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Sequential choices using signal detection theory can reverse classical predictions

John M. McNamara and Pete C. Trimmer

Abstract

The behavioural sciences have been strongly influenced for several decades by signal detection theory (also known as ‘error management theory’ and ‘ROC analysis’). The theory provides simple logic about how individuals should behave in order to maximise their expected payoff in a single decision; for instance, the theory predicts that as the probability of a particular danger increases, individuals should be more prone to avoiding that danger. However, such findings need not hold in situations where more than one decision will be made, and recent work has shown that when behaviour is allowed to depend on the energy reserves of the individual, the classical predictions can be reversed. Here, we use a simple analytic technique to show that even when the same behavioural rules are used at every reserve level, the predictions of classical signal detection theory (as though only a single decision will be made) are often reversed in a world where autocorrelation is high. The classical predictions are reversed because individuals will often make multiple decisions to achieve a goal, and the outcome of an action can influence the number of subsequent decisions that are required. The finding suggests that fundamental predictions should be altered across many of the behavioural sciences, not only in relation to signal detection theory, but also other single-decision models.

Keywords: signal detection theory, error management theory, state-dependence, evolution, sequential decision-making, ROC analysis

It's not what we do once in a while that shapes our lives. It's what we do consistently.

— Anthony Robbins

Background

Signal detection theory (SDT) has been strongly influential across the behavioural sciences, not least because of its simple logic. The theory assumes that there are two possible environmental conditions (e.g., safe or dangerous corresponding to the absence or presence of a predator) and that an individual must choose between two possible actions (e.g., forage or run), where the best choice of action depends on the environmental condition. Before the decision, the individual receives a signal, X , that is indicative of the environmental condition but does not perfectly delineate between conditions. There are two possible errors that could occur (in our example, foraging when dangerous, or running when there is no danger).

SDT assumes that the individual is aware of (or has evolved to behave *as if* it is aware of) the payoffs of the condition-action combinations, the background probability, p , of the environment being dangerous (prior to receiving the signal), and the distribution of signals from each condition. SDT identifies that the highest expected value is obtained by choosing to run whenever:

$$\frac{P(X|D)}{P(X|N)} > \frac{(1-p)(V_{NF} - V_{NR})}{p(V_{DR} - V_{DF})}, \quad (1)$$

and foraging otherwise (Green & Swets 1966). Here, $P(X|D)$ and $P(X|N)$ denote the probability densities of receiving a signal of strength X when danger is present or not respectively, and the V s are payoffs with subscripts denoting the situation (danger D , or no danger, N) and action (running away, R , or foraging, F). It is usually assumed that the V s are fixed values but, as pointed out by Getty (1995), they could also be functions of p ; this aspect is crucial to the point that we will make.

We assume that strong signals are indicative of danger, so the signals below the threshold (given by Equation 1 if the inequality were an equal sign) mean that the individual should forage. The threshold can thus be interpreted as the optimal level of ‘boldness’. SDT (also known as Error Management Theory in relation to evolved responses) has been cited in relation to a diverse range of behaviours, including food choice (e.g., McGuire et al. 2006), mate choice (e.g., Haselton & Nettle 2006), the evolution of plant defences (Orrock et al. 2015), immune function (Nesse 2005), and mental illnesses (Nettle & Bateson 2012).

Increasing the prior probability of danger, p , in Equation 1 supports the seemingly intuitive prediction that if predators are more likely, then the optimal threshold for response should be shifted to prompt evasive action at lower levels of danger signal (Figure 1). In other words, the focal individual should be more ready to run when the likelihood of danger is increased. This prediction, and its equivalent in other scenarios, has been identified in many texts (e.g., Green & Swets 1966, Quigley & Barrett 1999, Nesse 2005, Lynn & Barrett 2014).

In recent work we have shown that allowing boldness to depend on the reserves of the individual can disrupt, or even reverse, the predictions of SDT (Trimmer et al. 2017a, 2017b). Here, we go further by identifying that the complication of thresholds being reserve-dependent is not necessary; even without the possibility of death through starvation, the standard prediction of SDT can be reversed simply by an individual having sequential decisions to make. We provide a simple analytic example where an individual should use the *same threshold at every level of reserves*. That threshold should depend on the probability of danger that will be experienced at each time step. The model shows that the individual becomes less prone to run as the probability of danger increases. The effect exists because

reserves decrease if the individual chooses to run, so they would subsequently be exposed to the danger for a longer period to reach the reserve level that they could have achieved by foraging at the current time. This highlights an important general message. When the payoffs for a single decision are given and fixed, signal detection theory is perfectly sound. When individuals face a decision under risk, and this risk persists in the future, altering the risk alters future prospects and hence alters the payoffs for the decision. This then changes, and can reverse, predictions based on treating a single decision in isolation.

