

Two complementary models and an experimental test of how
receivers respond to multicomponent visual signals

by

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Abstract

Animals often communicate using elaborate displays containing multiple components, but it is unclear why these complex signals have evolved when one component might be sufficient to inform the receiver. In this thesis, I first briefly review this burgeoning field. I then evaluate how human receivers respond when faced with a signaller displaying a two-component signal, when each component differs in its probability of being associated with a binary outcome (desirable/undesirable). These tests were conducted under a broad range of conditions under which neither, one or both multicomponent signals were predicted to be followed according to a simple signal detection model. Signal detection theory identifies an optimal response once the receiver's learning is complete. However, I also considered a complementary modelling approach that predicts the same long-term response but uses exploration-exploitation theory to identify the optimal tradeoff between learning more about the nature of the signaller and using current information to reject it. The best supported statistical models for my data generally included both signal elements as significant predictors of acceptance. Indeed, receivers frequently attended to both forms of signal even under conditions when they are not predicted to do so by the signal detection model. The primary reason for this departure was that receiver learning was influential in shaping the response strategy of the volunteers. The exploration-exploitation model which makes assumptions about receiver learning was more successful in accounting for the observed behaviour and may therefore provide a promising starting point for future work on the study of multicomponent signals.

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Chapter 1: General Introduction

In this thesis, I combine empirical and theoretical approaches to make predictions and experimentally test whether receivers will use multicomponent signals. Specifically, I attempt to elucidate whether receivers would pay attention to more than one component within a multicomponent signal when one may provide sufficient information to make an informed response. The following general introduction is divided into four sections. The first section presents a brief history on the study of animal signals, introduces multicomponent signals, and provides key examples within literature. The second section explains signal detection theory and highlights its advantages and limitations for use within the study of animal communication. The third section introduces exploration-exploitation theory and explains how it can be used to model the behaviour of a payoff maximizing receiver that updates its beliefs using Bayesian learning. The final section is an overview of the goals and rationale behind the research for my thesis.

Multicomponent signals

The field of animal communication has long tried to understand the passage of information that occurs between animals. For consistency, any morphological or behavioral traits that function for communication will be referred to as *signals* in this thesis, however it is important to note that there are distinct differences between the types of selective pressures that influence *signal* evolution vs non-evolved traits/behaviours that provide information (“cues”) but are not under selection to do so (Maynard Smith & Harper, 2003). Signals that involve multiple components, or multicomponent signals (Candolin, 2003) are of interest from several perspectives, but a common question is why more than a single signalling component is ever selected for when they appear redundant. There has therefore been an extensive research effort to develop and test hypotheses to explain their presence in nature. Multicomponent signals are less the exception and more the rule. Indeed, they appear across multiple

communication systems including sexual selection (Darwin, 1871), parental care (Kim et al., 2011), foraging (Schaefer et al., 2004), predator avoidance (Ruxton et al., 2018) and in a wide variety of other contexts.

Several hypotheses exist as to why multicomponent signals may have evolved, although they are not necessarily mutually exclusive and different multicomponent signalling systems may have evolved for different reasons between species. It is worth mentioning that the difference between a signal with one component versus one containing multiple components is not always clear cut. Humans may be able to distinctly separate signal components that are viewed as a single unified signal by a natural animal receiver. Therefore, defining which signals are truly multicomponent can be problematic as it is possible to break down complex displays into nearly infinite components (Rowe, 1999). Furthermore, before describing a signal as multicomponent, one must rule out the possibility that components are expressed together for other non-adaptive reasons (i.e. pleiotropy). These problems are addressed by Hebets et al. (2016), who recommend a ‘systems approach’ to studying animal communication that includes how receivers perceive complex displays, interactions between components, and the function of each component compared to the integrated display.

Multicomponent signals may be selected because they enhance the detection and discrimination of signallers (Guilford & Dawkins, 1991; Rowe, 1999). For example, in begging signals between offspring and parents (i.e. parental care in birds, Kilner et al., 1999), the signal complexity may act to improve the efficacy with which an overall display conveys the true quality of the signaller (Endler et al., 2014). Multicomponent displays could contain components that are directed towards multiple receivers, with each component intended to convey information to a different receiver (Hebets & Papaj, 2005). Certain signal components may be unrelated to any underlying quality and instead only act as ‘amplifiers’ for their associated components and increase the receiver’s ability to assess the compound

signal (Hasson, 1989; Bogaardt & Johnstone, 2016). Thus, some signal components may simply attract receiver attention and/or increase the efficacy with which another signal is conveyed and do not contain useful information themselves (Endler et al., 2014). For example, bowerbirds construct extravagant bowers which entice females to approach, yet the birds themselves also possess ornaments and bright plumage which appear to signal their quality (Doucet & Montgomerie, 2003). Similarly, jungle fowl possess an array of ornaments and sexual behaviours, some of which do not appear correlated with mate quality (Smith et al., 2009).

There is a vast literature of empirical studies that have been conducted on multicomponent signals. In fact, attempts to understand how multiple cues influence learning a topic of investigation within psychology since has been the 1950s (Holzworth, 1999). Presently, a common protocol involves separating components within a multicomponent signal and presenting them to receivers both in unison and again individually. If receivers show a stronger (or more appropriate) response to both signals in unison, whether additively or synergistically, this suggests evidence in favor of receivers using multicomponent signals. For example, in predator avoidance, multicomponent deceptive signals have been shown to impede predator learning of the profitability of artificial snake-mimicking caterpillars (Skelhorn et al., 2015) and spider-mimicking moths (Wang et al., 2017) relative to either signalling component separately. Floral multimodal olfactory/visual signals have been shown to increase the accuracy with which foraging bumblebees (*Bombus impatiens*) correctly identify rewarding flowers compared to bumblebees that were only given access to either isolated component (Kulahci et al., 2008). In mate choice, female wolf spiders (*Schizocosa uetzi*) rely on males presenting both visual and vibratory components within multimodal sexual signals to appropriately respond (Hebets, 2005). Female side-blotched lizards (*Uta stansburiana*) achieve greater reproductive fitness from selecting males displaying multiple signals of quality, compared to males possessing only one such trait (Lancaster et

al., 2009). It is likely that this increased fitness can only be realized by attention to both signalling components. Empirical evidence is widespread that, compared to signallers with only individual components, multicomponent signals elicit a stronger and/or more appropriate response that could directly translate into fitness benefits to signaller and/or receiver.

Theoretical work on multicomponent signals is at best, a mixed bag of competing and complementary hypotheses. Complex signals could convey ‘multiple messages’ with each signalling component delivering a different piece of information (Moller & Pomiankowski, 1993; Johnstone, 1996). Signalling components could each contain information on the same quality yet differ in their reliability in honestly indicating the quality (Bradbury & Vehrencamp, 1998). In this respect, multiple components would be effectively redundant, and act simply as ‘backup signals’ (Johnstone, 1995) in cases when one component may not be informative enough. Multimodal sexual signals may have a selective benefit in fluctuating environments where transient selective pressures cause variation in the informative accuracy of certain components (Bro-Jørgensen, 2010). Criteria under which a preference for multiple signalling components could be evolutionarily stable has been proposed by Wilson et al., (2013), yet the general conclusion was that one signal is usually sufficient. However, when assessment costs are low, and signals are similar in their informative accuracy, signal detection models (see below) indicate that attention to bicomponent signals will benefit receivers (Fawcett & Johnstone, 2003; Sherratt & Holen, 2018).

Signal detection theory

The general premise of signal detection theory (SDT) finds an observer presented with a stimulus (or signal), that conveys information. The observer seeks to discriminate observations that might arise from a desirable signaller from that of noise or any distractions (an undesirable signaller) and respond

appropriately. Here, the appropriate response will be dependent not just on the likelihood the signaller is desirable, but also the payoffs from a correct decision (accept desirable signallers, reject undesirable ones) or incorrect decision (reject desirable signallers, accept undesirable ones). In the classical model with continuous signals, the probability distributions of an observation from a given type of desirable signaller and that of an undesirable signaller (distractor) with which it can be confused, are represented by Gaussian (normal) probability distributions with different means and equal variances. When the distributions overlap, the observer will be uncertain as to whether the observation is from a desirable or undesirable signaller, and thus there exists potential for type I and II errors, which are commonly referred to as ‘miss’ (rejection of desirable signaller) and ‘false alarm’ (acceptance of undesirable signaller), respectively. To optimally respond and thereby employ the payoff-maximizing combination of these errors, the observer should employ a single threshold (a decision boundary, x^*) beyond which they should treat signallers with $x > x^*$ as desirable. Naturally, other formulations of SDT models are possible, including cases in which signals are binary rather than continuous. Such a model is introduced in Chapter 2.

SDT has a rich history of multidisciplinary applications, beginning with its use in radar technology during WWII to distinguish the presence of enemy vessels from background noise (Peterson et al., 1954). It has been utilized extensively in psychology (Tanner & Swets, 1954) and psychophysics (Egan, 1975; Green & Swets, 1988) to model optimal decision-making tasks in humans. Still today, SDT has interesting and varied applications, including for example modelling the optimal conditions for eyewitness identification (Wixted & Mickes, 2014) to increase accuracy in correctly identifying offenders and reduce rates of false eyewitness testimony.

Ecology and evolution studies have co-opted SDT to make predictions about optimal animal behaviour. Early applications include modelling predator behaviour when faced with unprofitable

models (such as stinging Hymenoptera) and their Batesian mimics (Oaten et al., 1975). Behavioural ecologists have continued to find SDT effective for modelling predator decisions when faced with Batesian mimics that possess both one (McGuire et al., 2006) and two signalling traits (Kikuchi et al., 2015). Brood parasite rejection models have been used to predict the optimal threshold for a host parent to either accept or reject an egg in cases where parasitism (aggressive mimicry) is possible (Rodriguez-Girones & Lotem, 1999). This has been furthered using SDT to predict how recognition errors could be reduced by attending to multiple components within complex signals (Tibbets et al., 2020).

An SDT framework allows optimal behaviour to be modelled within a variety of contexts. However, in all SDT models the receiver (observer) is effectively assumed to possess ‘complete information’. That is, learning is not required for the receiver to be aware (or at least respond appropriately) to value and frequency of all available signals – the only source of uncertainty lies in the overlap of the appearance distributions of desirable and undesirable signallers. This is potentially problematic because some signals require repeated presentations before receivers can learn to estimate their true value and rate of occurrence. In fact, this challenge was observed in early tests of optimal foraging theory (Krebs et al., 1978) when modelling forager experience with differentially rewarding food patches. It was found that great tits (*Parus major*) required learning and may have exhibited partial preferences (McNamara & Houston, 1987) as they acquired experience sampling patches, rendering any model of their behaviour which did not include learning less predictive. Therefore, I aim to test the validity of this assumption of ‘complete information’ within SDT models in detail throughout Chapter 2 to demonstrate the potential effect of receiver learning.

Exploration/exploitation theory

Exploration/exploitation (E/E) models describe the trade-off between gathering information (exploring) and exploiting presently available information. E/E problems were originally framed as ‘multi-armed bandit’ models where a subject is faced with n ‘armed bandits’ (slot machines) with potentially differing rate of reward and the operator must choose a strategy to maximize its return. Subjects gather information by sampling each bandit to develop estimates of their profitability and then choose to exploit those which grant the highest reward. However, it is not immediately clear when a subject should switch from gaining more information about the payoffs of the different bandits (exploration) and exploiting its available information by choosing (what it believes to be) the best bandit (exploitation). An analytical solution for the optimal strategy for a particular type of multi-armed bandit problem has been identified, namely one with future discounting (Gittins & Jones, 1974). However, numerical solutions can be identified using stochastic dynamic programming for a much wider set of cases (see below).

Exploration-exploitation problems have important applications. For example, the question as to whether patients receiving a placebo in a clinical trial should be moved to the drug when initial information indicates the drug is effective (i.e. the optimal conditions to cease exploration) is a question that can be framed using bandit models with one known (placebo) and one unknown (drug) arm (Cohen et al., 2007). They are also an everyday dilemma. For example, should you go to the restaurant you have been to before and know is reasonably good (exploit), or should you visit a new one in the hope that it is even better (explore)? Indeed, the very same question has been framed in ecological terms – the problem as to whether a bird should stay in its current patch of known quality or explore new patches of unknown quality was solved and experimentally tested just as behavioral ecology was emerging as a separate discipline (Krebs et al., 1978). More recent applications in behavioral ecology have been used

to understand how superstitions (Skinner, 1948; Abbott & Sherratt, 2011) might develop, and why many species show age-dependent changes in neophobia (Sherratt & Morand-Ferron, 2018).

As noted above, numerical solutions for state-dependent optimal behaviour can be computed using dynamic programming (Houston et al., 1988). In the simplest formulation the state is information, but it can also include additional physiological state variables including hunger levels or toxin levels etc. (Aubier & Sherratt, 2020). Dynamic programming typically works backwards from the final decision, iteratively identifying the optimal solution at a given point in time for a given set of informational state variables (e.g. a given type of signaller was desirable on x occasions from n trials). At each stage, the receiver is assumed to behave optimally based on the information it has and update its information in the optimal manner according to the new information it receives. Thus, the receivers are assumed to update their beliefs through Bayesian learning, which describes the appropriate way to turn prior beliefs into posterior beliefs given new data (Bayes, 1764).

E/E may be a useful tool in animal signalling systems where learning is expected to significantly influence receiver behaviour; especially in cases where signal complexity has an impact on the speed with which learning occurs (Skelhorn & Rowe, 2016). To accurately assess information contained within signals, receivers may require significant learning through experience (more discussed in Chapter 2). The value of this information may change over time (Sherratt, 2011; Sherratt & Morand-Ferron, 2018) since new information is more valuable earlier on when it can be utilized, compared to later on when it has less future value. It is therefore important to determine how and why the optimal behaviour of receivers may change during these different stages. Sherratt (2011) used E/E to identify the optimal strategy for sampling unfamiliar prey, and it is this simple model I will seek to evaluate. Here, the choice was between pulling an arm of unknown reward (i.e. accepting the signaller, which may be

desirable or undesirable) or pulling an arm of known reward (rejecting the prey type and receiving a guaranteed payoff of 0). The quantitative form of this model will be described in Chapter 2.

Research goal and significance

As discussed, there is an ongoing debate within animal communication literature as to why signals have evolved to contain multiple components. There is a large body of evidence that suggests that receivers gain some sort of benefit from paying attention to multiple components (Rowe & Guilford, 1996, 1999; Marples & Roper, 1996; Lindstrom et al., 2001; Lancaster et al., 2009; Kikuchi et al., 2015; Skelhorn et al., 2015; Wang et al., 2017; Tibbets et al., 2020). However, recent empirical (Rubi & Stephens, 2016a,b) and theoretical (Wilson et al., 2013; Stephens, 2018) research claims that only the more reliable component within a multicomponent signal indicating the same underlying quality should be followed by payoff-maximizing receivers, at least under a broad range of conditions. This leaves the prevalence of multi-component signals in these instances something of a puzzle.

I hope that this thesis will be a significant contribution to the current body of literature by combining predictions from signal detection theory and exploration/exploitation theory to better understand if multicomponent signals would be attended to under a wide variety of conditions. My work emphasizes the importance of accounting for a receiver's learning phase and its impact on the development of asymptotic response strategies. I have collected data from multiple empirical experiments which tested the strategic responses of human receivers when presented with a bicomponent visual signal. I then modelled the behaviour of a payoff-maximizing receiver who uses Bayesian learning to identify the trade-off between exploring potentially rewarding signaller types and exploiting those known to be rewarding. By combining my empirical experiments with predictions from two theoretical models of optimal behaviour, I believe my work advances our understanding of

multicomponent signals, highlighting the limitations of signal detection models and the importance of receiver learning.

Chapter 2: Receivers learn to respond to one or both components of a two-component visual signal

Abstract

Animals often communicate using elaborate displays containing multiple components, but it is unclear why these complex signals have evolved when one component might be sufficient. Here, I test the predictions of two complementary models of how receivers should respond (accept/reject) to a two-component computer-generated signal when the signal components (colour and pattern) differ in their probability of being associated with a binary outcome (desirable/undesirable). The first model uses signal detection theory (SDT) to identify the optimal response of a receiver to a signaller, assuming complete information. The second model predicts the same long-term response but uses exploration-exploitation theory to identify the optimal trade-off between learning more about the nature of the signaller and using current information to reject it. Importantly, these experiments covered a broad range of conditions under which attending to none, one or two signal components was ultimately optimal from the SDT standpoint. When the difference in payoff from accepting or rejecting a given signaller type was high, then human receivers quickly learned to adopt the optimal strategy for the signaller predicted by SDT. However, when the difference in payoff was low, human receivers took longer to settle on a consistent strategy, a result readily explained by the exploration-exploitation model involving learning. This learning involved the early evaluation of strategies that attended to both colour and pattern, even when attention to one signal component was ultimately optimal. Thus, while SDT satisfactorily predicts the long-term payoff-maximizing response, exploration-exploitation models offer a more complete framework for understanding the responses of receivers to multi-component signals.

Introduction

Individuals (“receivers”) frequently attend to signals that provide valuable information about the nature of the signaller. For example, signals serve to indicate the suitability of mates (Darwin, 1871), the palatability of prey (Schaefer et al., 2004), and the needs of offspring (Kim et al., 2011; Jacob et al., 2011). Many of these signals involve combinations of several elements, that is they are *multicomponent* (see Candolin, 2003 for review) or *multimodal* (when the separate elements are perceived through different sensory modalities, Rowe & Guilford, 1996). For example, many insects employ multimodal anti-predator displays consisting of conspicuous colouration, unpleasant sounds and the discharge of pyrazine odour (Rowe & Guilford, 1999). Similarly, sexual signals among spiders often contain elements conveyed through seismic stridulations as well as visual displays (Hebets & Papaj, 2005). In these and many other cases, the complexity of the signals is well documented, but the reasons why receivers select for this complexity is poorly understood. Why for example, are multiple signals of unprofitability used to deter a predator and why do male spiders employ both visual and vibratory components in their sexual displays to attract a mate?

Many hypotheses have been proposed to understand the evolution of multicomponent signals (Hebets & Papaj 2005, Wilson et al., 2013, Chapter 1). Here, I focus on circumstances under which individual elements of a multicomponent signal each communicate the same underlying quality to a receiver. Multicomponent signals are particularly challenging to understand under these circumstances because one might expect that a second signal component would be effectively redundant with regard to decision making if the same decision would be made on the basis of the first signal component alone. Several models have explored this possibility (Schluter & Price, 1993; Bradbury & Vehrencamp, 1998, 2000; Fawcett & Johnstone, 2003; Wilson et al., 2013; Rubi & Stephens, 2016a, b; Sherratt and Holen, 2018). These models predict that attention to multicomponent signals is beneficial under some

conditions, but a consensus on whether attention to multicomponent signals in general is economically optimal has yet to be reached. Stephens (2018) for example argued that attention to multiple components is only optimal under a narrow range of parameter space. To date however, most empirical attention has focused on evaluating whether receivers attend to a single signalling trait when they are predicted to do so (e.g. see Rubi and Stephens, 2016a,b). To obtain a more complete picture, it is essential to test whether receivers attend to both signalling components, or neither signalling component, when they are predicted to do so.

The above-cited economic models differ in detail but several can be framed in terms of signal detection theory (hereafter referred to as SDT, Egan 1975; Green & Swets, 1988) in that they identify optimal decision rules for distinguishing two types of signaller based on two binary traits. Here, I test the predictions of the simplest SDT model with no assessment costs (see Sherratt & Holen, 2018). While SDT is a versatile and intuitive modelling framework, it does make some key assumptions which are not always met. In particular, signal detection models assume ‘complete information’ in that they presuppose that the receiver reacts as if it knows the model parameters and immediately adopts a discriminative strategy that maximizes its payoff. This may be true if the receiver’s responses to signals are “hard wired” by a long evolutionary history, and approximately true in cases where the learning phase is a small fraction of the total time the receiver has to make decisions. In reality however, the associations between signals and the desirability of the signaller may need to be learned by trial and error. As learning proceeds, receivers must make strategic decisions as to whether to further explore a type of signaller (by accepting it) or exploit their available information about its desirability and reject it. Exploration/exploitation models (also called “bandit models”) identify the optimal balance between gathering new information (exploration) and exploiting existing information (Cohen et al., 2007; Sherratt 2011). Since they seek to maximize payoff, these models generally lead to the same asymptotic

behaviour as SDT models when learning is complete (Figure 2.1). However, exploration-exploitation models show how receivers employing Bayesian learning would arrive at these optimal solutions, which may be fast or slow depending on the marginal benefit of rejection compared to acceptance. Thus, when rejecting a given type of signaller is clearly more beneficial compared to accepting it, then observers should rapidly learn this difference and subsequently reject the signaller. By contrast when the relative benefits of rejection and acceptance are much less clear-cut, then receivers might be expected to sample more of this type of signaller before making a final decision to reject the signaller, if at all.

