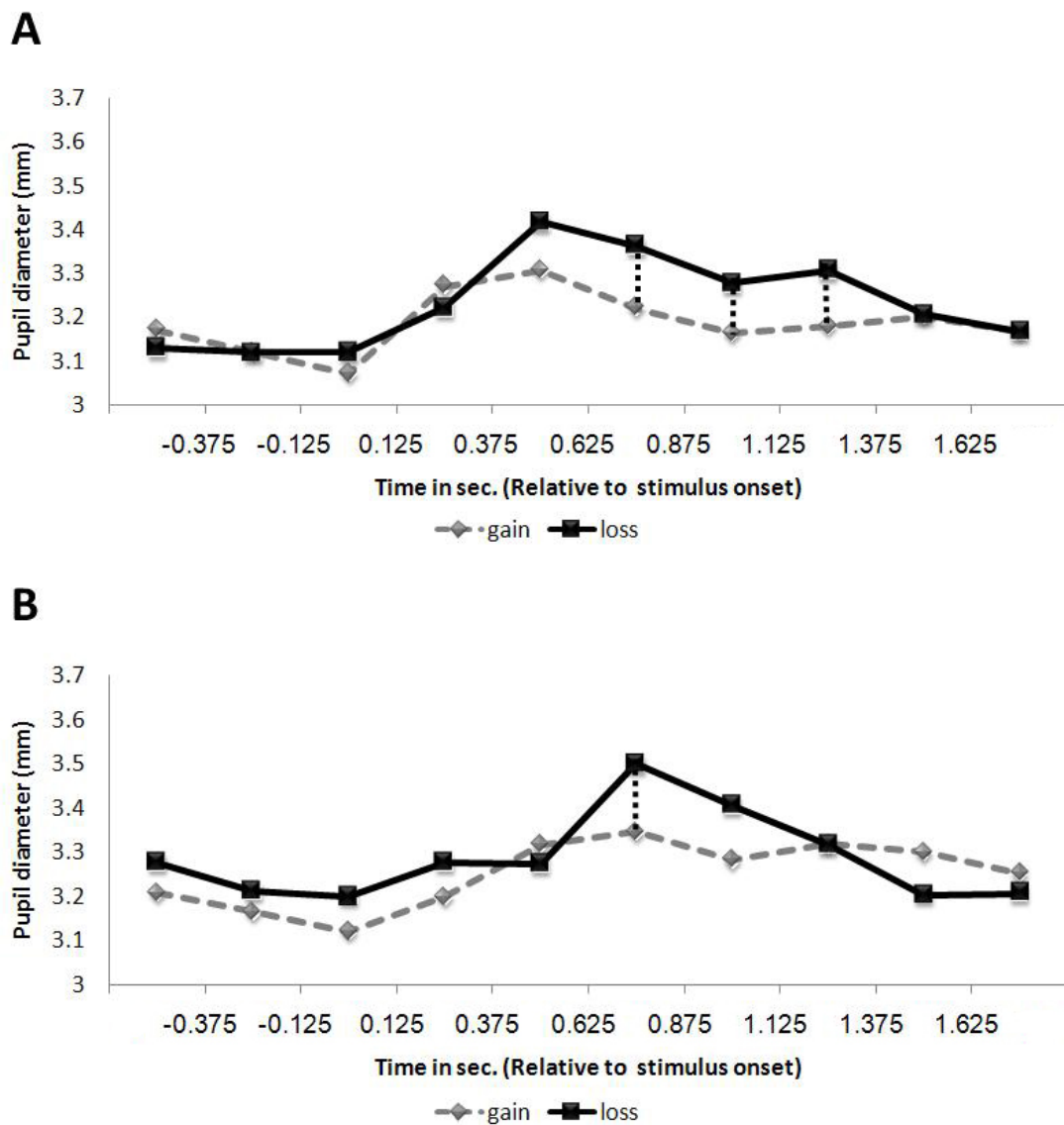
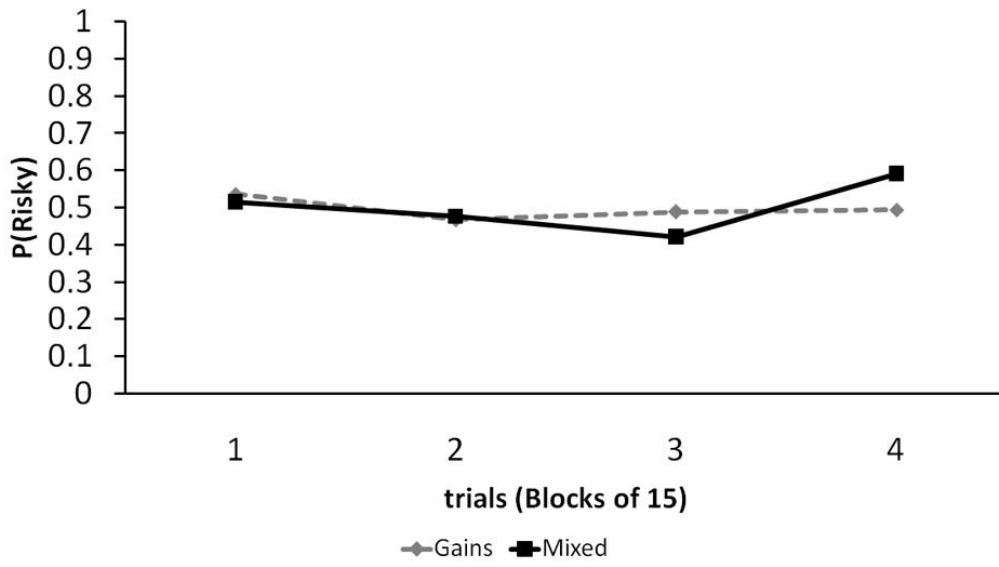
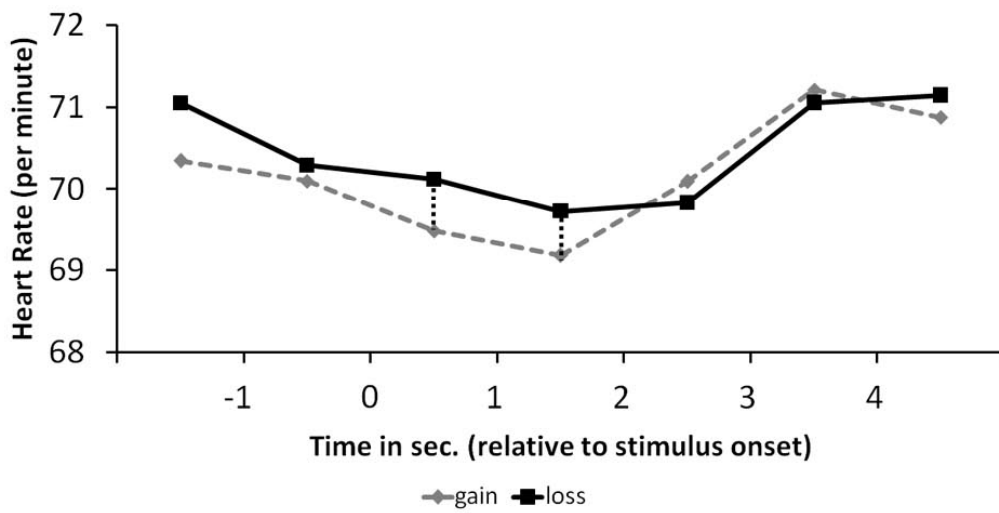
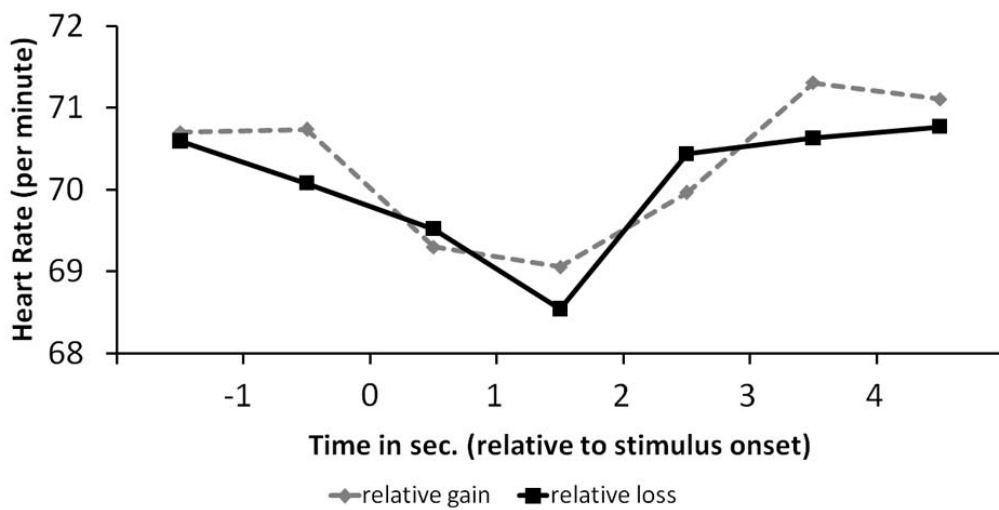