The Model

We assume that an individual makes repeated decisions about whether to forage, with the aim of reaching a reserve level that is suitable for reproduction. For simplicity, we discretise time and assume that the individual uses one unit of reserves per time step, and receives two units of food on occasions that it forages (i.e., reserves increase or decrease by one unit at each time step). At each time step, a predator is present with probability p , independent of other time steps. Prior to each decision, a signal is received that is somewhat indicative of whether a predator is present. Choosing to forage when a predator is present results in death. We also assume that in each time step there is a background probability of death by sources other than predation, δ , over which the individual has no control (e.g., disease). We also assume that the individual has sufficient reserves to ignore the possibility that it starves.

In order to reproduce an individual must first increase its reserves to some appropriate level (without dying first). To do so, it must first eventually raise its threshold by one unit (without dying), and then raise it by another unit, and so on. Thus the probability it raises reserves by k units is θ^k , where θ is the probability of eventually raising reserves by one unit. Thus whatever the value of k , the probability of

eventually raising reserves by this much is maximized by maximizing θ (Gilliam 1982; Houston & McNamara 1999). Thus we seek the strategy that maximises θ .

In a single time step, let a denote the probability that the individual chooses to run (and survives to make a future decision) and b denote the probability that the individual forages and survives (thus increasing its reserves). We illustrate the scenario in Figure 2.

The probability of reaching the next reserve level, θ , has two components: b (which we use to denote the probability of immediately moving up one reserve level) and $a\theta^2$, (from first moving down one reserve level but subsequently managing to increase by two steps, where a denotes the probability of initially moving down one level). i.e., $\theta = b + a\theta^2$. Thus, ignoring the root larger than 1,

$$\theta = \frac{1 - \sqrt{1 - 4ab}}{2a}.$$

Denoting the optimal cue threshold by x_T , we also have:

$$a = (1 - \delta)((1 - p)P(X \geq x_T|N) + pP(X \geq x_T|D)),$$

$$b = (1 - \delta)(1 - p)P(X < x_T|N).$$

Substituting, we can find the threshold that maximizes θ for any given p .

Results

With no background mortality ($\delta = 0$ provides a situation where future decisions are guaranteed so long as the individual is not killed by a predator), the optimal threshold increases monotonically with p , as shown in Figure 3. This trend is *completely the opposite of signal detection theory*, where boldness would monotonically reduce (becoming more prone to run from possible dangers) as the probability of danger increases. The SDT equation (1) is misleading because as p alters, the payoff values should also alter.

Although our results contradict classical SDT, they can be understood by suitable interpretation of equation 1, which is the standard equation of SDT. Increasing p in this equation has two opposing effects. It decreases the term $(1 - p)/p$. However, increasing the probability of danger also alters the individual's future prospects. In equation 1 the four V terms represent these future prospects; as p increases, these can change in a way as to more than compensate for the effect of $(1 - p)/p$. To gain some insight into this we consider the scenario again. Foraging in the face of danger results in death, so $V_{DF} = 0$. We also know that if the individual is one reserve unit short of gaining a particular payoff, α , (which would be achieved by foraging when safe) then $V_{NF} = \alpha$. We let $\theta(p)$ represent the probability of reaching the next reserve level under optimal behavior (i.e., for that value of p). Then we also know that $V_{NR} = V_{DR} = \alpha\theta^2(p)$ because, having run away, the individual would have a probability of $\theta^2(p)$ of subsequently reaching that higher level of reserves. Substituting gives,

$$\frac{(V_{NF} - V_{NR})}{(V_{DR} - V_{DF})} = \frac{(1 - \theta^2(p))}{\theta^2(p)}. \quad (2)$$

The probability of reaching the next level of reserves, $\theta(p)$, must decrease with p , so expression 2 becomes larger as p increases, and this can overwhelm the other terms in equation 1. When it does so, boldness should increase. This can be beneficial because boldness reduces the loss of reserves, and so reduces the number of occasions that danger will need to be faced. The influence of the number of occasions is crucial here; when the individual does not lose reserves by running, predictions of classical SDT apply.