The primary aim of this study was to evaluate how receivers respond to binary signals (colour and pattern, each with two variants) of signaller class (desirable or undesirable) when the signal components vary in the extent to which they are associated with desirability. Following Sherratt & Holen (2018), I consider conditions where the long-term optimal receiver strategy was predicted to be (i) ignore both signal components, (ii) pay attention to the form of only one signal component, and (iii) pay attention to the form of both signal components. To empirically test these models, I utilized human receivers presented with computer-generated signallers. Like many species, humans are called upon to make discriminative decisions widely in their daily lives; they are also visual foragers with a high capacity for learning and strategizing. As with many such experimental tests (e.g. Rubi & Stephens 2016a), the four types of signallers (2 colours x 2 patterns) were initially unfamiliar to the decision maker, as was their relative frequency. Thus, the receivers had to use their experience to estimate not only the probability that a given type of signaller was desirable, but also the probability of seeing it in future presentations (which affects the future value of information).

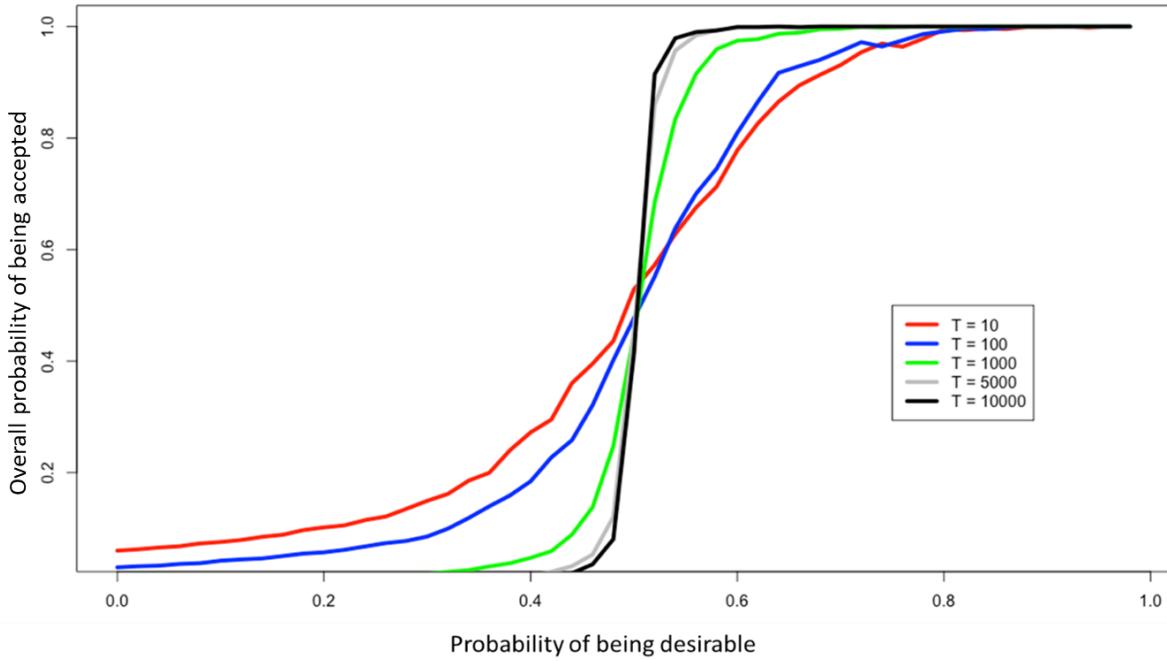


Figure 2.1 The overall probability that a signaller would be accepted by a payoff maximizing receiver that uses optimal exploration-exploitation rules, based on 1000 replicate forward iterations of the optimal set of sampling rules for a given probability of being desirable. Here we assume that the probability of encountering the signaller each time step is 1 (known to the receiver), while the payoffs from correct and incorrect acceptance are equal ($b = c = 1$). Extending the time horizon (T), receivers are able to sample more signallers and more accurately estimate the true probability that a signaller is desirable. Note that the relationship between acceptance rate and probability of being desirable is not a step function but sigmoidal, most especially when the time horizon is short. This smoothing arises because when signallers are of borderline profitability ($p \sim 0.5$ for $b = c$) receivers need to sample more of them to ascertain their best long-term strategy (accept or reject) and even then, mistakes are more likely to be made.

Methods

Signal detection model

Here, I begin by summarizing the SDT model (see Sherratt & Holen, 2018 for more details) which makes the long-term (asymptotic) predictions as to the types of signaller that should be accepted and rejected based on their component signalling traits. Consider a system containing desirable and undesirable signalers with a base probability ρ of a signaller being desirable. We assume that the appropriate decision on encountering a desirable signaller is to accept it (such that the difference in payoff from accepting and rejecting a desirable signaller, b , is positive), while the appropriate decision on encountering an undesirable signaller is to reject it (such that the difference in payoff from rejecting and accepting undesirable, c , is positive). Receivers can choose to accept or reject these signalers based on their appearance. Desirable and undesirable signalers have two signaling components, each in binary form. Let ij denote each signal combination, with signal components i and j each taking values of 0 and 1. Furthermore, let $d_{ij} = \Pr(ij | \text{desirable})$ and $u_{ij} = \Pr(ij | \text{undesirable})$ which indicate the probabilities of the signaller being of the form ij , conditional on it being desirable and undesirable. It is readily shown (e.g. Sherratt & Holen, 2018) that the receiver should accept the signaller ij if $u_{ij} / d_{ij} < \beta$ where $\beta = \rho b / (1-\rho) c$.

How are d_{ij} and u_{ij} related to the reliabilities of the signal elements? If the signal elements are conditionally independent, then the probability that the composite signal is from a given class of signaller (desirable or undesirable) will be the product of their marginal probabilities. Let form 1 be the form of each trait most associated with being desirable, where the marginal probabilities are such that $\Pr(i = 1 | \text{desirable}) = P_i$ and $\Pr(j = 1 | \text{desirable}) = P_j$. Assuming independence (and noting that, given its binary nature, $\Pr(i = 0 | \text{desirable}) = 1 - P_i$ and $\Pr(j = 0 | \text{desirable}) = 1 - P_j$) then:

$$\Pr(i = 1, j = 1 | \text{desirable}) = d_{11} = P_i P_j$$

$$\Pr(i = 0, j = 0 | desirable) = d_{00} = (1 - P_i)(1 - P_j)$$

$$\Pr(i = 1, j = 0 | desirable) = d_{10} = P_i(1 - P_j)$$

$$\Pr(i = 0, j = 1 | desirable) = d_{01} = (1 - P_i)P_j$$

Following earlier treatments (Bradbury and Vehrencamp, 1998; Fawcett and Johnstone, 2003; Rubi and Stephens, 2016a, b; Sherratt and Holen, 2018) we further assume that the probability a signal variant is associated with undesirability is equal to one minus the probability that it is associated with desirability and *vice versa*. This symmetry assumption is not essential, but it reduces the number of parameters.

Given the symmetry assumptions, analogous equations can be derived for the conditional probabilities associated with undesirable signallers such that:

$$\Pr(i = 1, j = 1 | undesirable) = u_{11} = (1 - P_i)(1 - P_j)$$

$$\Pr(i = 0, j = 0 | undesirable) = u_{00} = P_i P_j$$

$$\Pr(i = 1, j = 0 | undesirable) = u_{10} = (1 - P_i)P_j$$

$$\Pr(i = 0, j = 1 | undesirable) = u_{01} = P_i(1 - P_j)$$

Exploration/exploitation model

Here I briefly outline how one can identify the optimal strategy for a receiver that must make long-term payoff maximizing decisions as it learns about the probability a given signaller type is desirable, and seeks to estimate its frequency. See Sherratt (2011) and Sherratt & Morand-Ferron (2018) for more details and Appendix B for the associated RMarkdown code. We can assume that the receiver updates its beliefs regarding the probability that a given signaller is desirable through Bayesian learning, starting with a $\text{Beta}(a_D, b_D)$ distributed prior, which is the conjugate for the binomial (that is, following new information the posteriors will also follow a Beta distribution, albeit with different parameters, DeGroot 1970). Let the receiver find the signaller desirable on r occasions from n such signallers

accepted ($r \leq n$). Likewise, we assume that the receiver updates its beliefs concerning the probability that it will encounter the specific phenotype each trial after previously encountering y individuals of this signaller type from a total of x trials ($y \leq x$), starting with a Beta(a_E, b_E) distributed prior. We assume that the receiver knows the benefit of accepting desirable signallers b , the cost of accepting undesirable signallers - c (with rejection of both classes giving a payoff of 0) and the total number T of trials it has available. We further assume for simplicity that the observer learns separately about the profitability of alternative types of signallers that share some, but not all, aspects of appearance (so there is no generalization across traits, see Kikuchi & Sherratt, 2015).

The standard method for evaluating the optimal state-dependent (state variables x, y, r and n) decisions in a multistage decision process is dynamic programming (Houston et al., 1988; Mangel & Clark, 1988; Clark & Mangel, 2000). Let us define $S(x, y, r, n)$ as the maximum expected future payoff to the decision maker given informational state variables (x, y, r, n) assuming that it continues to adopt the optimal decision rules. The state variables x, y, r and n allow the decision maker to estimate both the expected probability of encountering a given signaller type per trial ($\pi_E = (\alpha_E + y)/(\alpha_E + \beta_E + x)$) and the expected probability that a given signaller type is desirable ($\pi_D = (\alpha_D + r)/(\alpha_D + \beta_D + n)$). Naturally, these expectations will change over time as information is gathered and approximate y/x and r/n when x and n are large.

Let $S_A(x,y,r,n)$ and $S_R(x,y,r,n)$ be the expected maximum future payoff from accepting (A) or rejecting (R) a signaller type which may be encountered in the next trial based on current informational variables x, y, r and n at the start of the time step. The receiver should choose to accept if $S_A(x,y,r,n) > S_R(x,y,r,n)$ and to reject if the reverse inequality holds (in the unlikely event of a tie, we can arbitrarily assume that it chooses to reject the item). Focusing solely on a given signaller type and looking to the future, the receiver can estimate its future payoff as:

$$S(x, y, r, n) = (1 - \pi_E) S(x+1, y, r, n) + \pi_E \{ \max [S_R(x, y, r, n), S_A(x, y, r, n)] \}$$

where

$$S_R(x, y, r, n) = S(x+1, y+1, r, n)$$

and

$$S_A(x, y, r, n) = \pi_D(S(x+1, y+1, r+1, n+1) + b) + (1 - \pi_D) (S(x+1, y+1, r, n+1) - c)$$

Substituting for S_R and S_A yields the dynamic programming equation (DPE), which allows one to compute the receiver's optimal decision under all conditions. The DPE can be solved numerically via backward induction, given that decision-makers all have a fixed time horizon of T . Under these conditions, we know that $S(x = T, y, r, n) = 0$ for all combinations of y , r , and n because there is no future to consider. We can then work backwards, starting with $x = T-1$ and evaluate the optimal decision under all possible combinations of y , r and n since it involves just a single time step. Following this, we can move to $x = T-2$, using the DPE to identify the maximum expected future payoff at $T-1$ and so on. Collectively, this approach identifies of the optimal decision (accept or reject) of a receiver with informational state variables x , y , r and n at any trial, knowing it has a time horizon of T .

To translate the (informational) state-dependent rules indicating whether a receiver with given experience should accept or reject a given signaller type, I ran a series of stochastic forward iterations, each with $T = 100$, $b = 1$, $c = 1$, assuming uniform (agnostic) priors for both the probability that an individual with a given combination of signals was desirable $\beta(\alpha_D = 1, \beta_D = 1)$ and the probability of the receiver encountering the signaller type each time step $\beta(\alpha_E = 1, \beta_E = 1)$. The forward iterations reflected a stochastic encounter and sampling process assuming that a given signaller type had a fixed probability of being desirable, and a fixed probability of being encountered per time step (determined by the base rate and signal reliabilities).

Experimental tests of models

A computer game was created in Microsoft® Visual Basic 6.0 in which human subjects were sequentially presented with a series of signallers, a proportion of which were desirable (the remainder being undesirable). Data collection took place at the University Centre and MacOdrum Library of Carleton University Campus during January-April 2019 (standard and extended trials) and July-August 2019 (flipped trials). Human volunteers (mainly undergraduates) were recruited by invitation as they passed. Consenting participants were shown a Microsoft® PowerPoint presentation outlining the rules of the game but given no information about its purpose in relation to signalling. Subjects were simply asked to accept/reject signallers in a way that maximized their score. All protocols were approved by Carleton University Research Ethics Committee.

The binary visual signals used to indicate the probability that the signaller was desirable were colour (red vs blue) and pattern (cross vs circle) – see Figure 2.2. I let the colour most strongly associated with a desirable signaller be denoted C+ (e.g. red) with the (conditional) probability of its occurrence in desirable signallers being denoted p_{C+} (> 0.5). Likewise, I let the pattern that most reliably indicated a desirable signaller be denoted P+ (e.g. cross), with association probability p_{P+} (> 0.5). Given the symmetry assumed, then the probabilities that undesirable signallers have the alternative colour (p_{C-}) and alternative pattern (p_{P-}) were set to be identical, such that $p_{C+} = p_{C-} = p_C$ and $p_{P+} = p_{P-} = p_P$. To generate signallers with these attributes, signallers were first set to be either desirable (probability ρ) or undesirable (probability $1-\rho$). Depending on their desirability they were then stochastically allocated a colour C+ or C- (probabilities p_C and $1-p_C$ respectively if desirable; $1-p_C$ and p_C respectively if undesirable) and pattern P+ or P- (probabilities p_P and $1-p_P$ if desirable; $1-p_P$ and p_P if undesirable). The combination of parameters ρ , p_C and p_P collectively determined the underlying probability of a given type of signaller being desirable and its frequency. Since signallers were stochastically generated,

there was inevitable variation not only in the order in which signallers were encountered, but also in their actual (realized) frequency and actual probability of being desirable.

A trial began with the presentation of a single square-shaped computer-generated prey placed at a random position on a white background, 11.2 cm × 11.2 cm. For each presentation, the volunteer could decide whether to accept the signaller item (by clicking on it) or move to the next screen (by clicking on the “Reject” button). Every screen contained a single signaller but the pace at which new signallers were presented was entirely set by the volunteer (the only way to move to a new screen was by pressing the “Next Screen” button). All volunteers were presented with the same fixed number of signallers, so there was no incentive to rush. The trial cumulative score was shown on the top of the screen. Accepting a desirable signaller yielded one point to the volunteer but accepting an undesirable signaller led to the deduction of a point. Since rejection yielded no points in either case then $b = c = 1$. To reinforce the change in total score (continuously displayed) accepting a signaller generated one of two distinct sounds depending on its desirability (cash register sound for desirable, buzzer sound for undesirable).

Experiment 1: Varying signal reliabilities and base rate

Trials were run for 3 different simulated environments, each with a different proportion of desirable signallers (or base rate, ρ), with $\rho = 0.25, 0.5$, and 0.75 . For each base rate, signals were tested at 3 different reliabilities ($p_C = 0.6, 0.75, 0.95$; $p_P = 0.6, 0.75, 0.95$) in a 3x3x3 factorial design (see Figure 2.3 for a depiction of treatment conditions). Trials were run so that all 27 combinations of signal reliabilities and base rates were tested within a single block, and this was repeated for a total of five blocks. Five different human volunteers participated in each of the 27 treatments (135 subjects in total). Each volunteer was presented with a total of 100 signallers; once all had been presented, the game ended.

Experiment 2: Extended trials at three different base rates

During experiment 1, it was clear that the human subjects took some time to learn the long-term payoffs from accepting each signaller phenotype, and some may have struggled to identify an optimal payoff-maximizing strategy upon completion of the trial. Extended trials were therefore conducted to evaluate the longer-term responses of volunteers, with subjects presented with a total of 200 signallers (twice that of experiment 1). Signal reliability was maintained at $p_C = p_P = 0.75$ for each trial and the base rates were $\rho = 0.25, 0.5$, and 0.75 (hence treatment combinations 5, 14 and 23 on Figure 2.3). Ten subjects were tested in each condition for a total of 30 subjects. Once all signallers had been presented, the trial ended.

Experiment 3: Flipped trials

To evaluate the extent of inherent biases for the colours or patterns used in the experiment, a set of trials were performed where signals were “flipped” (i.e. counterbalanced) so that those colours and patterns that were previously associated with desirability were now associated with undesirability and *vice versa*. Once again, treatments were chosen with parameters that would involve volunteers attending to colour alone, pattern alone, or both signals.

A total of 30 subjects were tested at one of two base rates ($\rho = 0.25, 0.75$) and one of three separate combinations of signal reliabilities ($p_C = 0.6, p_P = 0.95$; $p_C = 0.75, p_P = 0.75$; $p_C = 0.95, p_P = 0.6$) with five subjects tested for each of the six treatment combinations. Treatments were again separated into five temporal blocks. The flipped experiments were compared directly to that of the analogous treatments 3, 5, 7, 21, 23 and 25 of experiment 1 (see Figure 2.3). As before, each subject was presented with a total of 100 signallers; once all signallers had been presented, the trial ended.

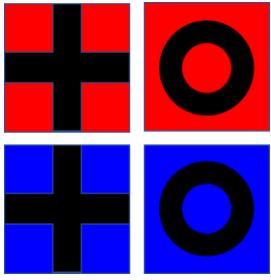


Figure 2.2 The four types of signaller separately presented to receivers. Signal combinations of colour (red or blue) and pattern (cross or circle) collectively indicated the signaller's likely class (desirable or undesirable). Standard trials were conducted with red and cross independently associated with being desirable. Flipped trials were conducted with these associations reversed, so that blue and circle were independently associated with desirability.

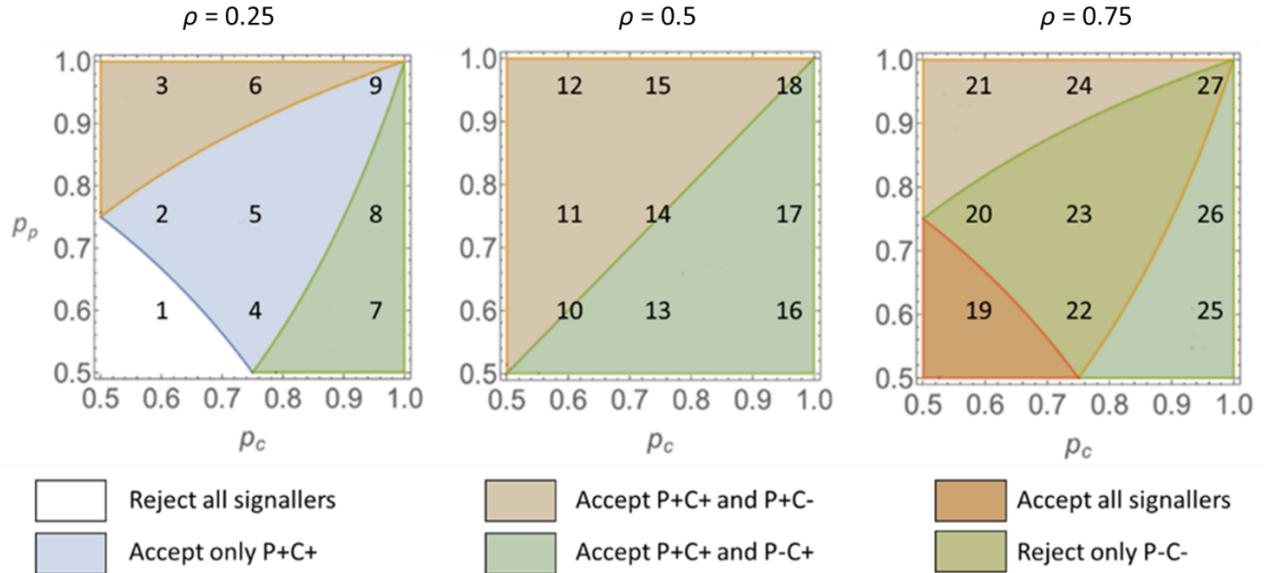


Figure 2.3 Optimal receiver response strategies under different base rate (ρ) and signal reliabilities p_c and p_p in Experiment 1. Numbers (1-27) represent each treatment combination. For each set of treatments, the benefit from accepting desirable signallers (b) and the cost from accepting undesirable signallers (c) were equal. Colours refer to whether signallers with given signal combinations (P+C+, P+C-, P-C+ and P-C-) should be accepted or rejected on encounter. Following only the most reliable signals is sometimes predicted over all parameter combinations (centre plot); however, there are combinations of reliability and base rate under which receivers should pay attention to both signals (highlighted in blue and dark green), or none at all (highlighted in white and dark brown).