Figure 5: Study 3 results. (A) Proportion of participants selecting the risky option in the two experimental conditions. Trials are presented in blocks of 15. (B) Average heart rate in the Mixed condition as a function of the event type (gain versus loss). Time zero denotes the outcome presentation onset. Significant differences are marked by black dotted lines. (C) Average heart rate in the All-Gains condition as a function of the event type (relative gain versus relative loss).

A**B****C**

Footnotes page

¹ Note that Tom et al. (2007) did not examine ANS responses but rather observed a negativity bias in the neuronal activation of several brain regions, including the anterior cingulate cortex (ACC) which is involved in the regulation of autonomic activity (Critchley, Mathias, & Dolan, 2001).

² Yet these findings have the possible problem of individuals not being able to clearly define the term risk independently from loss.

³ No gender differences was found for the behavioral or for the physiological responses in Study 1, as well as in the other studies reported in this paper. Thus, for conciseness, the data for females and males was collapsed.

⁴ Note that the simple individual differences hypothesis noted above predicts no negativity bias for the average decision maker. Yet one could still posit under the individual differences framework that the human ANS is more sensitive to losses than gains in robust settings (as demonstrated above), but in situations involving relatively small losses only some people exhibit behavioral loss aversion (see e.g., Harinck, Van Dijk, Van Beest, & Mersmann, 2007). This would conform to the main effect found, and also predict consistency between autonomic and behavioral responses to losses. This prediction is examined next.

⁵ While individuals tend to be risk neutral in low to moderate risk level, high risk levels lead to risk aversion (Erev et al., 2008; Holt & Laury, 2002)