The effect of background mortality, δ , is also illustrated in Figure 3. Background mortality reduces the worth of the future, so has the effect of making the individual less prone to run – though with very little effect once p is large enough to dominate mortality.

Discussion

Classical SDT is a very simple, abstract model. Many authors have assumed that the logical predictions are meaningful for their study systems. However, the assumption that only a single decision will be made is rarely the case for any real organism. We have shown that altering this assumption, to one where multiple decisions will be required to reach a goal, can lead to a reversal of the trends predicted by SDT.

Our result occurs because choosing to avoid any possible predators means that reserves will deteriorate; the individual would thus need to accept some risk in future time steps just to recover what it lost by the current decision (for a discussion of short-term versus longer term effects of choices in the context of SDT, see Getty et al. 1987). Avoidance of danger tends to be deleterious to reserves in many biological

decisions; e.g., an immune response uses trace minerals – so as the prevalence of a disease increases, it is possible that the optimal threshold may reduce, to help avoid wasting precious resources on false alarms. Our results suggest that, in the absence of death from other sources, an increased probability of infection by a disease will *increase the frequency* of mounted responses (because there are more cases to be detected), but *decrease the threshold* for responses danger (so as to reduce the waste of resources through false alarms). However, the direction of this effect should depend on the prevalence and effects of other dangers. Thus, our prediction may have widespread implications across the biological and psychological sciences.

Our simple demonstration that boldness can increase with the probability of danger concurs with the risk allocation hypothesis (Lima and Bednekoff 1999). One of the key simplifying assumptions in each case is that the prior probability of danger, p , will remain the same for all decisions; this is rarely the case in any real system. Previous work has shown that behavioural trends can depend on whether changes are believed to be transitory or permanent (McNamara & Houston 1994). Thus, in addition to the current probability, the level of autocorrelation should affect the strength of the effect that we describe (see also Higginson et al. 2012, Trimmer et al. 2017b). Classical SDT finds the optimal threshold for a single decision; we have seen that if the probability of danger is likely to persist for subsequent decisions, then the predicted effects on optimal thresholds can be reversed. This is because the probability of danger affects future expected payoffs, with extent being governed by the strength of autocorrelation. Reeve (1989) and Getty (1995) have noted that the effect of altering the background probability can have positive or negative effects, with Getty being explicit that the effect can hinge on how the (future) payoffs depend on the probability. This point seems to have gone largely unnoticed in the literature and our result is a specific case of Getty's result, identifying that reserves can mediate the effect. A more complex model allows the threshold to alter with reserve level and shows that boldness

increases as the risk of starvation increases (at lower reserves) (Trimmer et al. 2017b). Here, we have shown that the classical SDT predictions are reversed even when there is no risk of starvation and the same threshold is used at every reserve level.

We have shown this reversal of predictions in relation to SDT and our logic can clearly be applied to other single-decision models. For instance, the well-known diffusion model in forced choice tasks with two alternatives (Bogacz et al. 2006) shows how prior expectations (of danger, for instance) can translate to optimal decision thresholds for decisions which will be taken when sufficient information has been obtained (after some continuous period of time). Just like classical SDT, the usual assumption is that only one decision will be made – and the more likely the world is to be dangerous, the more likely the individual should be to quickly reach the decision to take evasive action. Setting such models in a wider context, where risks will sometimes need to be taken to achieve a goal (e.g., surviving for some period) will likely mean that some of the past predictions have been misleading, just as they have been with classical SDT. The behavioural sciences may therefore benefit from taking a fresh look at the predictions of models that have simplified scenarios down to a single decision.