Statistical Analysis

All statistical analyses were performed in R version 3.5.3 (R Core Team, 2019). For reproducibility, the raw data as well as annotated statistical code and output (formatted as an R Markdown document) are available in the Appendices.

Experiments 1 and 2

Generalized linear mixed models (GLMM) with binomial error (logit link) were fitted to the acceptance/rejection responses of our volunteers using the glmer function of the lme4 package (Bates et al., 2015). Although fitting an overarching model with high-order interactions was possible, for ease of interpretation I chose to fit a separate model to each of the 27 treatments and thereby evaluate the extent to which the differing model predictions were upheld under each separate set of conditions. When fitting models, the colour (red/blue) and pattern (circle/cross) of the signaller were treated as fixed effects, while the position in sequence in which the signaller was encountered (1-100) was treated as a covariate (mean-centred and rescaled to facilitate model convergence). The individual subject was treated as a random effect. The full model was:

$$\text{accepted} [0,1] \sim \text{colour} * \text{pattern} * \text{sequence} + (1|\text{ID})$$

which was compared with a simpler model lacking the colour term ($\text{accepted} \sim \text{pattern} * \text{sequence} + (1|\text{ID})$), a model lacking the pattern term ($\text{accepted} \sim \text{colour} * \text{sequence} + (1|\text{ID})$), a model lacking all colour*pattern interactions ($\text{accepted} \sim \text{colour} * \text{sequence} + \text{pattern} * \text{sequence} + (1|\text{ID})$), a model lacking all temporal changes in acceptance ($\text{accepted} \sim \text{colour} * \text{pattern} + (1|\text{ID})$) and the null model ($\text{accepted} \sim 1 + (1|\text{ID})$). Model selection was determined through small-sample Akaike Information Criteria (AICc) and associated weights (AICw), calculated using the MuMIn package (Barton, 2019). The importance of

particular predictors was further assessed by comparing models with and without the predictor using log-likelihood ratio tests (LRT). The random effect was considered intercept only to facilitate model convergence, and thus it controlled only for differences in the overall rate at which volunteers accepted signallers. When convergence warnings arose for any one of the six model estimates within a given treatment (which happened in 8 of 27 treatments), I controlled for the volunteer (ID) as a fixed effect for all candidate models within the treatment (Bolker, 2014). The ΔAICc and associated weights from the fit of these fixed effect models were very similar to those from fitting the respective mixed effects models in cases where the fit of both model types was possible.

Under conditions for which no signal component should be attended to (i.e. all signallers accepted, or all rejected), it was expected that the null model with a constant acceptance rate independent of signaller would be best supported. Conversely, in those instances in which the form of only a single signal component (colour or pattern) mattered long-term, then I expected its effect to be evident in the best supported model, and that there would be no evidence for the effect of the other signalling component in influencing acceptance. In cases where the variants of both signal components influenced the decision to accept a given signaller type, then I expected to see a colour*pattern interaction in the best supported model (since three types of signaller should be accepted and one rejected or *vice-versa*). If separate effects of colour and pattern were evident but no colour*pattern interaction, then this would represent separate additive contributions towards the decision to accept a given type of signaller based on its signal components. In these cases, both signal components would be attended to, but not in the strict manner predicted by the signal detection model where combinations of traits should be always accepted or never accepted. Naturally, any role of sequence, whether as a main effect or part of an interaction, reflects a changing acceptance rate of one type of signaller or another over time.

Experiment 3: Flipped Trials

To determine the effect of changing the nature of the reliable colours and patterns, I used the binary variables r_c (0/1) and r_p (0/1) to represent whether the signaller exhibited the more reliable colour and/or more reliable pattern. Here the reliable colour and pattern differed according to whether the experiment was “flipped” or “not flipped”. Thus, $r_c = 1$ was used for red and 0 for blue in non-flipped trials in Experiment 1, yet $r_c = 0$ was used for red and 1 for blue in flipped trials generated in this experiment. Likewise, $r_p = 1$ was used for cross and 0 for circle in non-flipped trials and $r_p = 0$ was used for cross, 1 for circle in flipped trials. Defining the reliable colour and pattern in this way we fitted the following full model for each of the six treatments namely accepted[0,1] $\sim r_c * r_p * \text{sequence} + r_c * r_p * \text{flipped} + (1|\text{ID})$. In total six additional simpler models were compared, paralleling the models fitted in Experiment 1. Any effect of flipping (elucidated using log likelihood ratio tests comparing the above full model to the same model lacking the flipping term) would indicate that the acceptance rates of signallers was at least in part affected by the precise set of signals used to indicate desirability.

Results

Experiment 1

Figure 2.4 shows the proportion of each type of signaller that were desirable in each of the 27 treatment combinations and the corresponding proportion of each type of signaller that were ultimately accepted. Figure 2.5 shows the fitted responses to each of the four signaller types for each treatment.

Overall, the acceptance rates tended to match the probability of signallers being desirable (since $b = c$ then any signaller with a probability of being desirable of higher than 0.5 should be accepted, see Figure 2.4). However, the full model was often best at accounting for the entire history of acceptance rates of volunteers in a given treatment. For example, in treatment 3 volunteers ultimately appeared to

accept those signallers with a cross, independent of their colour. Reassuringly, the SDT model predicts that in this particular case the best supported model would contain pattern only; however, the full model with an interaction between colour and pattern had a better fit than the pattern only model ($\Delta\text{AICc} = 8.7$). Likewise, in treatment 7 receivers appeared to accept signallers that were red independent of pattern. In accordance with SDT model predictions, the colour only model was among the two best fit models, yet the full model with an interaction had a slightly better fit ($\Delta\text{AICc} = 4.1$). In treatment 9 where accepting only C+P+ was optimal (Figure 2.3), receivers tended to accept only those signallers with red crosses; here the additive and full models had most support ($\Delta\text{AICc} = 4.1$). No signaller was predicted to be accepted in treatment 1 and here the AICw of most of the fitted models were non-negligible (> 0.001) with the exception of the null model and full model without learning for which there was no evidence.

Table 2.1 summarizes the best supported models when fitting the 27 separate generalized linear models to the short-trial data. There was evidence of learning, as indicated by a significantly better fit of the full model compared to the fit of the same model without sequence in 19 of the 27 treatments. Note that, as described above, in many treatments volunteers used both colour and pattern (the full model had the greatest support) even when they were predicted to pay attention to just one of these signals long-term. This likely arose because receivers had to evaluate a range of rules for acceptance based on signaller appearance, including those that turned out to be suboptimal.

Experiment 2

The overall acceptance rates of signallers in the extended trials are shown in Figure 2.6, while the fits of the generalized linear models are shown in Figure 2.7. In the first set of extended trials (equivalent to treatment 5 when only P+C+ was predicted to be accepted), the full model was most supported ($\text{AICw} = 1$); see Table 2.2. Comparing the full model with sequence against the same model

lacking sequence, learning continued to be significant ($LRT X^2_4 = 104.9, P < 0.001$). Moreover, the full model explained significant variance compared to both the colour only model ($LRT X^2_4 = 276.2, P < 0.001$) and the pattern only model ($LRT X^2_4 = 132.8, P < 0.001$). As expected, the fitted acceptance rates of P+C+ increased over time, while the acceptance rate of all the other forms of signaller decreased as more were encountered (Figure 2.7a).

When $\rho = 0.5, b = c = 1$ in the extended trials, the desirability of two types of signaller (red circle and blue cross) was borderline, with each having an expected probability of being desirable of 0.5, while red crosses were generally desirable and blue circles were generally undesirable. Because of this, following colour (red), pattern (cross) or both all had similar payoffs. Here, it was found that the full model and the model without learning were best supported ($AIC_w = 0.987$ and 0.013 respectively), although including the effect of learning provided a significantly better fit ($LRT X^2_4 = 16.7, P < 0.001$). Moreover, the full model explained significant variance compared to the colour only model ($LRT X^2_4 = 215.5, P < 0.001$) and pattern only model ($LRT X^2_4 = 198.9, P < 0.001$). As expected, the acceptance rate of C+P+ was high and the acceptance rate of C-P- was low, with acceptance rates of the two other signaller types being intermediate (Figure 2.7b).

In the third set of extended trials (equivalent to treatment 23 where all but C-P- were predicted to be accepted), the full model was best supported ($AIC_w = 0.999$). Learning continued to be significant ($LRT X^2_4 = 23.8, P < 0.001$) and the full model explained significant variance compared to the colour only model ($LRT X^2_4 = 305.1, P < 0.001$) and pattern only model ($LRT X^2_4 = 183.3, P < 0.001$). By the end of the experiment, the fitted acceptance rates of signallers was above 0.5 for all signaller types except C-P- (Figure 2.7c).

To help highlight the effect of learning, Figure 2.8 identifies signaller acceptance proportions at different stages within the trial. During the initial stage, when receivers encountered only a few ($n < 10$)

of each signaller type, each phenotype's acceptance is relatively even. As the trial progressed and more was learned relating to signaller desirability and frequency of encounter, the overall acceptance rates of each signaller type begin to differentiate to reflect the predicted asymptotic strategies.

Experiment 3: Flipped Trials

Across all treatments, the acceptance rates of signallers in flipped and non-flipped trials were broadly comparable, such that for example signallers with a cross tended to be accepted as desirable in treatment 21 of the original (non-flipped) trials, while signallers with a circle tended to be accepted when the reliability of the colour pattern combination was reversed (see Figure 2.9). However, differences were also evident. Recognizing the specific colour and pattern associated with desirability did not significantly improve the model in two (5 and 23) of the six treatments (see Table 2.3). In the remaining four treatments, three showed a significant effect of flipping as part of a model that included a three-way interaction with the two signalling traits associated with desirability (Table 2.3). No consistent patterns were evident however, since the effect of flipping varied between treatments. More importantly, the qualitative conclusions arising from these experiments remained the same. Thus, fitting the six models to the flipped trials alone indicated that the full model (4 out of 6 treatments) or additive model (2 out of 6 treatments) was best supported in explaining variation in acceptance rates (see Table 2.4).

Exploration/exploitation model

To compare the entire suite of observations with exploration-exploitation predictions, I ran 100 forward iterations under the conditions specified for each of the 27 treatments (three base rates, three colour and three pattern reliabilities). Figure 2.10 shows the predicted probability of accepting a given signaller type on encounter over all 108 possible conditions (27 treatments x 4 signaller types) and the observed probability of accepting the signaller type over the full duration of the experiment. In general,

the observed acceptance rates were relatively consistent with those predicted by the exploration-exploitation model. Signallers with a high likelihood of being desirable were indeed accepted at high rates as predicted by the model, while signallers with a low likelihood of being desirable were rapidly rejected. For those signallers with a probability of being desirable closer to 0.5, the predicted and observed acceptance rates were more intermediate as a consequence of receivers requiring more sampling before identifying an optimal response. These intermediate responses are not predicted by SDT, which predict all or nothing acceptance rates of a given type of binary signaller. The probability of signallers being presented per time step during the experiment also affected model predictions (and observations). Those signallers encountered frequently were predicted to have acceptance rates closer to 0 or 1 (dependent on profitability) and this prediction was generally supported (Figure 2.11). Likewise, the acceptance rate of infrequently encountered signallers was predicted to be more variable, and this was also evident.

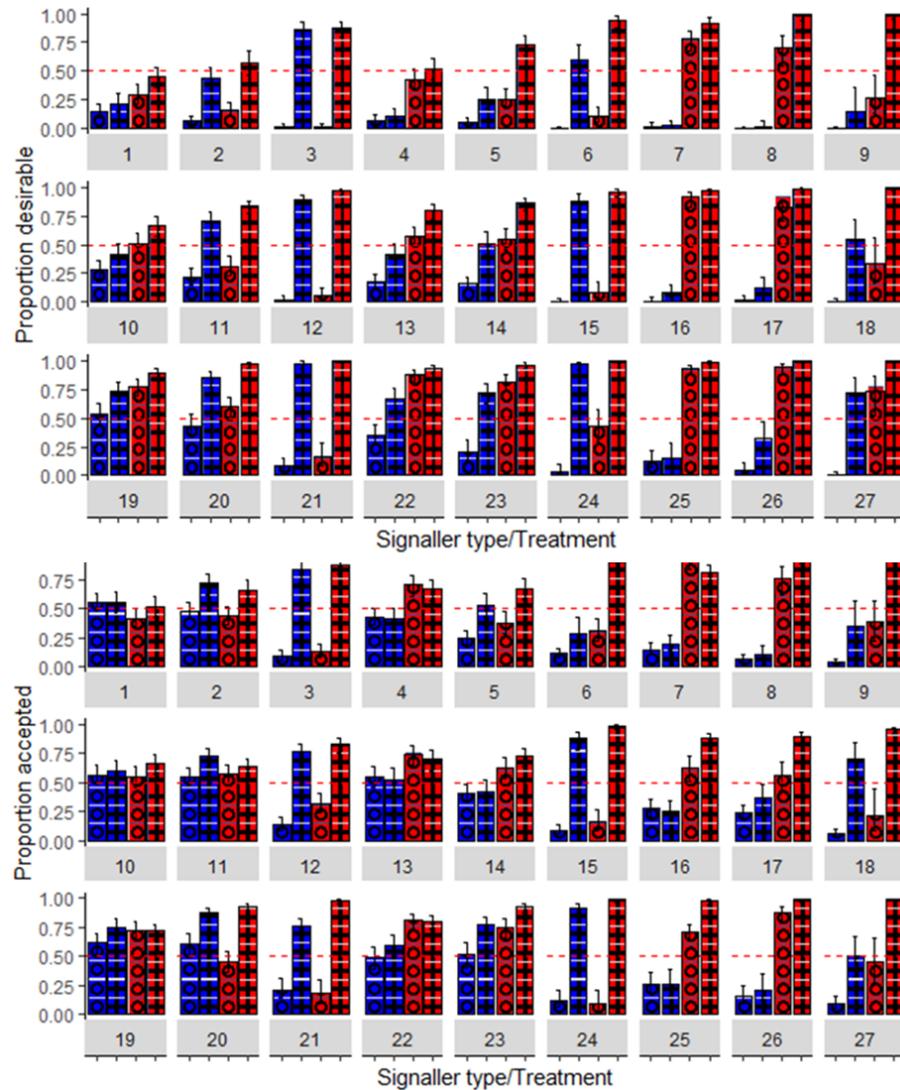


Figure 2.4 The proportion of four types of signaller that were desirable (hence profitable to accept, above) and the proportion of each signaller type accepted for each treatment over the course of Experiment 1 (below). The colours and patterns on the bars correspond to the specific signaller phenotypes. The dotted red line indicates a proportion of 0.5 and the error bars show one standard error.

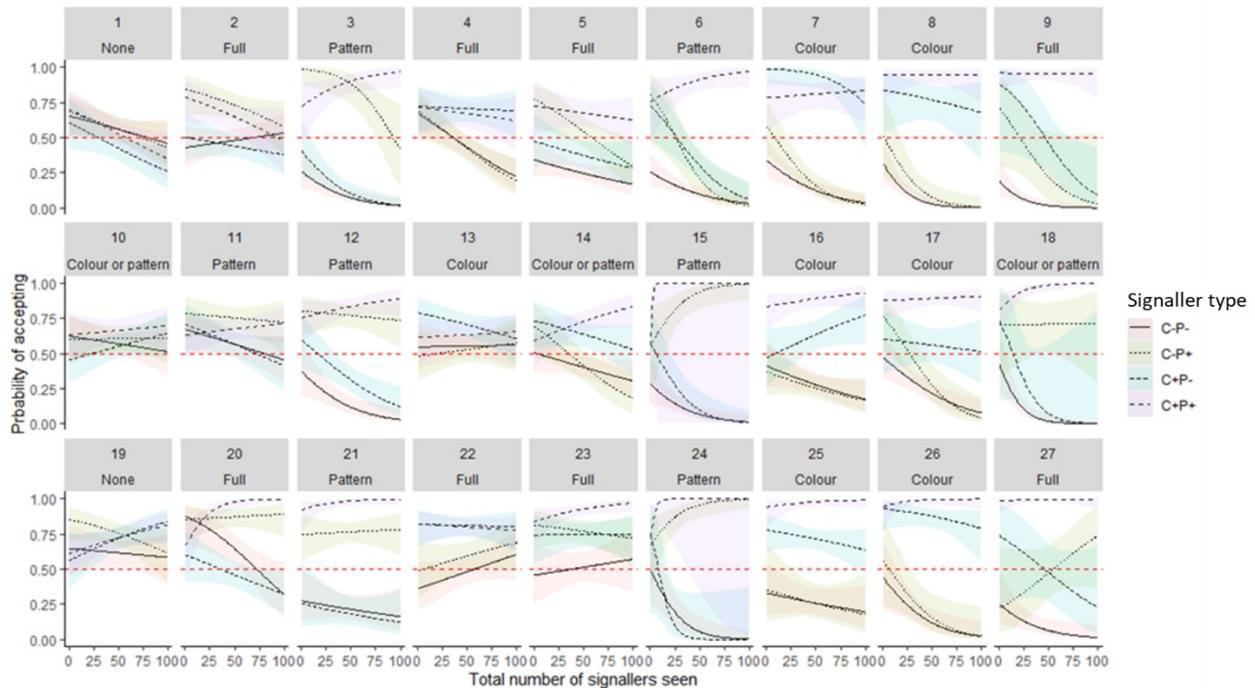


Figure 2.5 The fits of generalized linear mixed models to the 27 treatments in Experiment 1, showing the acceptance rate of each signaller type as more of this signaller type is encountered. The treatment number and predicted SDT optimal response are given in grey bars. Coloured ribbons show 95% confidence intervals of the fitted model.

Table 2.1 Fits of the GLMM to 27 treatments within Experiment 1, each involving 5 human volunteers choosing whether to accept a sequence of 100 signallers with a given colour and pattern. The SDT predicted response (see Figure 2.3) is compared with the best supported model of acceptance (lowest AIC_c) of six candidate models namely null, only follow pattern, only follow colour, additive model (no colour:pattern interaction), full model and full model with no temporal component. Evidence of learning was assessed by comparing the fit of full model with temporal changes in the acceptance rates to a reduced model lacking these temporal changes (Full nl) using an LRT. Where warnings were raised concerning the fit of any of the candidate mixed effects models due to singular fits, the best candidate model was identified by treating individual volunteer as a fixed effect rather than a random effect.

Treatment	SDT predicted best supported model	Observed best supported model	Best supported model weight	Evidence of learning	Singular fit
1	Null	Colour	0.674	Y	N
2	Full	Pattern	0.602	N	N
3	Pattern	Full	0.93	Y	Y
4	Full	Colour	0.845	Y	N
5	Full	Full	0.695	Y	N
6	Pattern	Full	1	Y	N
7	Colour	Full	0.814	Y	Y
8	Colour	Additive	0.840	Y	Y
9	Full	Full	0.824	Y	N
10	Colour or pattern	Null	0.566	N	N

11	Pattern	Pattern	0.684	N	N
12	Pattern	Additive	0.571	Y	N
13	Colour	Full (nl)	0.460	N	N
14	Colour or pattern	Full	0.518	Y	N
15	Pattern	Full	0.990	Y	Y
16	Colour	Full	0.626	N	N
17	Colour	Full	0.943	Y	N
18	Full	Additive	0.785	Y	Y
19	Null	Colour	0.542	Y	N
20	Full	Full	0.999	Y	N
21	Pattern	Full (nl)	0.589	N	N
22	Full	Colour	0.590	N	N
23	Full	Full (nl)	0.574	N	N
24	Pattern	Full	0.998	Y	Y
25	Colour	Full (nl)	0.879	N	N
26	Colour	Full	0.925	Y	Y
27	Full	Additive	0.6	Y	Y

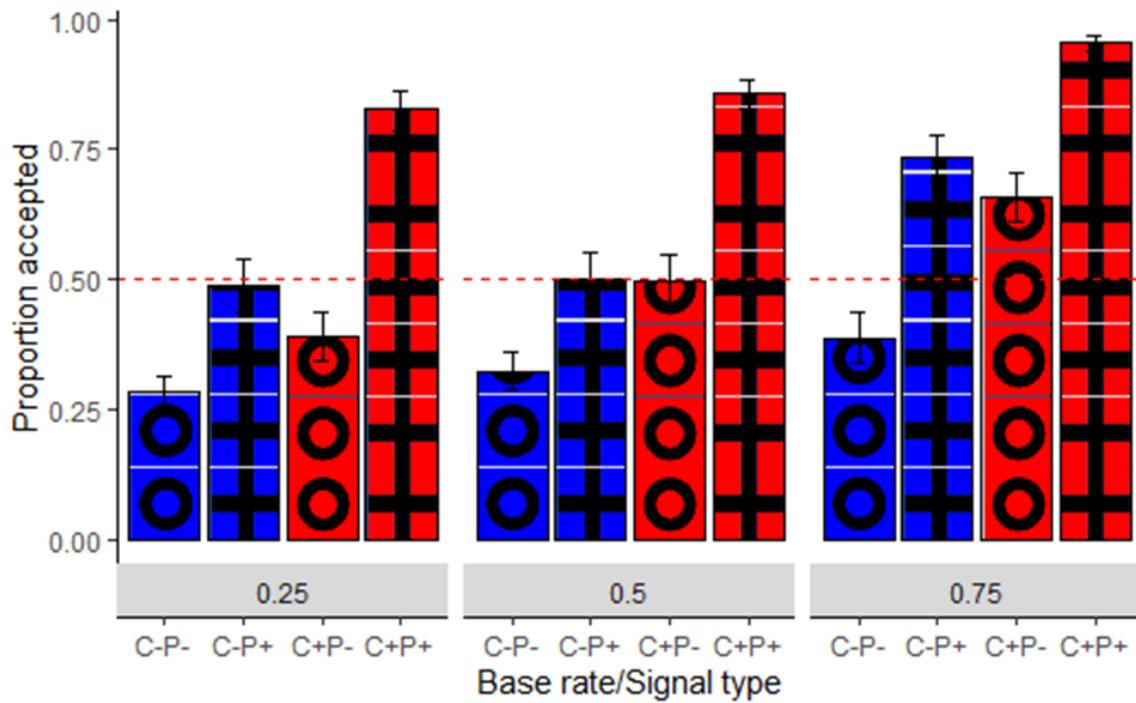


Figure 2.6 The proportion of signallers of each type that were accepted for each base rate with signal reliabilities $p_c = p_p = 0.75$ (treatments 5, 14 and 23) over the course of the extended trials (Experiment 2) with 200 signallers presented. The values (0.25, 0.5, 0.75) of base rate ρ are given in grey. The colours and patterns on the bars correspond to the specific signaller phenotypes presented. Error bars show one standard error.

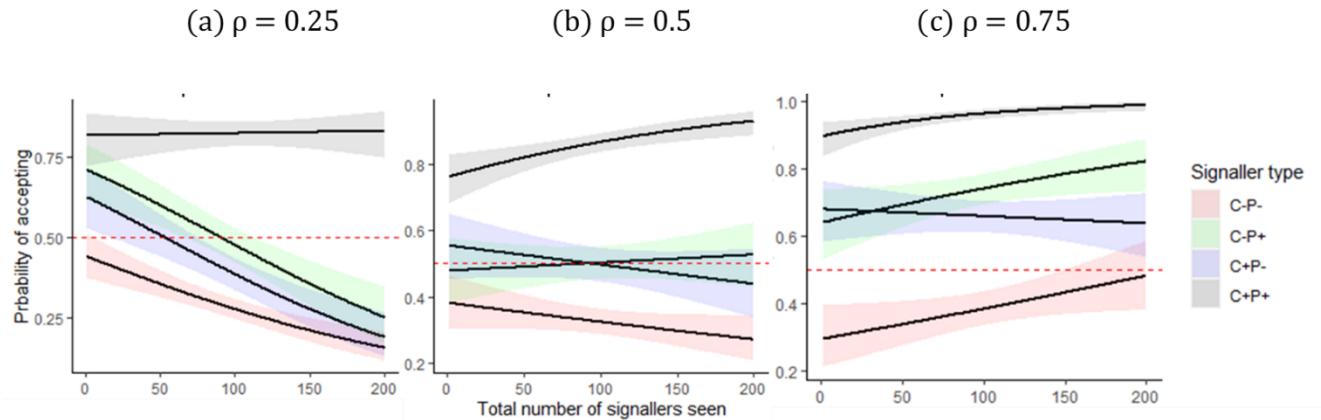


Figure 2.7 The separate fits generalized linear mixed models in the extended trials (Experiment 2) showing how the probability of accepting each signaller changes over time. Results are shown for each base rate ($\rho = 0.25, 0.5, 0.75$). Coloured ribbons show 95% confidence intervals of the fitted model.

Table 2.2 Fit of the six candidate GLMMs to the data from extended trials (Experiment 2), each involving 10 human volunteers choosing whether to accept a sequence of 200 signallers with particular colours and patterns. Base rates (ρ) 0.25, 0.5 and 0.75 exemplify conditions which are identical to treatments 5, 14 and 23, respectively from Experiment 1 (Figure 1). See Table S1 legend and main text for a description of the candidate models fitted. The best supported model was the full model with colour:pattern interactions. Analysis of deviance confirms the importance of attending to the specific combination of colour and pattern, in that in all cases the colour:pattern interaction was highly significant in itself and often as part of a three-way interaction with sequence. * P <0.05, ** P < 0.01 and *** P < 0.001.

Base rate (ρ)	SDT predicted best supported model	Observed best supported model	Best supported model weight	Analysis of deviance comparing models of increasing complexity							
				Colour	Pattern	Sequence	Colour: Pattern	Colour: Sequence	Pattern: Sequence	Colour: Pattern: Sequence	
0.25	full	full	0.999	***	**	***	***	ns	ns	***	
0.5	Colour and/or Pattern	full	0.987	***	***	ns	***	ns	ns	ns	
0.75	full	full	0.999	***	***	*	***	ns	ns	*	

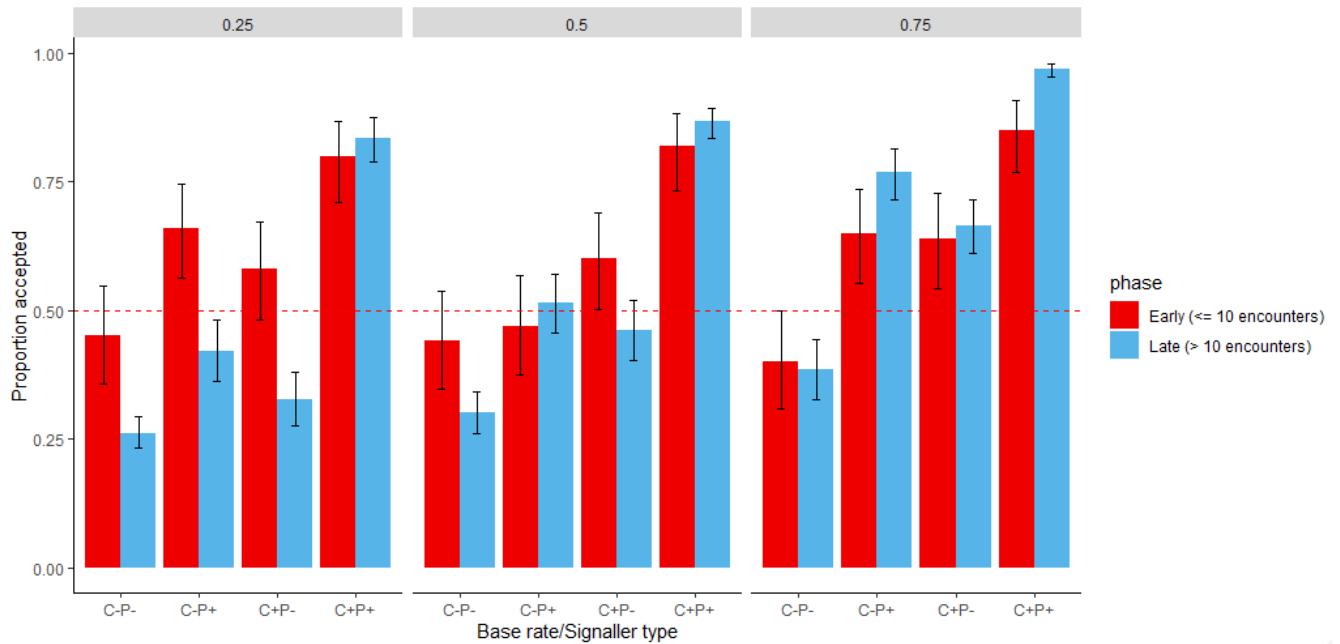


Figure 2.8 The proportion of signallers that were accepted within the extended trials (Experiment 2).

Blue bars indicate the proportions after which 10 signallers of each type had been encountered, when observers are relatively experienced with the four signaller types. These acceptance proportions are compared to those during the phase of the trial where the receiver had encountered only 10 presentations of each signaller type, and when it was predicted that learning would impact the stability of acceptance proportions (red bars). In general, acceptance rates improved for signallers that were on average profitable and reduced for signallers that were on average unprofitable. Error bars show one standard error.

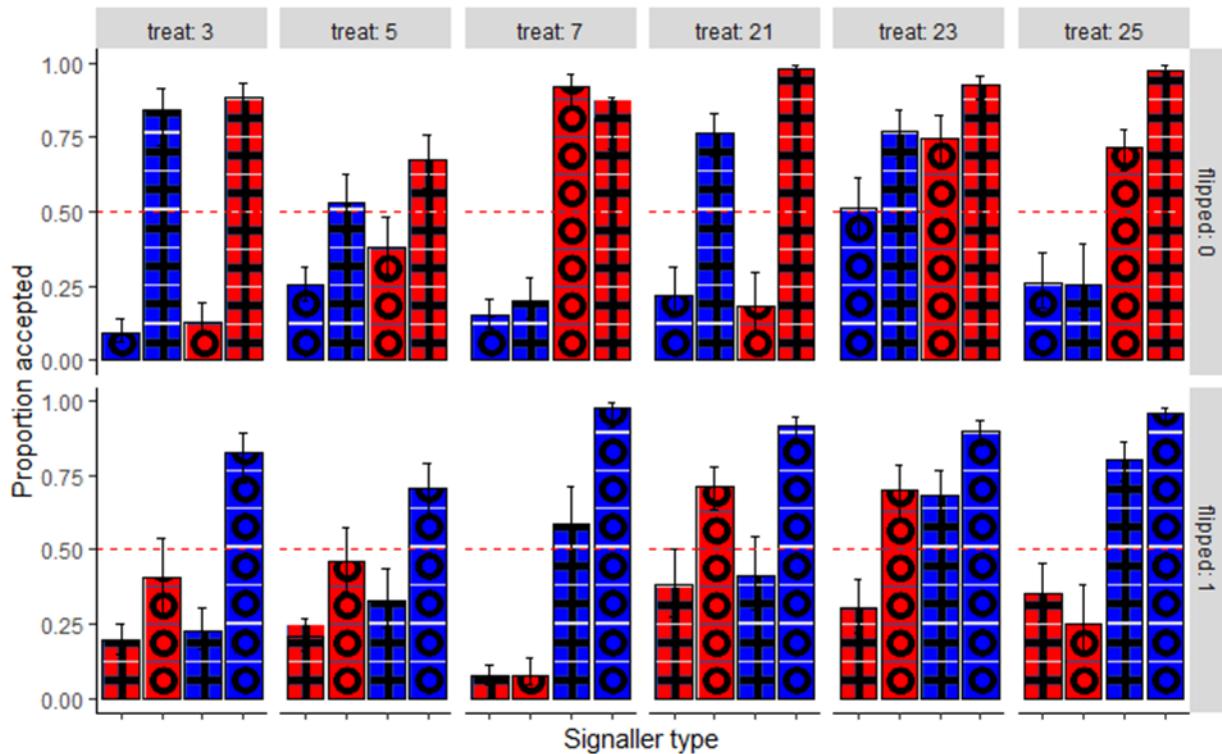


Figure 2.9 The proportion of signallers of each type that were accepted for each treatment in the original (Experiment 1, flipped = 0) and flipped (Experiment 3, flipped = 1) experiments. Colours and patterns on the bars correspond to the actual signaller phenotypes that were presented during each set of experimental trials (red and cross were the reliable signaling trait in the Experiment 1, blue and circle were the reliable signaling trait in Experiment 3). In general, there was a strong correspondence in acceptance rates within comparable treatments (red cross = blue circle, red circle = blue cross etc.). Error bars show one standard error.

Table 2.3 Fits of the GLMM to the six short treatments and corresponding flipped data. The SDT predicted response (see Figure 2.3) is compared with the best supported model of acceptance (lowest AIC_c) of seven candidate models: null, only follow pattern, only follow colour, additive model, full model and full model with no learning component (Full nl) and full model with flipping (Full flipped). Evidence of learning was further assessed by comparing the fit of full model with temporal changes in the acceptance rates to a reduced model lacking these temporal changes using an LRT. Evidence of flipping was further assessed by comparing the fit of full model with flipping to the same model lacking the flipping term using LRT. All seven candidate models could be fit using the mixed effect model except treatment 7 which did not converge on the null model and full model without learning.

Treatment	SDT predicted best supported model	Observed best supported model	Best supported model weight	Evidence of learning	Evidence of flipping effect
3	Pattern	Full (flipped)	1	Y	Y
5	Full	Full	0.976	Y	N
7	Colour	Full (flipped)	1	Y	Y
21	Pattern	Full (flipped)	1	Y	Y
23	Full	Full (nl)	0.409	N	N
25	Colour	Full (flipped)	0.899	Y	Y

Table 2.4 Fits of the GLMM to only the six flipped treatments. The SDT predicted response (see Figure 1) is compared with the best supported model of acceptance (lowest AIC_c) of six candidate models namely null, only follow pattern, only follow colour, additive model, full model and full model with no temporal component (Full nl). Evidence of learning was further assessed by comparing the fit of full model with temporal changes in the acceptance rates to a reduced model lacking these temporal changes using an LRT. All six candidate models were fit using the mixed effect model, except treatment 25 which did not converge on the full model without learning.

Treatment	SDT predicted best supported model	Observed best supported model	Best supported model weight	Evidence of learning?
3	Pattern	Full	0.923	Y
5	Full	Additive	0.843	Y
7	Colour	Full	0.94	Y
21	Pattern	Full	0.984	Y
23	Full	Additive	0.569	N
25	Colour	Full	0.999	Y

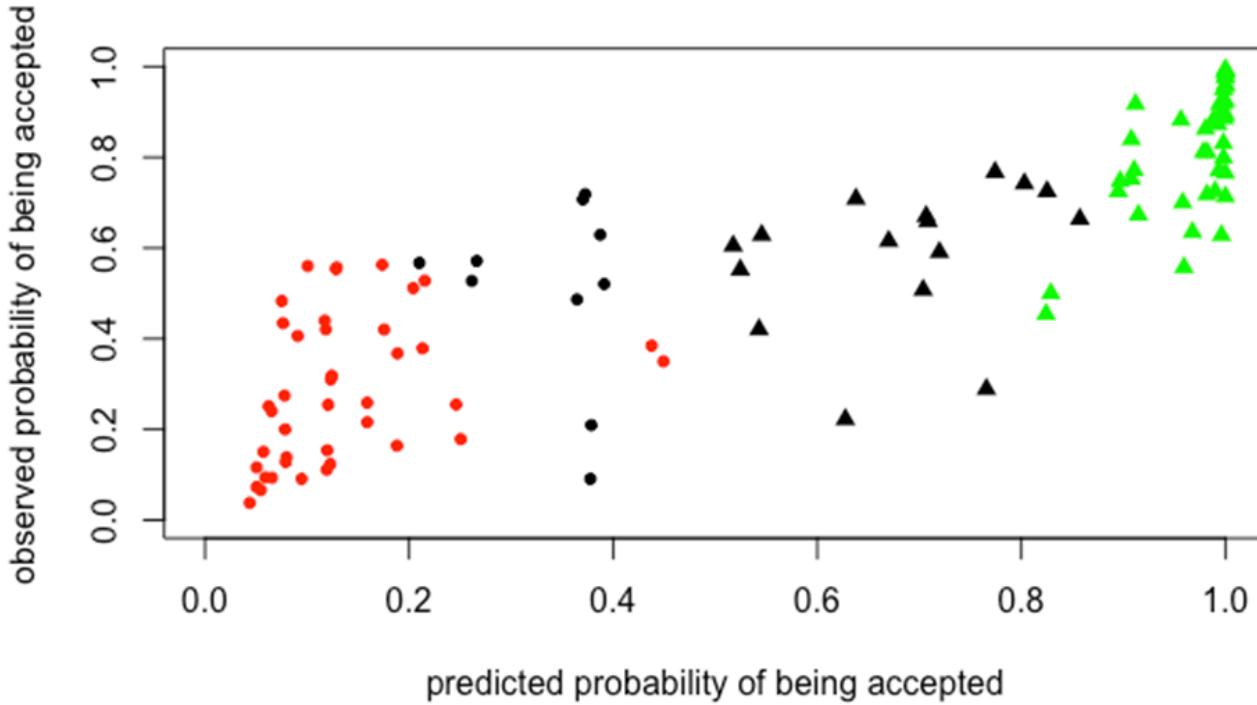


Figure 2.10 The predicted average proportion of signallers accepted and the observed proportion of signallers accepted in the exploration-exploitation model over all the 27 treatments ($4 \times 27 = 108$ data points). Here, I assumed that volunteers initially had uniform Bayesian priors and that $b = c = 1$. Green points represent cases where the signaller had a high probability of being profitable ($\text{Pr}(\text{desirable}|s_{ij}) > 0.7$) and red points represent cases where the signaller had a low probability of being profitable ($\text{Pr}(\text{desirable}|s_{ij}) < 0.3$). Intermediate cases are given in black. Triangles represent signallers that would ultimately be profitable (since $b = c$) to accept ($\text{Pr}(\text{desirable}|s_{ij}) > 0.5$), circles represent signallers that would on average be unprofitable to accept ($\text{Pr}(\text{desirable}|s_{ij}) < 0.5$).

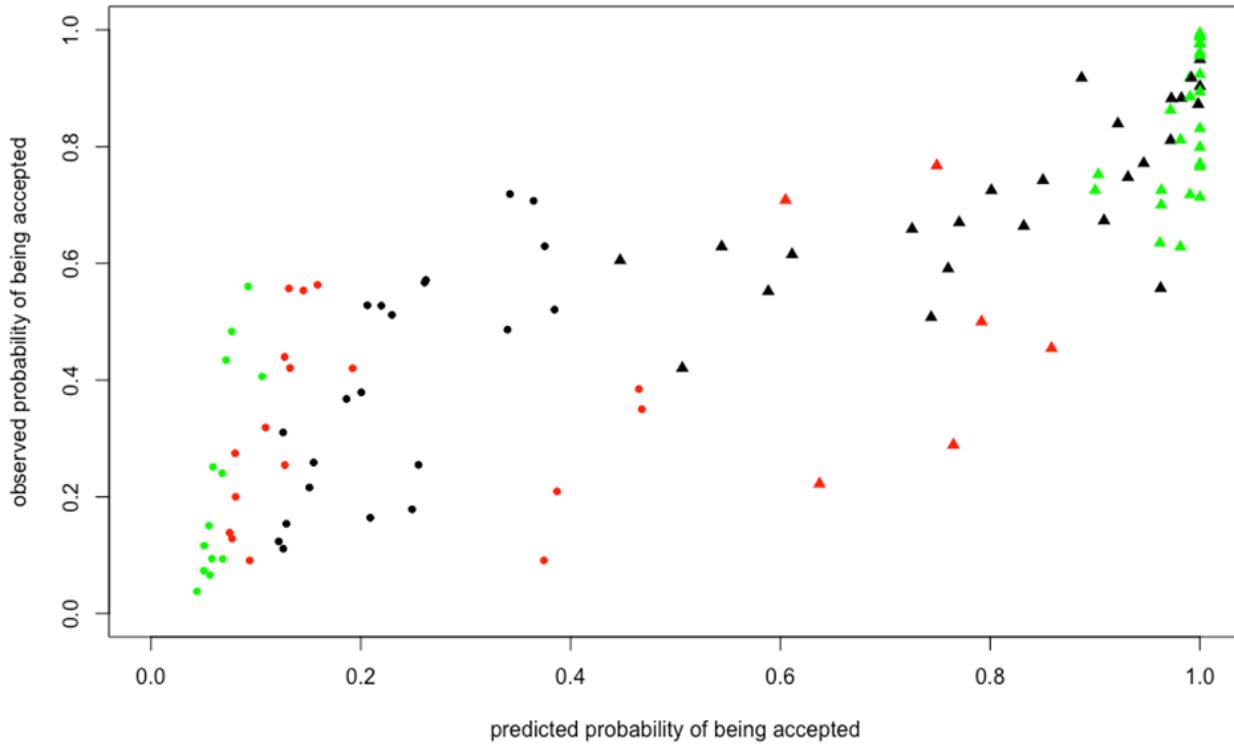


Figure 2.11 The predicted average proportion of signallers accepted and the observed proportion of signallers accepted in our exploration-exploitation model over all the 27 treatments. Here, I assumed that volunteers initially had uniform Bayesian priors and that $b = c = 1$. Green points represent cases where the signaller had a high probability of being encountered per presentation (> 0.3) and red points represent cases where the signaller has a low probability of being encountered (< 0.1). Intermediate cases are given in black. Triangles represent signallers that would ultimately be profitable (since $b = c$) to accept ($\Pr(\text{desirable} | s_{ij}) > 0.5$), circles represent signallers that would on average be unprofitable to accept ($\Pr(\text{desirable} | s_{ij}) < 0.5$).