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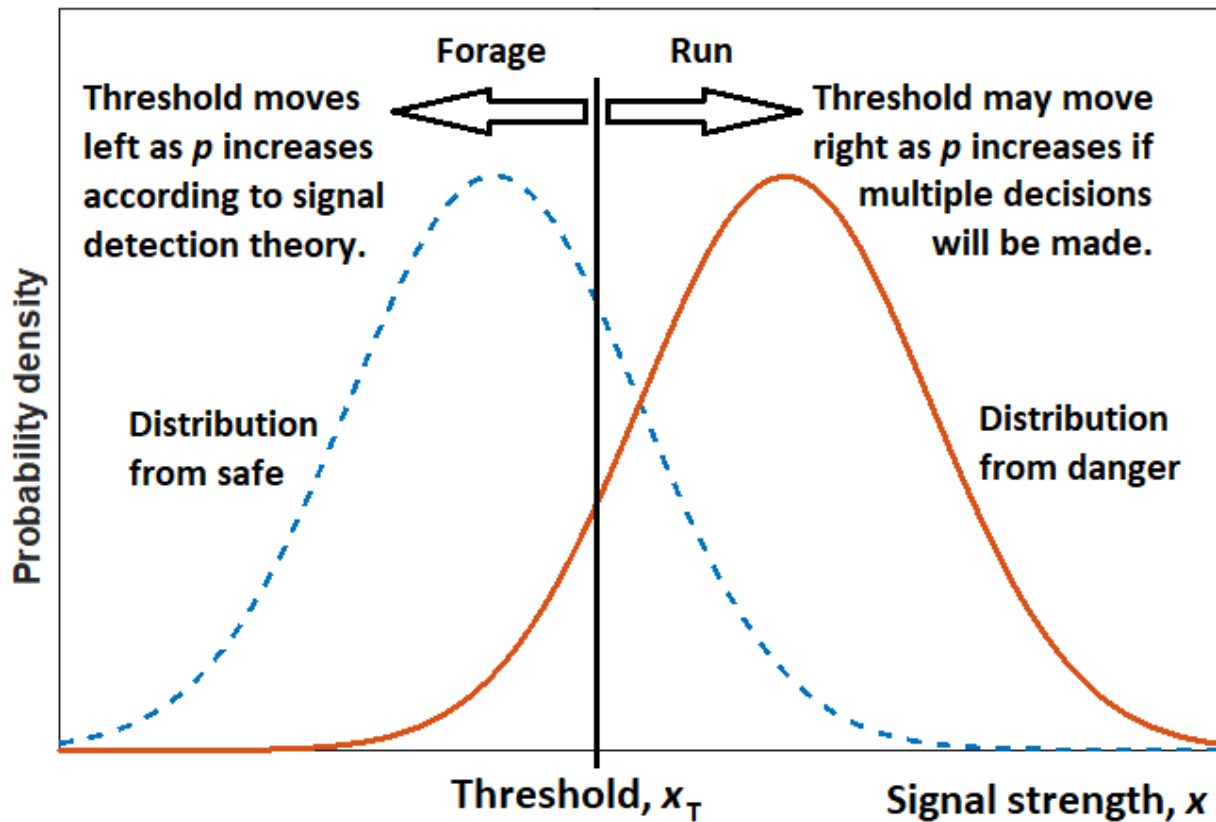


Figure 1: We consider a scenario where the distributions of signals under safe or dangerous situations mean that a threshold should be used to choose behaviour, with evasive action (running away) being chosen if a high signal is received. Classical signal detection theory identifies that the optimal threshold, x_T , should move left (making an individual more ready to run away) as the probability of danger, p , increases. Thus, as danger increases, the actions of an individual should tend to appear less 'bold'. However, our analysis shows that if a series of decisions will be made using the threshold, always with the same probability of danger, p , then the optimal threshold will instead move to the right.

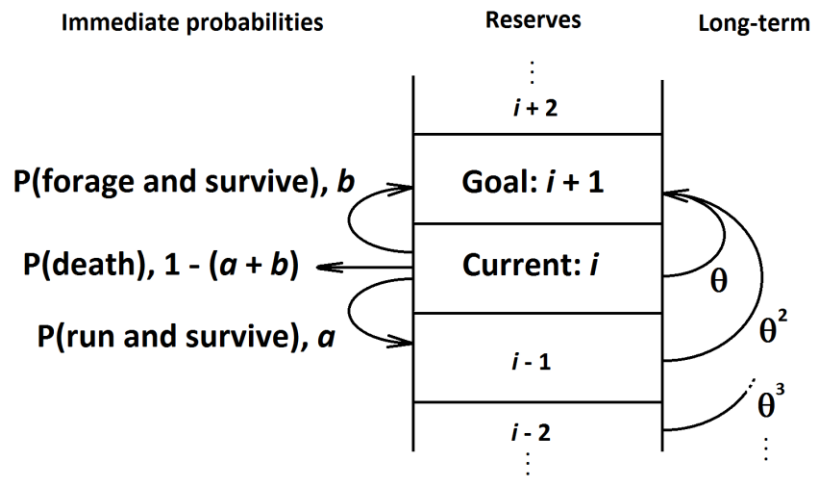


Figure 2: The level of boldness affects the immediate probabilities of increasing or decreasing reserves by 1 unit, and the probability of being killed. We are interested in the behavioural strategy that maximises the long-term probability of reaching the next reserve level without being killed by a predator or through background mortality (i.e., the optimal level of boldness).