Discussion

Receivers frequently need to discriminate between signallers based on their traits. While the evolution of multicomponent and multimodal signals have been the topic of many comprehensive reviews (Rowe, 1999; Candolin, 2003; Hebets & Papaj, 2005), to my knowledge no study has empirically investigated receiver economics under the complete range of conditions in which paying attention to no signal element, only one element or two signal elements is predicted to be optimal from a purely “economic” (Rubi & Stephens, 2016a) standpoint. While most experimental effort has been aimed at evaluating whether receivers attend to the single most reliable signalling trait when they are expected to do so (e.g. Rubi & Stephens 2016a, b), I believe that it is of just as much interest to ask whether receivers pay attention to two signalling traits when they are predicted to do so.

I found evidence that receivers attend to both signalling traits under many of the conditions predicted by SDT. Thus, a full model containing interactions in which acceptance rates were dependent on the specific combination of colour and pattern, was often the best supported model. Intriguingly however, the full model was often supported when receivers were predicted to attend to just one signalling element. This result most likely arose because volunteers had to learn how to respond and were therefore testing a range of tentative hypotheses based on the variants of both signalling components before settling on a strategy that appeared consistent with maximizing their gain. For example, a volunteer that avoids blue at first but then settles on avoiding circles may give the impression that both colour and pattern are attended to, when eventually only pattern matters to the receiver. This is a plausible explanation because I found strong evidence that acceptance rates of signallers changed over time, indicating that learning was occurring. Moreover, repeated forward iterations of the optimal exploration-exploitation rules under conditions identical to those of the experimental treatments

frequently produced sample data to which the full model had greatest support, even when the optimal strategy eventually settled on accepting signallers based on just their colour, or just their pattern.

Signal complexity may influence the rate at which receivers arrive at optimal decision-making strategies (Skelhorn et al., 2015; Skelhorn & Rowe, 2016; Tibbets et al., 2020). Dog owners have long exploited this phenomenon, using both verbal and gestural commands to reinforce their messages. However, as Lotem (2013) noted, behavioral ecologists have tended to focus on identifying optimal behavioral strategies rather than the evolution of the learning mechanisms that lead to these strategies. Indeed, experiments to test predictions of SDT often take steps to educate receivers prior to formal experimentation. For example, Rubi & Stephens (2016a) did not use the first 400 presentations of signals to blue jays in their analysis, allowing the birds time to identify a payoff maximizing strategy. Likewise, McGuire et al. (2006) showed their human volunteers screen shots of collections of desirable and undesirable signallers before the formal experiment began so that they could directly see the extent to which the signallers differ. Kikuchi et al. (2015) also presented human subjects with exemplars of costly models and beneficial mimics side by side before subjects participated in trials. In both studies, there was clear evidence that learning continued to take place despite the prior information provided.

The response of receivers to some signallers may be innate, such that for example receivers may evolve a strong prior that a given type of signaller is desirable or undesirable. Mantids for example, have been shown to express an innate aversion to ants (Nelson et al., 2006). Likewise, some species of passerine bird exhibit innate avoidance of aposematic prey even when they are hand-reared and have no prior experience with them (Exnerova et al., 2007). In cases where responses are less ‘hard-wired’, learning may still take up only a small proportion of the total interaction time. However, in many cases more flexible responses may be necessary which comprise a significant portion of the interactions. For

example, signals of mate quality are evaluated differentially depending on the frequency and quality of potential mates and the state of the evaluating receiver (Schneider et al., 2016).

SDT is a versatile and powerful modelling framework (see Getty, 1985; Rodriguez-Gironés & Lotem, 1999; Holen & Johnstone, 2004; Kloock & Getty 2019 for some example applications). In cases where signallers were predominantly desirable or undesirable and commonly encountered, the SDT model described provided reasonable approximations of receiver behaviour in that their long-term acceptance rates were close to 0 or 1 and matched the predicted outcome. For example, in experiment 1 the C+P+ signallers that had a probability of being desirable greater than 0.8 and a probability of encounter greater than 0.4 per time step (8 treatments in total) had a mean acceptance rate of 0.97 (se 0.01). Likewise, C-P- signallers that had a probability of being desirable of less than 0.2 and a probability of encounter of greater than 0.4 per time step (7 treatments) had a mean acceptance rate of 0.11 (se 0.03). This asymmetry (deviations of 0.11 vs. 0.03 from 0 and 1) no doubt arises because receivers that discover signallers are generally undesirable must change their behaviour and stop accepting them, whereas those that discover signallers tend to be desirable can continue accepting them and are increasingly re-assured they are making the correct decision. Despite the success of SDT in predicting certain receiver responses, the acceptance rates of rarer signallers of borderline profitability was not 0 or 1 as predicted by the SDT model, but somewhat intermediate. Far from being sub-optimal, this is precisely what one would expect if receivers are making strategic decisions as to whether to accept a signaller type as they learn about their profitability while estimating their frequency. By using exploration-exploitation models, we can identify just how a payoff-maximizing receiver should respond to signallers in circumstances that are less than clear-cut; notably when information is limited and the differences in payoff are small.

In sum, I have presented clear evidence that receivers often attend to more than one signal component. This is often the economically rational thing to do because it maximizes payoff, whether receivers must learn associations, or not. The extended trials were particularly telling, highlighting conditions under which all signallers but C-P- tended to be accepted and other conditions under which no signaller except C+P+ tended to be accepted. In other cases, early attention to both signalling components makes sense from a strategic perspective even if ultimately receivers learn that following one is sufficient, or if signalling components do not convey useful information. The overall conclusions were robust to the choice of colour or pattern that most reliably indicates desirability, in that similar results arose when the signal combinations that most reliably indicated desirability were flipped.

Note that while the exploration-exploitation model I have presented readily explains the intermediate acceptance rates of receivers, it does not allow for the possibility that individuals generalize their experiences. Instead it simply treats the four signaller types as distinct and identifies the optimal acceptance strategy for each type. Just as with the SDT model, the rules that emerge such as “follow colour” or “follow colour and pattern” were simply a consequence of the set of signaller types that prove to be acceptable and those that do not. However, the human volunteers were engaging in an even more sophisticated exploratory strategy as they learned about signallers than the one modelled here. This is evidenced by the fact that the acceptance rate of a signaller encountered for the first time in extended trials ($n = 10$ human subjects per treatment) was not 100% but only 60-75% (Figure 2.12) - a result also reflected in the estimated intercepts of the fitted GLMMs (Figure 2.7). Exploration-exploitation models, or less computational reinforcement learning algorithms, that allow receivers to simultaneously compare evidence for alternative models such as colour matters, pattern matters and both colour and pattern matters may help us get closer to understanding the way receivers with limited information learn how to respond to multicomponent signals.

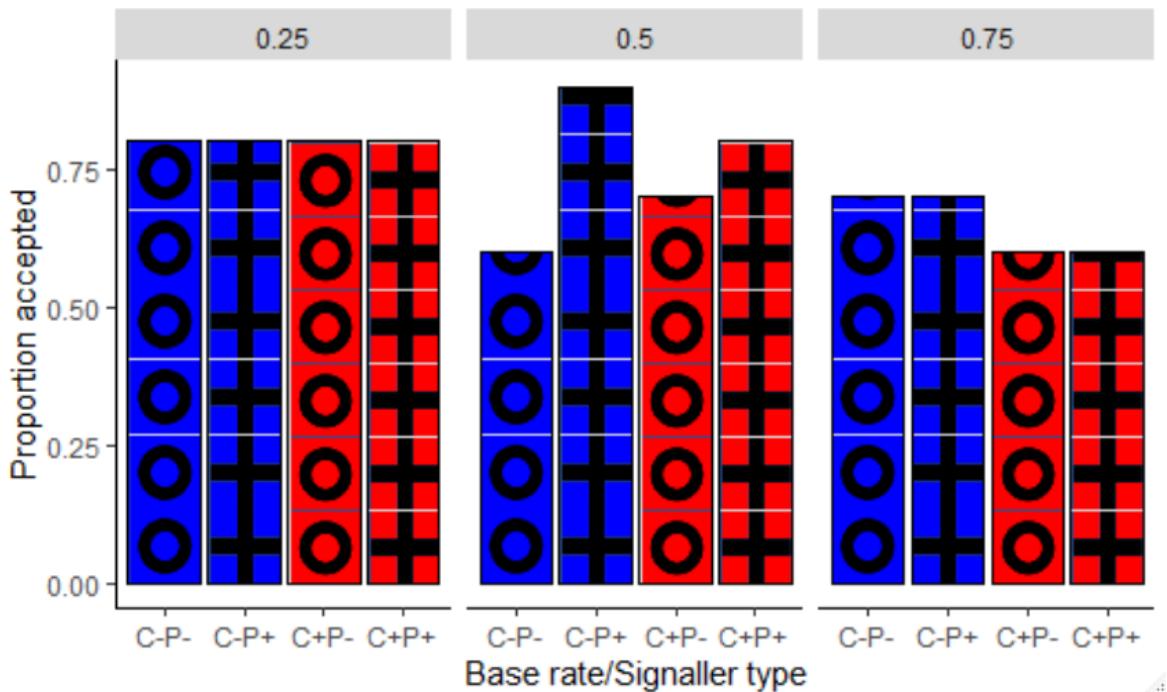


Figure 2.12 The proportion of each signaller type accepted by human volunteers on their first encounter with this signaller type in the extended trials (Experiment 2, $n = 10$ volunteers for each base rate, indicated by grey bars). Even a completely novel signaller type was not always accepted on first encounter, which could suggest that the volunteers were generalizing their experiences and/or exploring the benefits of more complex acceptance strategies.

Chapter 3: General Discussion

Key results

In Chapter 2, when faced with simulated multicomponent signals (Figure 2.2), human receivers tended to pay attention to the form of both signalling components when deciding whether to accept or reject. By ultimately accepting only one signaller type, or by accepting all but one, their decisions necessarily require attention to both signal components. In Experiment 1, I explored a broad parameter space in which a range of different receiver strategies were predicted by a standard SDT model (Figure 2.3). I found that in many cases, the empirical data qualitatively matched these predictions (Figure 2.4, Figure 2.5). Notably, receivers tended to accept desirable signallers and reject undesirable ones (the proportion of signallers that were desirable matched the observed proportion of signallers accepted in Figure 2.4; Table 2.1). However, while receivers ultimately attend to both components when predicted to do so (ultimately accepting one type of signaller, or three types of signaller), they also attended to multiple traits when they were not predicted to do so!

Learning was shown to consistently influence how receivers responded to signallers (Table 2.1). Because of this, I conducted subsequent extended experimental trials (Experiment 2) to allow more time for responses to stabilize. I found cases where receivers again relied on both colour and pattern when choosing to respond (particularly $\rho = 0.25$ and $\rho = 0.75$ in Figure 2.6). The results from fitting GLMMs to the data from Experiment 2 revealed that under all the tested conditions, receivers relied on both signal components (Table 2.2); however, the best supported model continued to include learning as a significant term. The effect that learning had on responses throughout the experiment is illustrated in Figure 2.8. Fits of separate models to the responses of individual participants within the extended trials (not shown) indicated that when colour and pattern were equally reliable (notably, when $\rho = 0.5$), individual receivers varied in their strategies, with some using only colour and others using pattern.

To account for any inherent biases among the tested colours or patterns, I conducted a third set of trials (Experiment 3) on a subset of treatments where the signals associated with desirable and undesirable signallers were “flipped”. The results were qualitatively similar (Figure 2.9, Table 2.4). While there was evidence that flipping did impact responses, it was not in a consistent manner across treatments and the same general conclusions (i.e. attention to both traits and learning) held (Table 2.3).

I ran forward iterations to compare predictions from the exploration/exploitation model to the experimental observations. The asymptotic predictions from the exploration/exploitation model when time horizon was extended remarkably resembles the predictions from SDT when learning is complete (Figure 2.1). That is, when receivers have longer to learn about the relative payoffs of each available resource, they should spend more effort to explore and therefore become increasingly certain that they are making correct decisions. In general, the model-predicted acceptance rates matched those of the observed receivers, but it is worth mentioning that this resemblance deviated at intermediate levels of signal desirability (Figure 2.10) and encounter frequency (Figure 2.11). This result is precisely what we should expect because relatively rare signallers of borderline profitability are more difficult for receivers to accurately appraise, causing variability in their responses.

Limitations and future directions

While the exploration/exploitation model allowed learning to be incorporated, it did not account for generalization among the different signaller types. This is a potentially significant omission as receivers appeared to reject the first signaller presented in some trials, which could suggest that observers are generalizing in an attempt to make informed responses to novel signals (Figure 2.12). E/E problems involve considerable computational resources to solve, and receivers are clearly not “doing the math”. An alternative, and often simpler, set of modelling tools to identify how a receiver adopts an optimal response strategy is through using heuristics (i.e. learning rules of thumb) (Real, 1991; Lotem,

2013; Quiñones et al., 2020). The use of heuristics may allow receivers to make informed decisions about novel signals but also guide them as to how they should treat more familiar signallers. It is quite likely that in most cases, instead of selection acting on optimal behavioural strategies, it instead acts on learning mechanisms which allow an organism to develop such a strategy (Lotem, 2013).

In the experiments conducted, the benefits from accepting desirable signallers (b) and costs from accepting bad signallers (c) were fixed, with both set at 1. While this was set by convenience because it simplifies the problem for receivers, a natural extension of this work is to explore the effects of pushing the ratio b/c away from 1 since it will rarely if ever be precisely equal to 1. The payoffs from accepting desirable and undesirable signallers are a key component when identifying optimal decisions in SDT models and altering these payoffs can change which signals should be attended to (Sherratt & Holen, 2018). For example, when $b \gg c$ then all signallers should be accepted, but if $b \ll c$ then all signallers should ultimately be rejected. In addition, the SDT model was tested under a fixed time horizon of $T = 100$ (Experiment 1 and 3) and $T = 200$ (Experiment 2). Naturally, the amount of signallers a receiver may encounter over its lifetime is likely to vary substantially from this value. For example, a predator evaluating prey signals could encounter hundreds of signallers over their lifetime, whereas a female bird may only evaluate a handful of males signalling their quality as a mate. In these cases, it is of interest to evaluate the impact of increasing (or decreasing) the time horizon to emulate a range of explicit biologically relevant conditions.

The state of the evaluating receiver has been shown to directly influence the value of signal content. For example, Schneider et al. (2006) show that males evaluate female signals differentially throughout the mating season, with a decrease in selectivity as the season progresses. Additionally, Katz & Naug (2015) found that the energetic state of foraging bumblebees influences risk-taking behaviour within exploration/exploitation tasks. The risk of sampling unknown or relatively unrewarding signallers

could be learned and implemented through adaptive decision making (Skelhorn et al., 2016). Further evidence suggests that state dependence is likely to play a role in the valuation of signals, a concept that has been demonstrated in the context of mimicry (Aubier & Sherratt, 2011). Furthermore, the SDT model I have described makes the critical assumption that attention to signal components does not come with an assessment cost or a rejection cost. While this assumption makes modelling receiver behaviour simpler and may hold up in certain contexts, there are cases which have been suggested where taking extra time to evaluate multiple signal components may result in a time/energy or opportunity cost (Fawcett & Johnstone, 2003). A step to further validate the robustness of the conclusions presented here could include the effect of state dependence and include assessment/rejection costs in a more comprehensive model of optimal receiver behaviour.

Appendix A

Analysis of empirical experiments

James Voll

1/08/2020

I start by loading all the required libraries.

```
library(Matrix)
library(lme4)
library(MuMin)
library(dplyr)
library(lattice)
library(ggplot2)
library(DescTools)
library(tibble)
library(readxl)
library(ggtextures)
library(LaplaceDemon)
```

Experiment 1

This is the first of three experiments conducted to test whether receivers would rely on more than one signal within multicomponent signals when deciding how to respond. In each experiment, signallers possessed bicomponent signals of colour (red/blue) and pattern (cross/circle). The signals indicated whether the signaller was profitable to accept (desirable) with colour signal reliability pc and pattern signal reliability pp. Experiment 1 was conducted at three levels of each signal reliability, such that $pc = 0.6, 0.75, 0.95$ and $pp = 0.6, 0.75, 0.95$. I simulated conditions where the frequency of desirable signallers in the environment was varied, with the base rate of desirable signallers being 0.25, 0.5 or 0.75. Combining the 3 levels of each signal reliability, and 3 levels of base rate, the responses of volunteers at a total of 27 treatment configurations were evaluated (3x3 factorial design). This combination of parameters includes conditions where attending to the form of 0, 1 or 2 signals elements is the optimal strategy.

I begin by reading the data.

```
# Master file for experiment 1
setwd("C:/Users/James/Documents")
MasterFileJames <- read.table("MasterFileJames.txt", header = TRUE)
```

To construct Wilson's confidence intervals for the probability of a receiver accepting each signaller type, I aggregate the data according to signal combination (4 types) and treatment (1-27).

```

adata <- aggregate(attacked ~ pt + treat, data = MasterFileJames, sum)
acceptances<- adata$attacked # the number of signallers encountered

edata <- aggregate(attacked ~ pt + treat, data = MasterFileJames, length)
encounters <- edata$attacked # the number of signallers encountered that were accepted

binomci <- cbind(adata, encounters)
colnames(binomci) <- c("pt", "treat", "acceptances", "encounters")
CItable <- as.data.frame(BinomCI(acceptances, encounters, conf.level = 0.95, method = "wilson"))
finalpcalc <- cbind(binomci, CItable$est, CItable$lwr.ci, CItable$upr.ci)
colnames(finalpcalc) <- c("pt", "treat", "acceptances", "encounters", "propaccepted", "Lower_95_CI", "Upper_95_CI")
head(finalpcalc)

##      pt treat acceptances   encounters propaccepted Lower_95_CI Upper_95_CI
## 1 C-P-    1        79       141    0.5602837  0.4778354  0.6395343
## 2 C-P+    1        67       119    0.5630252  0.4733184  0.6487902
## 3 C+P-    1        50       119    0.4201681  0.3353441  0.5099850
## 4 C+P+    1        63       121    0.5206612  0.4323901  0.6076607
## 5 C-P-    2        86       178    0.4831461  0.4108698  0.5561344
## 6 C-P+    2        69        96    0.7187500  0.6217410  0.7989259

```

The graph constructed below shows the long-term average acceptance rate of each type of signaller in each of the 27 treatments. Displayed are the proportion of signallers of each type that were accepted by receivers within each treatment. The error bars show Wilson's binomial confidence intervals.

```

# adding signal images
cp<- "C:/Users/James/Documents/p-c-.png"
cP<- "C:/Users/James/Documents/p+c-.png"
Cp<- "C:/Users/James/Documents/p-c+.png"
CP<- "C:/Users/James/Documents/p+c+.png"

images <- as.vector(rep(c(cp,cP,Cp,CP),27))

## ggplot with colour and patterns on bars
ggplot(finalpcalc, aes(pt, y = propaccepted)) +
  geom_textured_bar(stat = "identity", image = images) +
  labs(x = "Signaller type/Treatment", y = "Proportion accepted") +
  facet_wrap(~treat, strip.position = "bottom", ncol = 9) +
  geom_errorbar(aes(ymin = Lower_95_CI, ymax = Upper_95_CI), width = 0.2) +
  geom_hline(aes(yintercept = 0.5), col = "red", lty = 2) +
  theme(axis.text.x=element_blank()) +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
        panel.background = element_blank(), axis.line = element_line(colour = "black"))

```

While these data show how many of each signaller type were accepted across experimental conditions, it does not show whether the signallers were indeed desirable on average. To see if receiver behaviours

reflects the underlying conditions, we can compare these proportions accepted with the actual proportion of signallers that were desirable.

```

ndatas<- aggregate(nice~ pt + treat, data = MasterFileJames, sum)
ndatal<- aggregate(nice~ pt + treat, data = MasterFileJames, length)
propg<- ndatas[,3]/ndatal[,3]
finalpropg<- cbind(ndatas,propg)

# To construct Wilson's confidence intervals for the proportion of signallers that
# were desirable to accept
agnice <- (aggregate(nice ~ pt + treat, data = MasterFileJames, sum))
numnice <- agnice$nice # the number of desirable signallers

agtotalnice <- aggregate(nice ~ pt + treat, data = MasterFileJames, length)
total <- agttotalnice$nice # the total number of signallers

binomcigood <- cbind(agnice, total)
colnames(binomcigood) <- c("pt", "treat", "nice", "total")
CItable <- as.data.frame(BinomCI(numnice, total, conf.level = 0.95, method = "wilson"))
finalpcalcgood <- cbind(binomcigood, CItable$est, CItable$lwr.ci, CItable$upr.ci)
colnames(finalpcalcgood) <- c("pt", "treat", "nice", "total", "Proportion_Good", "Lower_95_CI", "Upper_95_CI")

ggplot(finalpcalcgood, aes(x = pt, y = propg)) +
  geom_textured_bar(stat = "identity", image = images) +
  labs(x = "Signaller type/Treatment", y = "Proportion desirable", fill = "Signal Type") +
  facet_wrap(~treat, ncol = 9, strip.position = "bottom") +
  geom_errorbar(aes(ymin = Lower_95_CI, ymax = Upper_95_CI), width = 0.2) +
  theme(axis.text.x=element_blank()) +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(), panel.background = element_blank(), axis.line = element_line(colour = "black")) +
  geom_hline(aes(yintercept=0.5), col = "red", lty=2)

```

Comparing between the true proportion of profitable signallers and the observed proportion of each signaller type accepted across treatments, it seems as if the receivers are ultimately correctly estimating the profitability of the signallers.

Modelling how receivers choose to respond to signallers (GLMM)

The main goal in analyzing the results of these experiments was to elucidate whether receivers rely on both signal components when deciding how to respond to a multicomponent signal under the conditions predicted. We can begin to answer this by modelling whether or not a signaller was accepted (**attacked**) in relation to the colour and/or pattern of the signaller (**t1** and **t2**, respectively). Since learning is likely to be involved, the sequence in which signallers were seen by receivers (**ic**) and possible differences observed among different volunteers (**ID**) need to be considered. Below shows an example of the output from one treatment (23). While individuals should preferably be considered as random effect (they are a subset of population of volunteers that could have been chosen), here I also include **ID** as a fixed factor

because including it as a random effect in glmer was not always possible due to lack of convergence. Since individuals may respond in different ways to different signaller types, I fit a model with an individual intercept for each type of signaller.

```
#GLMM (can change data to analyze original short or flipped only trials)
rdata <- subset(MasterFileJames, treat == 23)
rdata$ic <- scale(rdata$i, center = TRUE, scale = TRUE) # mean-centre sequence to assist with convergence

null<- glmer(attacked ~ 1 + (1|ID), family = binomial,
             data = rdata, control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))
colour<- glmer(attacked ~ t1*ic + (1|ID), family = binomial,
                data = rdata, control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))
pattern<- glmer(attacked ~ t2*ic + (1|ID), family = binomial, data = rdata, control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))
nolearn<- glmer(attacked ~ t1*t2 + (1|ID), family = binomial, data = rdata,
                 control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))
)
additive<- glmer(attacked ~ t1*ic+t2*ic + (1|ID), family = binomial,
                  data = rdata, control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))
full <- glmer(attacked ~ t1*t2*ic + (1|ID), family = binomial, data = rdata,
               control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))
AICc(null, colour, pattern, additive, full, nolearn)

##          df      AICc
## null      2  516.0047
## colour    5  490.5529
## pattern   5  482.8329
## additive  7  463.2056
## full      9  464.4083
## nolearn   5  461.7386

round(Weights(AICc(null, colour, pattern, additive, full, nolearn)), 3)

##  model weights
## [1] 0.000 0.000 0.000 0.275 0.151 0.574

anova(full, nolearn, test = "LRT")

## Data: rdata
## Models:
## nolearn: attacked ~ t1 * t2 + (1 | ID)
## full: attacked ~ t1 * t2 * ic + (1 | ID)
##          Df      AIC      BIC  logLik deviance Chisq Chi Df Pr(>Chisq)
## nolearn  5 461.62 482.69 -225.81     451.62
## full     9 464.04 501.97 -223.02     446.04 5.5762      4     0.2331
```

Respective GLMs in the case of non-convergence

```

#GLM
null<- glm(attacked ~ 1 + as.factor(ID), family = binomial, data = rdata)
colour<- glm(attacked ~ t1*ic + as.factor(ID), family = binomial, data = rdata)
pattern<- glm(attacked ~ t2*ic + as.factor(ID), family = binomial, data = rdata)
nolearn<- glm(attacked ~ t1*t2 + as.factor(ID), family = binomial, data = rdata)
additive<- glm(attacked ~ t1*ic+t2*ic + as.factor(ID), family = binomial, data = rdata)
full <- glm(attacked ~ t1*t2*ic + as.factor(ID), family = binomial, data = rdata)

AICc(null, colour, pattern, additive, full, nolearn)

##          df      AICc
## null      5 509.8632
## colour    8 485.0004
## pattern   8 476.7039
## additive 10 457.5207
## full      12 458.8776
## nolearn   8 456.4344

round(Weights(AICc(null, colour, pattern, additive, full, nolearn)), 3)

## model weights
## [1] 0.000 0.000 0.000 0.310 0.157 0.533

anova(full, nolearn, test = "LRT")

## Analysis of Deviance Table
##
## Model 1: attacked ~ t1 * t2 * ic + as.factor(ID)
## Model 2: attacked ~ t1 * t2 + as.factor(ID)
##   Resid. Df Resid. Dev Df Deviance Pr(>Chi)
## 1       488     434.24
## 2       492     440.14 -4    -5.9042  0.2064

```

I expect the interaction **t1:t2** to be significant (either alone, or part of a three-way interaction with **ic** if substantial changes in acceptance rates took place as a consequence of learning) in cases where receivers rely on the specific combination of colour and pattern to influence their decision of how to respond.

What this looks like with respect to learning

We can plot the probability of accepting a signaller of each type over the course of the trial to elucidate how quickly receivers respond to the desirability of each type of signaller.

```

#Experiment 1 GLM plots
rdata <- subset(MasterFileJames)

#GLM for predicting
pglm <- glm(attacked ~ pt * i * as.factor(treat), family = binomial, data = rdata)

## Warning: glm.fit: fitted probabilities numerically 0 or 1 occurred

```

```

#Plot basic GLM
ndata <- with(rdata, expand.grid(pt = unique(pt), i = unique(i), treat = unique(treat)))
ndata <- add_column(ndata, fit = predict(pg1m, newdata = ndata, type = 'response'))

ilink <- family(pg1m)$linkinv

## add fit and se.fit on the **link** scale
ndata <- bind_cols(ndata, setNames(as_tibble(predict(pg1m, ndata, se.fit = TRUE)[1:2]),
                                     c('fit_link','se_link')))

ndata <- mutate(ndata,
               fit_resp = ilink(fit_link),
               right_upr = ilink(fit_link) + (1.96 * se_link)),
               right_lwr = ilink(fit_link) - (1.96 * se_link))

prediction <- as.vector(c(rep("None",400), rep("Full", 400), rep("Pattern", 400),
                           rep("Full", 400), rep("Full", 400), rep("Pattern", 400),
                           rep("Colour", 400), rep("Colour", 400), rep("Full", 400),
                           rep("Colour or pattern", 400), rep("Pattern", 400), rep("Pattern", 400),
                           rep("Colour", 400), rep("Colour or pattern", 400),
                           rep("Pattern", 400), rep("Colour", 400), rep("Colour", 400),
                           rep("Colour or pattern", 400), rep("None", 400), rep("Full", 400),
                           rep("Colour", 400), rep("Colour or pattern", 400),
                           rep("Pattern", 400), rep("Full", 400), rep("Full", 400),
                           rep("Pattern", 400), rep("Colour", 400), rep("Colour", 400),
                           rep("Full", 400)))

ggplot(ndata, aes(x = i, y = fit, fill = pt)) +
  geom_line(aes(linetype = pt)) +
  scale_color_manual(values=c("red", "green", "blue", "black")) +
  geom_ribbon(data = ndata, aes(ymin = right_lwr, ymax = right_upr), alpha = 0.1) +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
        panel.background = element_blank(), axis.line = element_line(colour = "black")) +
  geom_hline(aes(yintercept=0.5), col = "red", lty=2) +
  facet_wrap(~as.factor(treat) + ~factor(prediction), ncol = 9) +
  labs(y = 'Prbability of accepting',
       x = 'Total number of signallers seen')

```

Extended trials

Upon completion of Experiment 1, it became clear that the receivers often struggled to arrive at a stable strategy where they were consistently responding in a similar way to each signaller type by the end of the trial. Since SDT predictions rely on observations to be taken from a period of stable responding, I increased the number of signallers presented within the trial to 200 and maintained equal signal reliability for each signal such that $pc = pp = 0.75$. Here, the main emphasis of the extended trials was to see whether the acceptance/rejection strategies predicted by SDT would emerge when the base rate was altered.

```
setwd("C:/Users/James/Documents")
MasterFileExtended <- read.table("MasterFileExtended.txt", header = TRUE)
#Selecting data for each of the 3 base rates (p = 0.25, 0.5, 0.75)
rdata <- subset(MasterFileExtended, p == 0.25)
rdata$ic <- scale(rdata$i, center = TRUE, scale = TRUE)

null<- glmer(attacked ~ 1 + (1|ID), family = binomial,
              data = rdata, control=glmerControl(optimizer="bobyqa", optCtrl=list(max
fun=2e5)))
colour<- glmer(attacked ~ t1*ic + (1|ID), family = binomial,
               data = rdata, control=glmerControl(optimizer="bobyqa",optCtrl=list(m
axfun=2e5)))
pattern<- glmer(attacked ~ t2*ic + (1|ID), family = binomial,
                 data = rdata, control=glmerControl(optimizer="bobyqa",optCtrl=list(
maxfun=2e5)))
full <- glmer(attacked ~ t1*t2*ic + (1|ID), family = binomial, data = rdata,
               control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))
nolearn<- glmer(attacked ~ t1*t2 + (1|ID), family = binomial, data = rdata,
                  control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))
)
additive<- glmer(attacked ~ t1*i+t2*ic + (1|ID), family = binomial,
                  data = rdata, control=glmerControl(optimizer="bobyqa",optCtrl=list(
maxfun=2e5)))

## fixed-effect model matrix is rank deficient so dropping 1 column / coefficient

## Warning in checkConv(attr(opt, "derivs"), opt$par, ctrl =
## control$checkConv, : Model failed to converge with max|grad| = 0.00462462
## (tol = 0.001, component 1)

## Warning in checkConv(attr(opt, "derivs"), opt$par, ctrl = control$checkConv, : M
odel is nearly unidentifiable: very large eigenvalue
## - Rescale variables?

full <- glmer(attacked ~ t1*t2*ic + (1|ID), family = binomial, data = rdata,
               control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

summary(full)
```

```

## Generalized linear mixed model fit by maximum likelihood (Laplace
## Approximation) [glmerMod]
## Family: binomial ( logit )
## Formula: attacked ~ t1 * t2 * ic + (1 | ID)
## Data: rdata
## Control:
## glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 2e+05))
##
##      AIC      BIC  logLik deviance df.resid
## 2044.1  2094.5 -1013.0   2026.1     1991
##
## Scaled residuals:
##    Min     1Q Median     3Q    Max
## -7.4925 -0.5612 -0.2944  0.5930  3.1937
##
## Random effects:
## Groups Name        Variance Std.Dev.
## ID      (Intercept) 1.019     1.01
## Number of obs: 2000, groups: ID, 10
##
## Fixed effects:
##             Estimate Std. Error z value Pr(>|z|)
## (Intercept) -1.10645   0.33156 -3.337 0.000846 ***
## t1          0.47923   0.15013  3.192 0.001413 **
## t2          1.11694   0.15098  7.398 1.38e-13 ***
## ic          -0.54965   0.08913 -6.167 6.96e-10 ***
## t1:t2       1.31366   0.23736  5.534 3.12e-08 ***
## t1:ic       -0.21848   0.15044 -1.452 0.146440
## t2:ic       -0.03281   0.15332 -0.214 0.830531
## t1:t2:ic    0.80575   0.24152  3.336 0.000849 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##            (Intr) t1     t2     ic   t1:t2  t1:ic  t2:ic
## t1         -0.158
## t2         -0.162  0.346
## ic          0.059 -0.121 -0.145
## t1:t2      0.096 -0.629 -0.608  0.065
## t1:ic      -0.029  0.161  0.058 -0.570 -0.102
## t2:ic      -0.033  0.069  0.141 -0.575 -0.080  0.331
## t1:t2:ic   0.017 -0.099 -0.072  0.351  0.061 -0.622 -0.629
## AICc(null,colour,pattern,additive,full,nolearn)

##      df      AICc
## null      2 2517.206
## colour    5 2312.268
## pattern   5 2168.867
## additive  7 2081.868

```

```

## full      9 2044.147
## nolearn   5 2140.275

round(Weights(AICc(null, colour, pattern, additive, full, nolearn)), 3)

## model weights
## [1] 0 0 0 0 1 0

```

Graphing GLMs for each treatment

Plots are constructed using the code below to illustrate how acceptance rates on each signaller type changed throughout the course of the trial.

```

#Parsing data by base rate (p = 0.25, 0.5, 0.75)
rdata <- subset(MasterFileExtended)

#GLM for predicting
pglm <- glm(attacked ~ pt * i * p, family = binomial, data = rdata)
summary(pglm)

##
## Call:
## glm(formula = attacked ~ pt * i * p, family = binomial, data = rdata)
##
## Deviance Residuals:
##      Min        1Q    Median        3Q       Max
## -2.7887  -0.9159   0.3501   0.9289   1.9464
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept) 0.0855516 0.2433871  0.352  0.72521 .
## ptC-P+      0.7238201 0.4080651  1.774  0.07610 .
## ptC+P-      0.1939151 0.3983615  0.487  0.62641
## ptC+P+      0.7065274 0.4603944  1.535  0.12488
## i          -0.0131249 0.0022466 -5.842 5.15e-09 ***
## p          -1.2228280 0.5163261 -2.368  0.01787 *
## ptC-P+:i   -0.0031782 0.0037719 -0.843  0.39944
## ptC+P-:i   -0.0003302 0.0036113 -0.091  0.92714
## ptC+P+:i   0.0110142 0.0041839  2.632  0.00848 **
## ptC-P+:p   0.4967558 0.8051539  0.617  0.53725
## ptC+P-:p   1.6601960 0.7811079  2.125  0.03355 *
## ptC+P+:p   2.7218086 0.8802862  3.092  0.00199 **
## i:p        0.0222803 0.0045825  4.862 1.16e-06 ***
## ptC-P+:i:p 0.0074441 0.0073578  1.012  0.31167
## ptC+P-:i:p -0.0042047 0.0069305 -0.607  0.54405
## ptC+P+:i:p -0.0055513 0.0083140 -0.668  0.50432
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)

```

```

## Null deviance: 8138.7 on 5999 degrees of freedom
## Residual deviance: 6399.7 on 5984 degrees of freedom
## AIC: 6431.7
##
## Number of Fisher Scoring iterations: 5

#Plot basic glm
ndata <- with(rdata, expand.grid(pt = unique(pt), i = unique(i), p = unique(p)))
ndata <- add_column(ndata, fit = predict(pg1m, newdata = ndata, type = 'response'))

ilink <- family(pg1m)$linkinv

## add fit and se.fit on the **link** scale
ndata <- bind_cols(ndata, setNames(as_tibble(predict(pg1m, ndata, se.fit = TRUE)[1:2]),
                                     c('fit_link','se_link')))

ndata <- mutate(ndata,
               fit_resp = ilink(fit_link),
               right_upr = ilink(fit_link) + (1.96 * se_link),
               right_lwr = ilink(fit_link) - (1.96 * se_link))

ggplot(ndata, aes(x = i, y = fit, fill = pt)) +
  geom_line(lty = 1, col = "black", size = 1) +
  scale_fill_manual(values=c("red", "green", "blue", "black")) +
  geom_ribbon(data = ndata, aes(ymin = right_lwr, ymax = right_upr), alpha = 0.1) +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
        panel.background = element_blank(), axis.line = element_line(colour = "black")) +
  geom_hline(aes(yintercept=0.5), col = "red", lty=2) +
  facet_wrap(~as.factor(p)) +
  labs(y = "Prbability of accepting",
       x ="Total number of signallers seen",
       fill = "Signaller type")

```

Graphing proportion of each signaller accepted for extended trials. These plots are constructed to illustrate the proportion of acceptance rates on each signaller type.

```

success <- (aggregate(attacked ~ pt + p, data = MasterFileExtended, sum))
successes <- success$attacked

trialdata <- aggregate(attacked ~ pt + p, data = MasterFileExtended, length)
trials <- trialdata$attacked

```

```

#Making a table for Wilson's binomial conf interval
binomci <- cbind(success, trials)
colnames(binomci) <- c("pt", "p", "attacks", "trials")

CItable <- as.data.frame(BinomCI(successes, trials, conf.level = 0.95, method = "wilson"))
finalpcalc <- cbind(binomci, CItable$est, CItable$lwr.ci, CItable$upr.ci)

colnames(finalpcalc) <- c("pt", "p", "attacks", "trials", "Proportion_Attacked",
                           "Lower_95_CI", "Upper_95_CI")

#Plotting proportion of each prey attacked with Wilson's Binomial CI for each base rate

images <- as.vector(rep(c(cp,cP,Cp,CP),3))

ggplot(finalpcalc, aes(x = pt, y = Proportion_Attacked)) +
  geom_textured_bar(stat = "identity", image = images) +
  labs(x = "Base rate/Signal type", y = "Proportion accepted") +
  facet_wrap(~factor(p), strip.position = "bottom") +
  geom_errorbar(aes(ymin = Lower_95_CI, ymax = Upper_95_CI), width = 0.2) +
  geom_hline(aes(yintercept = 0.5), col = "red", lty = 2) +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
        panel.background = element_blank(), axis.line = element_line(colour = "black"))

```

Flipped trials

Under standard conditions, I consistently used red and cross as desirable signals and blue and circle as undesirable signals. To exclude the possibility of an existing inherent bias for accepting red vs blue or cross vs circle, I subsequently conducted *flipped trials* on a subset of the treatment configurations (treatments 3, 5, 7, 21, 23, and 25) where the signal profitability was flipped. **t1** and **t2** are used to represent the “more reliable” signal which differed between flipped and normal trials. Here, the goal is to see whether changing which signals are desirable will alter which signals are followed between the two experiments.

```

#Flipped MasterFile
setwd("C:/Users/James/Documents")
MasterFileFlipped <- read.table("MasterFileFlipped.txt", header = TRUE)

## selecting only the relevant treatments from the regular MasterFile
normtreat <- rbind(subset(MasterFileJames, treat == 3),
                     subset(MasterFileJames, treat == 5),
                     subset(MasterFileJames, treat == 7),
                     subset(MasterFileJames, treat == 21),
                     subset(MasterFileJames, treat == 23),
                     subset(MasterFileJames, treat == 25))