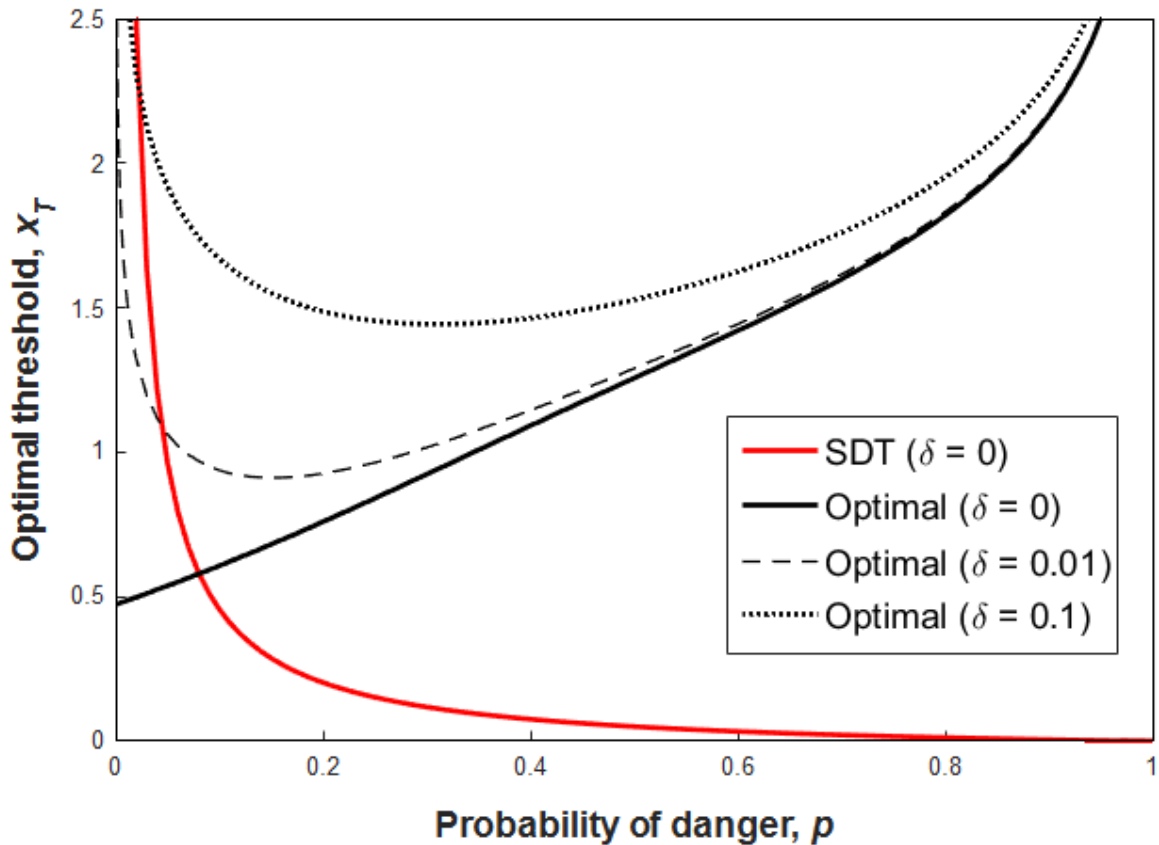


Figure 3: Contrasting the predictions of boldness with the optimal (multiple decision) calculations. With no background mortality, as p increases, the optimal threshold (i.e., boldness) increases; i.e., the individual forages when they would otherwise have run. The monotonic upward trend is entirely contrary to SDT, which predicts a monotonic decrease in boldness. With non-zero background mortality, the optimal boldness decreases for small predation probabilities but then monotonically increasing as p comes to dominate. The SDT line has been calculated against baseline payoffs relating to $p = 0.1$, with one reserve level to go, using the optimal payoffs (that would be measured by an observer if behaviour evolved to be optimal). A similar monotonic downward trend occurs for the SDT line, irrespective of which value of p is chosen. Introducing non-zero background mortality to the SDT case also produces a similar monotonic downward trend, with a slower asymptote to zero (not shown). [Signals normally distributed with unit variance and means $\mu_N = 0$, $\mu_D = 2$.]