```

```

flipped <- as.vector(c(rep(0,3000),(rep(1,3000)))))

#Combining the two datasets
combined <- cbind(rbind(normtreat,MasterFileFlipped),flipped)

#Select data to plot
fdatas<- aggregate(attacked~ pt + treat + flipped, data = combined, sum)
fdata1<- aggregate(attacked~ pt + treat + flipped, data = combined, length)
fpropa<- fdatas[,4]/fdata1[,4]
finalf<- cbind(fdatas,fpropa)

#To construct Wilson's confidence intervals for the proportion of signallers that were desirable to accept
attackf <- (aggregate(attacked ~ pt + treat + flipped, data = combined, sum))
numattackf <- attackf$attacked # the number of signallers accepted

totalf <- aggregate(attacked ~ pt + treat + flipped, data = combined, length)
numtotalf <- totalf$attacked # the total number of signallers

binomcif <- cbind(attackf, numtotalf)
colnames(binomcif) <- c("pt", "treat", "flipped", "attacked", "total")
CItablef <- as.data.frame(BinomCI(numattackf, numtotalf, conf.level = 0.95, method = "wilson"))
finalpcalcf<- cbind(binomcif, CItablef$est, CItablef$lwr.ci, CItablef$upr.ci)
colnames(finalpcalcf) <- c("pt", "treat", "flipped", "attacked", "total", "Proportion_Attacked", "Lower_95_CI", "Upper_95_CI")

#Images for plotting
bluecircle<- "C:/Users/James/Documents/p-c-.png"
bluecross<- "C:/Users/James/Documents/p+c-.png"
redcircle<- "C:/Users/James/Documents/p-c+.png"
redcross<- "C:/Users/James/Documents/p+c+.png"

imagesf <- as.vector(c(rep(c(bluecircle,bluecross,redcircle,redcross),6),rep(c(redcross,redcircle,bluecross,bluecircle),6)))

#Plotting flipped and non-flipped trials together
ggplot(finalpcalcf, aes(x = pt, y = Proportion_Attacked)) +
  geom_textured_bar(stat = "identity", position = "dodge2", image = imagesf) +
  labs(x = "Signaller type", y = "Proportion accepted") +
  facet_grid((flipped ~ treat), labeller = label_both) +
  geom_errorbar(aes(ymin = Lower_95_CI, ymax = Upper_95_CI), width = 0.2) +
  theme(axis.text.x=element_blank()) +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(), panel.background = element_blank(), axis.line = element_line(colour = "black")) +
  geom_hline(aes(yintercept=0.5), col = "red", lty=2)

```

```

#Analyzing the fit of potential models for combined flipped/non-flipped data
rdata <- subset(combined, treat == 7)
rdata$ic <- scale(rdata$i, center = TRUE, scale = TRUE)

flipnull<- glmer(attacked ~ 1 + flipped + (1|ID), family = binomial, data = rdata,
control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

## singular fit

flipcolour<- glmer(attacked ~ t1*ic + t1*flipped + (1|ID), family = binomial, data = rdata,
control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

flippattern<- glmer(attacked ~ t2*ic + t2*flipped + (1|ID), family = binomial, data = rdata,
control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

## singular fit

nolearn<- glmer(attacked ~ t1*t2 + (1|ID), family = binomial, data = rdata, control =
=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

flipnolearn<- glmer(attacked ~ t1*t2*flipped + (1|ID), family = binomial, data = rd
ata, control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

## singular fit

flipfull<- glmer(attacked ~ t1*t2*ic + t1*t2*flipped + (1|ID), family = binomial, d
ata = rdata,control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

## singular fit

full<- glmer(attacked ~ t1*t2*ic + (1|ID), family = binomial, data = rdata,
control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

flipfullno3way<- glmer(attacked ~ t1*t2*ic + t1*t2*flipped - t1:t2:flipped + (1|ID)
, family = binomial, data = rdata, control=glmerControl(optimizer="bobyqa", optCtrl
=list(maxfun=2e5)))

flipfullsimple<- glmer(attacked ~ t1*t2*ic + flipped + (1|ID), family = binomial, d
ata = rdata, control=glmerControl(optimizer="bobyqa", optCtrl=list(maxfun=2e5)))

AICc(flipnull,flipcolour,flippattern,nolearn,flipnolearn,flipfull,full,flipfullno3w
ay,flipfullsimple)

##          df      AICc
## flipnull     3 1254.8980
## flipcolour    7  674.9351
## flippattern   7 1192.2878
## nolearn       5  767.3430
## flipnolearn   9  734.2530
## flipfull      13  645.9781
## full          9  679.9284

```

```

## flipfullno3way 12  668.5672
## flipfullsimple 10  672.6417

round(Weights(AICc(flipnull,flipcolour,flippattern,nolearn,flipnolearn,flipfull,full,flipfullno3way,flipfullsimple)),3)

## model weights
## [1] 0 0 0 0 0 1 0 0 0

anova(full, flipfull, test = "LRT")

## Data: rdata
## Models:
## full: attacked ~ t1 * t2 * ic + (1 | ID)
## flipfull: attacked ~ t1 * t2 * ic + t1 * t2 * flipped + (1 | ID)
##          Df AIC BIC logLik deviance Chisq Chi Df Pr(>Chisq)
## full      9 679.75 723.92 -330.87   661.75
## flipfull 13 645.61 709.41 -309.80   619.61 42.138      4  1.562e-08 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

#Comparable GLMs (in the case of singular fit)
flipnull<- glm(attacked ~ flipped + as.factor(ID), family = binomial, data = rdata)
flipcolour<- glm(attacked ~ t1*ic + t1*flipped + as.factor(ID), family = binomial,
data = rdata)
flippattern<- glm(attacked ~ t2*ic + t2*flipped + as.factor(ID), family = binomial,
data = rdata)
flipnolearn<- glm(attacked ~ t1*t2*flipped + as.factor(ID), family = binomial, data =
rdata)
nolearn<- glm(attacked ~ t1*t2 + as.factor(ID), family = binomial, data = rdata)
full <- glm(attacked ~ t1*t2*ic + as.factor(ID), family = binomial, data = rdata)
flipfull <- glm(attacked ~ t1*t2*ic + t1*t2*flipped + as.factor(ID), family = binomial,
data = rdata)
flipfullno3way<- glm(attacked ~ t1*t2*ic + t1*t2*flipped - t1:t2:flipped + as.factor(ID),
family = binomial, data = rdata)
flipfullsimple<- glm(attacked ~ t1*t2*ic + flipped + as.factor(ID), family = binomial,
data = rdata)

AICc(flipnull,flipcolour,flippattern,flipnolearn,nolearn,flipfull,full,flipfullno3way,flipfullsimple)

##                df      AICc
## flipnull      10 1258.6308
## flipcolour    14  675.7911
## flippattern   14 1196.7861
## flipnolearn   16  738.9338
## nolearn       13  763.3015
## flipfull      20  650.1680
## full          17  675.5726
## flipfullno3way 19  671.6814
## flipfullsimple 17  675.5726

```

```

round(Weights(AICc(flipnull,flipcolour,flippattern,flipnolearn,nolearn,flipfull,full,flipfullno3way,flipfullsimple)),3)

## model weights
## [1] 0 0 0 0 0 1 0 0 0

anova(flipfull, full, test = "LRT")

## Analysis of Deviance Table
##
## Model 1: attacked ~ t1 * t2 * ic + t1 * t2 * flipped + as.factor(ID)
## Model 2: attacked ~ t1 * t2 * ic + as.factor(ID)
##   Resid. Df Resid. Dev Df Deviance Pr(>Chi)
## 1      980    609.31
## 2      983    640.95 -3   -31.639 6.234e-07 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

#Graphs showing proportion desirable for only flipped trials

cp<- "C:/Users/James/Documents/p-c-.png"
cP<- "C:/Users/James/Documents/p+c-.png"
Cp<- "C:/Users/James/Documents/p-c+.png"
CP<- "C:/Users/James/Documents/p+c+.png"

images <- as.vector(rep(c(CP,Cp,cP,cp),6))

ndatas<- aggregate(nice~ pt + treat, data = MasterFileFlipped, sum)
ndatal<- aggregate(nice~ pt + treat, data = MasterFileFlipped, length)
propg<- ndatas[,3]/ndatal[,3]
finalpropg<- cbind(ndatas,propg)

# To construct Wilson's confidence intervals for the proportion of signallers that
# were desirable to accept
agnice <- (aggregate(nice ~ pt + treat, data = MasterFileFlipped, sum))
numnice <- agnice$nice # the number of desirable signallers

agtotalnice <- aggregate(nice ~ pt + treat, data = MasterFileFlipped, length)
total <- agtotalnice$nice # the total number of signallers

binomcigood <- cbind(agnice, total)
colnames(binomcigood) <- c("pt", "treat", "nice", "total")
CItable <- as.data.frame(BinomCI(numnice, total, conf.level = 0.95, method = "wilson"))
finalpcalcgood <- cbind(binomcigood, CItable$est, CItable$lwr.ci, CItable$upr.ci)
colnames(finalpcalcgood) <- c("pt", "treat", "nice", "total", "Proportion_Good", "Lower_95_CI", "Upper_95_CI")

ggplot(finalpcalcgood, aes(x = pt, y = propg)) +
  geom_textured_bar(stat = "identity", image = images) +
  labs(x = "Signaller type/Treatment", y = "Proportion desirable", fill = "Signal T"

```

```

ype") +
  facet_wrap(~treat, ncol = 9, strip.position = "top") +
  geom_errorbar(aes(ymin = Lower_95_CI, ymax = Upper_95_CI), width = 0.2) +
  theme(axis.text.x=element_blank()) +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(), panel.background = element_blank(), axis.line = element_line(colour = "black")) +
  geom_hline(aes(yintercept=0.5), col = "red", lty=2)

```

Generalization

```

#A breakdown of which types of signallers were rejected on first encounter
rdata<- subset(MasterFileExtended, ranka == 1)

s<- aggregate(attacked~ pt + p, data = rdata, sum)
l<- aggregate(attacked~ pt + p, data = rdata, length)
propa<- s[,3]/l[,3]
rdata <- cbind(s,propa)

cp<- "C:/Users/James/Documents/p-c-.png"
cP<- "C:/Users/James/Documents/p+c-.png"
Cp<- "C:/Users/James/Documents/p-c+.png"
CP<- "C:/Users/James/Documents/p+c+.png"

images <- as.vector(rep(c(cp,cP,Cp,CP),3))

ggplot(rdata,aes(x=pt, y=propa)) +
  geom_textured_bar(stat = "identity", image = images) +
  facet_wrap(~p) +
  labs(x = 'Base rate/Signaller type',
       y = 'Proportion accepted') +
  theme(panel.grid.major = element_blank(), panel.grid.minor = element_blank(),
        panel.background = element_blank(), axis.line = element_line(colour = "black"))

```

Appendix B

DPE and related analyses

James Voll

1/08/2020

Dynamic Programming Equations

Here I begin by identifying the optimal response (accept or reject) of a payoff-maximizing receiver when it encounters a signaller with which it is relatively unfamiliar at a certain stage in the experiment. The array $S(x,y,r,n)$ refers to its expected future reward at time step x having encountered y such signallers in the past (y less than or equal to x) and accepted n of them (n less than or equal to y) with r of them being profitable (r less than or equal to n). x , y , r , and n represent the informational state variables available to the receiver when it makes its decision. The array $A(x,y,r,n)$ refers to the optimal action of the receiver on encounter with this relatively unfamiliar type of signaller (1 = accept, 0 = reject). x and y allow the estimation of the likelihood of encountering this signaller type per time step and r and n allow the estimation of the likelihood that the signaller type will be profitable. The receiver may have prior beliefs as to the probability of encountering the prey type per time step and its probability of being profitable to accept and these beliefs are updated by experience in a Bayesian manner.

```
T<- 100      # Time horizon
ap<- 1; bp<- 1 # Bayesian priors for profitability of the unfamiliar signaller
aq<- 1; bq<- 1 # Bayesian priors for probability of encounter of the signaller per
time step
b<- 1; c<- 1  # benefit and cost of profitable vs. unprofitable experience

S<- array(0, dim = c(T+1,T+1,T+1,T+1)) # Expected future payoff S(x,y,r,n)
A<- array(0, dim = c(T+1,T+1,T+1,T+1)) # Optimal Action [1 = Accept, 0 = Reject] wi
th state (x,y,r,n)

# As with all discrete dynamic programming algorithms, we work backwards from the l
ast step
for (x in (T-1):0) {           # time step x
  for (y in x:0) {             # number of encounters with unfamiliar signaller type
    for (n in y:0) {           # number of unfamiliar signaller type accepted n
      for (r in n:0) {         # number of unfamiliar signaller type accepted that w
ere profitable r

        xi<- x + 1; yi<- y + 1; ni<- n + 1; ri<- r + 1;
        # 1 needs to be added to the index of state variables because the index o
f the array starts at 1

        pc<- (ap+r)/(ap+bp+n) # estimated probability that the object is profitab
```

```

le (beliefs follow a Beta)
    qc<- (aq+bq)/(aq+bq+x) # estimated future probability of seeing the novel
object per time step

    payignore<-S[xi+1,yi+1,ri,ni] # time and encounters go up, but no information
about the signaller is gained
    payexplore<-pc*(b+S[xi+1,yi+1,ri+1,ni+1])+(1-pc)*(-c+S[xi+1,yi+1,ri,ni+1])
) # estimated benefits depend on beliefs

    if (payexplore >= payignore) {
        maxpay<- payexplore
        A[xi,yi,ri,ni]<- 1
    } else {
        maxpay<- payignore
        A[xi,yi,ri,ni]<- 0
    }#if
    S[xi,yi,ri,ni]<- qc*maxpay + (1-qc)*(S[xi+1,yi,ri,ni])
    #estimated future payoff also depends on the likelihood of encounter
}#r
} #n
} #y
} #x

```

Experimental Conditions

In all experiments, the benefit b was always 1 if the signaller was profitable, and the cost was 1 if the signaller was unprofitable. However, in each of the 27 treatments (3 base rates x 3 colour reliabilities x 3 pattern reliabilities) as the base rate and reliabilities changed, so too did the probability of encountering each signaller type per time step and the probability that each signaller type was profitable. We can calculate the expected encounter probabilities and expected profitability of signaller types in each of the 27 treatments. We can also determine the mean probabilities actually experienced by experimental subjects. Observed and expected probabilities may differ (albeit slightly) from expectations due to sample variation. For good measure, and as an additional confirmation that the experimental conditions resulted in the predicted conditional probabilities of given types of signaller (e.g. C+P+) being good, I determine both and compare the two.

Expected values

To calculate the expected probabilities that a given signaller type (e.g. C+P+) is good and its expected probability of encounter per time step, we can use simple probability theory along with Bayes rule to convert reliabilities $P(C+|good)$ and $P(P+|good)$ to $P(Good|C+P+)$ as follows.

```

pcon<- c(0.25,0.5,0.75) # base rate combinations used in experiments
pccon<- c(0.6,0.75,0.95) # colour reliability combinations p(C+/good)
ppcon<- c(0.6,0.75,0.95) # pattern reliability combinations p(P+/good)

# here are some vectors set up to collect the data
treatv<- numeric(108); pv<- numeric(108); ppv<- numeric(108); pcv<- numeric(108)

```

```

ptv<- character(108); propgv<- numeric(108); qindexv<- numeric(108)

# For notational convenience 1's and 0's are used to represent the more (+) and Less (-) reliable traits
# The first trait refers to colour, the second to pattern so phenotype 10 is C+P-
treat<- 0
for (p in pcon) {
  for (pc in pccon) {
    for (pp in ppcon) {

      # a count through the 27 treatments as the base rate and signal reliabilities are altered
      treat<- treat + 1

# Combined conditional probabilities of trait combinations in good signallers (assuming independence)
# Given the binary nature then we know that P(C-/good) = 1-P(C+/good)
      s11g = pc * pp
      s10g = pc * (1 - pp)
      s01g = (1 - pc) * pp
      s00g = (1 - pc) * (1 - pp)
#Assuming symmetry, so that P(C+/good) = P(C-/bad), we can calculate the same trait combination probabilities for bad signallers
      s11b = (1 - pc) * (1 - pp)
      s10b = (1 - pc) * pp
      s01b = pc * (1 - pp)
      s00b = pc * pp
#Conditional probabilities of the P(good/sij) can be calculated through Bayes Law:
      gs11 = s11g * p / (s11g * p + s11b * (1 - p))
      gs10 = s10g * p / (s10g * p + s10b * (1 - p))
      gs01 = s01g * p / (s01g * p + s01b * (1 - p))
      gs00 = s00g * p / (s00g * p + s00b * (1 - p))
# The encounter probability with each of the signaller types is simply:
      qs11<- p*s11g+(1-p)*s11b
      qs10<- p*s10g+(1-p)*s10b
      qs01<- p*s01g+(1-p)*s01b
      qs00<- p*s00g+(1-p)*s00b

# Here we seek to populate a data frame 4 values at a time (since there are 4 signaler types per treatment)
# Of particular interest are the expected profitabilities of the signaller phenotypes, and their expected rates of encounter
# For each combination of base rate and signal reliabilities
i<- (treat-1)*4
treatv[(i+1):(i+4)]<- treat
pv[(i+1):(i+4)]<- p
ppv[(i+1):(i+4)]<- pp
pcv[(i+1):(i+4)]<- pc
ptv[(i+1):(i+4)]<- c("C-P-", "C-P+", "C+P-", "C+P+")

```

```

propgv[(i+1):(i+4)]<- c(gs00,gs01,gs10,gs11)
qindexv[(i+1):(i+4)]<- c(qs00,qs01,qs10,qs11)
} # pc
} # pp
} # p
expectations<- data.frame(treatv,pv,ppv,pcv,ptv,propgv,qindexv)
head(expectations)

##   treatv    pv    ppv    pcv    ptv      propgv qindexv
## 1      1 0.25 0.60 0.6 C-P-  0.12903226  0.3100
## 2      1 0.25 0.60 0.6 C-P+  0.25000000  0.2400
## 3      1 0.25 0.60 0.6 C+P-  0.25000000  0.2400
## 4      1 0.25 0.60 0.6 C+P+  0.42857143  0.2100
## 5      2 0.25 0.75 0.6 C-P-  0.06896552  0.3625
## 6      2 0.25 0.75 0.6 C-P+  0.40000000  0.1875

```

Observed values

The above shows how the expected probabilities can be calculated, but the realized probabilities can differ due to sample variation. The actual encounter probabilities and probabilities of being profitable require us to read the experimental data and sum the experiences of subjects with a given signaller phenotype in each treatment.

```

# MF is the RecodedMasterfileComplete
# The file was recoded simply to include the sequence of encounter with a given signaller phenotype in an experiment

library(readxl)
MF <- read_excel("/Users/James/Documents/RecodedMasterfileComplete.xlsx")
head(MF)

## # A tibble: 6 x 12
##       ID     p     pc     pp     i   nice     t1     t2 attacked pt   treat
##   <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <dbl> <chr> <dbl>
## 1  8936  0.25  0.6   0.6   1     0     0     0     0     1 C-P-    1
## 2  8936  0.25  0.6   0.6   2     0     1     1     1     1 C+P+    1
## 3  8936  0.25  0.6   0.6   3     0     0     0     0     0 C-P-    1
## 4  8936  0.25  0.6   0.6   4     0     0     1     1     1 C+P+    1
## 5  8936  0.25  0.6   0.6   5     0     0     1     0     0 C-P+    1
## 6  8936  0.25  0.6   0.6   6     0     0     1     0     0 C-P+    1
## # ... with 1 more variable: ranka <dbl>

# here we can calculate the overall probability of a given phenotype (4 different pt's) in a given treatment (1-27) were profitable
ndatas<- aggregate(nice~ pt + treat, data = MF, sum)
ndatal<- aggregate(nice~ pt + treat, data = MF, length)
propg<- ndatas[,3]/ndatal[,3]

# Likewise, for future comparison, we can calculate the overall probability of a given phenotype in a given treatment being attacked

```

```

adatas<- aggregate(attacked~ pt + treat, data = MF, sum)
adata1<- aggregate(attacked~ pt + treat, data = MF, length)
propa<- adatas[,3]/adata1[,3]

# the overall probability of encountering each phenotype in a given treatment can be readily calculated from the number of observations
# note that the count of observations sums over 5 subjects each with a total of 100 encounters, so to obtain the average probability we divide the sum by 500
probenc<- ndatas[,3]/500

# Here we have the mean conditions observed in the experiments
observations<- cbind(ndatas,propg, propa, probenc)

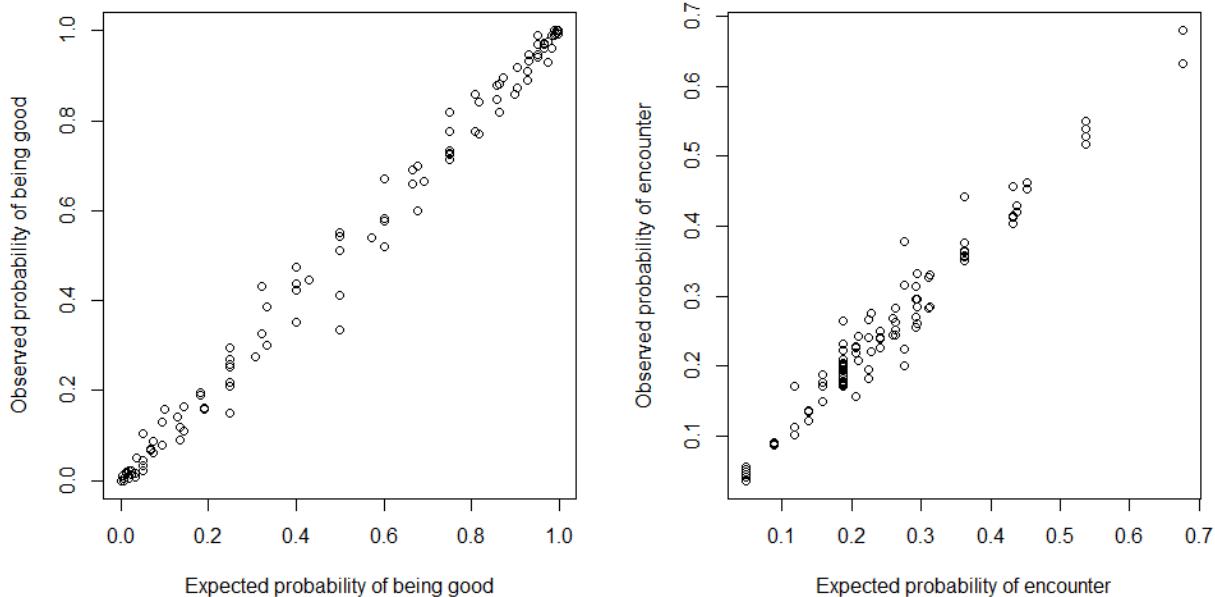
```

An obvious first question is whether the observations match the expectations. This is readily demonstrated with the two relevant plots:

```

par(mfrow=c(1,2))
plot(expectations$propgv, observations$propg, xlab = "Expected probability of being good", ylab = "Observed probability of being good")
plot(expectations$qindexv, observations$probenc, xlab = "Expected probability of encounter", ylab = "Observed probability of encounter")

```



How do the predictions of the DPE and observations match up?

So now we have (a) the predicted optimal response of a receiver under all possible informational conditions (b) the relevant expected probabilities of encounter and probabilities of being profitable for given base rates and signal reliabilities and (c) the actual probabilities observed following stochastic implementation (they match quite well). I now wish to ascertain how well the DPE (i.e. the exploration-exploitation) model predictions match the observations. To do this, I implement *FORWARD ITERATION* which employs the optimal response rules of receivers in response to a series of stochastic encounters (based on overall observed acceptance probabilities) over T time steps with a given type of

signaller with given probability of being profitable (based on observed probabilities of the signaller being good). If it is profitable it gains b, but if it is unprofitable it loses c.

```

# FORWARD ITERATION
# I will use the observed probability of encounter and profitability

maxz<- 108 # number of values of pg (27 treatments x 4 phenotypes)
maxi<- 1000 # individual replicates per set of conditions

# I create some helpful arrays for total accepted and total encountered in each replicate and the mean proportion accepted per replicate
finN<- numeric(maxi); finE<- numeric(maxi); apz<- numeric(maxz);
# some other arrays to show how the mean responses of receivers in the forward iteration change over time
cmeans<- matrix(NA,maxz,T); cn<- matrix(NA,maxz,T); cmeanslimit<- matrix(NA,maxz,T)

# counting over each of the 108 different sets of conditions
for (z in 1:maxz) {

  # the observed probability of a phenotype being good and its observed probability of encounter
  realp<- observations$propg[z]
  realq<- observations$probenc[z]

  # creates a matrix for the behaviour of each replicate receiver (maxi) over all possible encounters (T)
  asig<- matrix(NA,maxi,T)

  for (i in 1:maxi) {
    y1<- 1 # encounters
    r1<- 1 # number good accepted
    n1<- 1 # total number accepted

    for (s in 1:T) {
      g<- runif(1)

      # is a signaller of this form encountered in this time step?
      if (g < realq) {enc<- 1} else {enc<-0}

      # would the receiver accept it if encountered? We look at the DPE solution derived above
      if (A[s, y1, r1, n1] == 1) {at<- 1} else {at<-0}

      if (enc == 1) {y1<- y1 + 1} # encounters
      if ((enc == 1) & (at == 1)) {n1<- n1 + 1} # acceptances on encounter
      if ((enc == 1) & (at == 1) & (runif(1) < realp)) {r1<- r1 + 1} # profitable when accepted

      if ((enc == 1) & (at == 1)) {asig[i,y1]<- 1} # encountered and accepted
      if ((enc == 1) & (at == 0)) {asig[i,y1]<- 0} # encountered and rejected
    }
  }
}

```

```

} #s

# take one off because the index started at 1
finN[i] = n1-1
finE[i] = y1-1
} #i

apz[z]<- mean(finN/finE, na.rm=TRUE) # mean probability of accepting signaller phenotype on encounter
cmeans[z,]<- colMeans(asig, na.rm = TRUE, dims = 1) # mean proportion of acceptance s of this signaller at that point in time
cn[z,]<- colSums(!is.na(asig)) # mean number of observations ignoring the NAs

}

```

Having run forward iterations, it is now time to compare the DPE (exploration-exploitation) predictions with observations. To begin with we can simply plot the predicted proportion of the signaller types accepted in each of the 108 conditions vs the actual proportion accepted. Let's take a look:

```

par(mfrow = c(1,1))
plot(apz, observations$propa, xlab = "predicted probability of being accepted",
      ylab = "observed probability of being accepted", pch = 20)

```

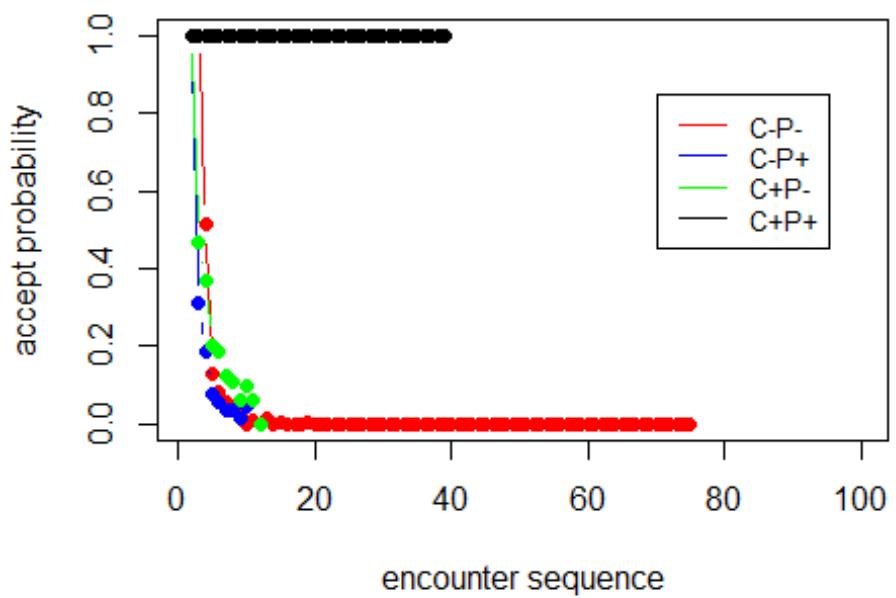
One might wonder how receivers arise at these decisions, i.e. how they use their experiences to guide their behaviour. For any given treatment (here I show treatment 9) we first ensure that there are enough encounters (≥ 10) with a signaller type to base the mean on, and then we can portray the mean probability of accepting for each of the four signaller phenotypes in the treatment.

```

for (z in (1:maxz)) {
  for (j in (1:T)) {
    if (cn[z,j] >= 10) {cmeanslimit[z,j] = cmeans[z,j]} else {cmeanslimit[z,j] = NA}
  }
}

trt<- 9
j<- 1:T
y1<- cmeanslimit[1+(trt-1)*4,j]
y2<- cmeanslimit[2+(trt-1)*4,j]
y3<- cmeanslimit[3+(trt-1)*4,j]
y4<- cmeanslimit[4+(trt-1)*4,j]
plot(j, y1, type="b", pch=19, col="red",
      ylim = c(0,1),
      xlab="encounter sequence", ylab="accept probability")
lines(j, y2, pch=19, col="blue", type="b")
lines(j, y3, pch=19, col="green", type="b")
lines(j, y4, pch = 19, col = "black", type = "b")
legend(70, 0.85, legend = c("C-P-", "C-P+", "C+P-", "C+P+"),
      col=c("red", "blue", "green", "black"), cex = 0.8, lty = 1)

```



References

- Abbott, K.R., & Sherratt, T.N. (2011). The evolution of superstition through optimal use of incomplete information. *Animal Behaviour*, 82, 85–92.
- Aubier, T. G., & Sherratt, T. N. (2020). State-dependent decision-making by predators and its consequences for mimicry. *American Naturalist*. In press.
- Barton, K. (2019). MuMIn: Multi-Model Inference. R package version 1.43.6.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). “Fitting Linear Mixed-Effects Models Using lme4.” *Journal of Statistical Software*, 67(1), 1–48.
- Bayes, T. (1764). An essay toward solving a problem in the doctrine of chances. *Phil. Trans. R. Soc. B*, 53, 370-418.
- Beatty, C. D., Bain, R. S., & Sherratt, T. N. (2005). The evolution of aggregation in profitable and unprofitable prey. *Animal Behaviour*, 70(1), 199–208.
- Bogaardt, L. & Johnstone, R. A. (2016). Amplifiers and the origin of animal signals. *Proc. R. Soc. Lond. B*, 283(1832), 1–6.
- Bolker, B. M. (2014). Linear and generalized linear mixed models. In G.A. Fox, S. Negrete-Yankelevich, & V.J. Sosa, (Eds.), *Ecological statistics: contemporary theory and application* (pp. 310-334). Oxford University Press, USA.
- Bradbury, J. W. & Vehrencamp, S. L. (1998). Principles of Animal Communication. First Edition Sunderland, Massachusetts: Sinauer.
- Bradbury, J. W. & Vehrencamp, S. L. (2000). Economic models of animal communication. *Animal Behaviour*, 59(2), 259–268.
- Bro-Jørgensen, J. (2010). Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology and Evolution*, 25(5), 292–300.
- Candolin, U. (2003). The use of multiple cues in mate choice. *Biological Reviews of the Cambridge Philosophical Society*, 78(4), 575–595.
- Clark, C. & Mangel, M. (2000). Dynamic modeling in behavioral ecology. Princeton University Press.
- Cohen, J. D., McClure, S. M., & Yu, A. J. (2007). Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. *Phil. Trans. R. Soc. B*, 362(1481), 933–942.
- Darwin, C. (1871). The descent of man, and relation to sex. Murray, London.

- DeGroot, M. (1970). Conjugate Prior Distributions. Pages 155-189. In: Statistical Decision Theory. Wiley Classics.
- Egan, J.P. (1975). Signal Detection Theory and ROC-analysis. Academic Press, New York.
- Endler, J. A., Gaburro, J., & Kelley, L. A. (2014). Visual effects in great bowerbird sexual displays and their implications for signal design. *Proc. R. Soc. Lond. B*, 281(20140235), 1–9.
- Fawcett, T. W. & Johnstone, R. A. (2003). Optimal assessment of multiple cues. *Proc. R. Soc. Lond. B*, 270(1524), 1637–1643.
- Gittins, J. C. & Jones, D. M. (1974). A dynamic allocation index for the sequential design of experiments. In *Progress in statistics* (ed. J. Gans), pp. 241–266. Amsterdam, The Netherlands: North-Holland.
- Green, D.M. & Swets, J.A. (1988). Signal detection theory and psychophysics. New York: Wiley.
- Guilford, T. & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour*, 42(1), 1–14.
- Hasson, O. (1989). Amplifiers and the handicap principle in sexual selection: A different emphasis. *Proc. R. Soc. Lond. B*, 235(1281), 383–406.
- Hebets, E. A. (2005). Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behavioral Ecology*, 16(1), 75–82.
- Hebets, E. A. & Papaj, D. R. (2005). Complex signal function: Developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.*, 57(3), 197–214.
- Hebets, E. A., Barron, A. B., Balakrishnan, C. N., Hauber, M. E., Mason, P. H., & Hoke, K. L. (2016). A systems approach to animal communication. *Proc. R. Soc. Lond. B*, 283, 20152889.
- Holen, & Johnstone. (2004). The Evolution of mimicry under constraints. *The American Naturalist*, 164(5), 598.
- Holzworth, R. J. (1999). Annotated Bibliography of Cue Probability Learning Studies. *The Brunswik Society*.
- Houston, A., Clark, C., McNamara, J., & Mangel, M. (1988). Dynamic models in behavioural and evolutionary ecology. *Nature* 332, 29–34.
- Johnstone, R. A. (1995). Honest advertisement of multiple qualities using multiple signals. *Journal of Theoretical Biology*, 177, 87-94

- Johnstone, R. A. (1996). Multiple displays in animal communication “backup signals” and “multiple messages.” *Phil. Trans. R. Soc. B*, 351, 329–338.
- Katz, K. & Naug, D. (2015). Energetic state regulates the exploration-exploitation trade-off in honeybees. *Behavioral Ecology*, 26(4), 1045–1050.
- Kikuchi, D. W., Malick, G., Webster, R. J., Whissell, E., & Sherratt, T. N. (2015). An empirical test of 2-dimensional signal detection theory applied to Batesian mimicry. *Behavioral Ecology*, 26(4), 1226–1235.
- Kilner, R. M., Noble, D. G., & Davies, N. B. (1999). Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, 397(6721), 667–672.
- Kim, S.-Y., Noguera, J. C., Morales, J., & Velando, A. (2011). The evolution of multicomponent begging display in gull chicks: sibling competition and genetic variability. *Animal Behaviour*, 82(2011), 113–118.
- Kloock, C. T., & Getty, T. (2019). A mathematical model of aggressive mimicry. *Behavioral Ecology*, 30(1), 134–141.
- Krebs, J. R., Kacelnik, A., & Taylor, P. (1978). Test of optimal sampling by foraging great tits. *Nature*, 275(5675), 27-31.
- Kulahci, I. G., Dornhaus, A., & Papaj, D. R. (2008). Multimodal signals enhance decision making in foraging bumblebees. *Proc. R. Soc. Lond. B*, 275(1636), 797–802.
- Lancaster, L. T., Hipsley, C. A., & Sinervo, B. (2009). Female choice for optimal combinations of multiple male display traits increases offspring survival. *Behavioral Ecology*, 20(5), 993–999.
- Lindstrom, L., Rowe, C., & Guilford, T. (2001). Pyrazine odour makes visually conspicuous prey aversive. *Proc. R. Soc. Lond. B*, 268, 159–162.
- Lotem, A. (2013). Learning to avoid the behavioral gambit. *Behavioral Ecology*, 24(1), 13.
- Mangel, M. & Clark, C. (1988). Dynamic modeling in behavioral ecology. Princeton University Press.
- Marple, N. M. & Roper, T. J. (1996). Effects of novel colour and smell on the response of naive chicks towards food and water. *Animal Behaviour*, 51, 1417-1424.
- Maynard Smith, J. & Harper, D. 2003. Animal Signals. Oxford University Press, Oxford.
- McGuire, L., Van Gossum, H., Beirinckx, K., & Sherratt, T. N. (2006). An empirical test of signal detection theory as it applies to Batesian mimicry. *Behavioural Processes*, 73, 299–307.

- McNamara, J. M. & Houston, A. I. (1987). Partial preferences and foraging. *Animal Behaviour*, 35(4), 1084–1099.
- Moller, A. P., & Pomiankowski, A. (1993). Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.*, 32, 167–176.
- Oaten, A., Pearce, C. E. M., & Smyth, M. E. B. (1975). Batesian mimicry and signal detection theory. *Bulletin of Mathematical Biology*, 37, 367–387.
- Penney, H. D., Hassall, C., Skevington, J. H., Lamborn, B., & Sherratt, T. N. (2013). The relationship between morphological and behavioral mimicry in hover flies (Diptera: Syrphidae). *The American Naturalist*, 183(2), 281–289.
- Peterson, W., Birdsall, T., & Fox, W. (1954). The theory of signal detectability. *Transactions of the IRE Professional Group on Information Theory*, 4(4), 171–212.
- Quiñones, A. E., Leimar, O., Lotem, A., & Bshary, R. (2020). Reinforcement learning theory reveals the cognitive requirements for solving the cleaner fish market task. *American Naturalist*, 195(4), 664–677.
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Real, L. A. (1991). Animal choice behavior and the evolution of cognitive architecture. *Science*, 253(5023), 980–986.
- Rodríguez-Gironés, M. A., & Lotem, A. (1999). How to detect a cuckoo egg: A signal-detection theory model for recognition and learning. *The American Naturalist*, 153(6), 633–648.
- Rowe, C. (1999). Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour*, 58, 921–931.
- Rowe, C. & Guilford, T. (1996). Hidden colour aversions in domestic chicks triggered by pyrazine odours of insect warning displays. *Nature*, 383, 520–522.
- Rowe, C., & Guilford, T. (1999). The evolution of multimodal warning displays. *Evolutionary Ecology*, 13, 655–671.
- Rubi, T. L., & Stephens, D. W. (2016a). Should receivers follow multiple signal components? An economic perspective. *Behavioral Ecology*, 27(1), 36–44.
- Rubi, T. L., & Stephens, D. W. (2016b). Does multimodality per se improve receiver performance? An explicit comparison of multimodal versus unimodal complex signals in a learned signal following task. *Behav. Ecol. Sociobiol.*, 70(3), 409–416.

- Ruxton GD, Allen W, Sherratt TN & Speed MP (2018). Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry. Second Edition Oxford University Press.
- Schaefer, H. M., Schaefer, V., & Levey, D. J. (2004). How plant-animal interactions signal new insights in communication. *Trends in Ecology and Evolution*, 19(11), 577–584.
- Schlüter, D. & Price, T. (1993). Honesty, perception and population divergence in sexually selected traits. *Proc. R. Soc. Lond. B*, 253(1336), 117–122.
- Schneider, J. M., Zimmer, S. M., Gatz, A. L., & Sauerland, K. (2016). Context- and state-dependent male mate choice in a sexually cannibalistic spider. *Ethology*, 122(3), 257–266.
- Sherratt, T. N. (2011). The optimal sampling strategy for unfamiliar prey. *Evolution*, 65(7), 2014–2025.
- Sherratt, T. N., & Holen, Ø. H. (2018). When should receivers follow multiple signal components? A closer look at the “flag” model. *Behavioral Ecology*, 29(4), e6–e8.
- Sherratt, T. N., & Morand-Ferron, J. (2018). The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Animal Behaviour*, 138, 59–67.
- Skelhorn, J., Halpin, C. G., & Rowe, C. (2016). Learning about aposematic prey. *Behavioral Ecology*, 27(4), 955–964.
- Skelhorn, J., Holmes, G. G., Hossie, T. J., & Sherratt, T. N. (2015). Multicomponent deceptive signals reduce the speed at which predators learn that prey are profitable. *Behavioral Ecology*, 27(1), 141–147.
- Skinner, B.F. (1948). ‘Superstition’ in the pigeon. *Journal of Experimental Psychology*, 38(2), 168–172.
- Smith, C. L., Van Dyk, D. A., Taylor, P. W., & Evans, C. S. (2009). On the function of an enigmatic ornament: wattles increase the conspicuousness of visual displays in male fowl. *Animal Behaviour*, 78, 1433–1440.
- Stephens, D. W. (2018). Corrigendum: Reply to Sherratt and Holen: Goldilocks and the half-empty glass. *Behavioral Ecology*, 29(4), 1001–1001.
- Tanner, W.P. & Swets, J.A. (1954). A decision-making theory of visual detection. *Psychological Review*. 61(6), 401–409.
- Tibbetts EA, Liu M, Laub EC, Shen S-F. 2020 Complex signals alter recognition accuracy and conspecific acceptance thresholds. *Phil. Trans. R. Soc. B*, 375, 20190482.
- Wang, M. Y., Vasas, V., Chittka, L., & Yen, S. H. (2017). Sheep in wolf’s clothing: multicomponent traits enhance the success of mimicry in spider-mimicking moths. *Animal Behaviour*, 127, 219–224.

- Wilson, A. J., Dean, M., & Higham, J. P. (2013). A game theoretic approach to multimodal communication. *Behav. Ecol. and Sociobiol.*, 67(9), 1399–1415.
- Wixted, J.T. & Mickes, L. (2014). A signal-detection-based diagnostic-feature-detection model of eyewitness identification. *Psychological Review*, 121(2), 262-276.