Subjective Estimates of Opportunity Cost in Rats Working for Rewarding Brain Stimulation

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ABSTRACT

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The principal goal of psychophysics is to describe the functions that transform the objective variables into their subjective equivalents. The matching law has been used to describe the function translating the objective strength of a rewarding stimulus (e.g., the concentration of a sucrose solution) into its subjective impact. In contrast, the psychophysics of the cost of a reward has been little studied. This is a salient lacuna.

The present experiments examine opportunity cost, the price paid for a reward in terms of the time taken away from competing activities, such as procurement of alternate rewards, resting, grooming, and exploration. The reward is electrical stimulation delivered to the medial forebrain bundle. It is the subjective interpretation of these values (reward strength and cost) that an animal uses for goal selection. A widely held assumption is that the animal computes the payoff of a goal (an index of how worthwhile it is for it to choose a goal) as the ratio of the subjective reward strength to the subjective cost required to obtain the goal. This assumption is the basis for the present experiments: changes in subjective reward strength (manipulated by the frequency of stimulation) are used to compensate for changes in opportunity costs by the animal, and changes in opportunity costs are used to compensate for changes in reward strength.

The present experiments estimate the function that transforms objective opportunity costs into subjective opportunity costs under the assumed definition of

payoff. In Experiment I, the change in frequency required to offset a constant proportional change in price is determined, providing an estimate of the first derivative of the subjective-price function. This experiment demonstrates that as the time intervals are shortened, subjective opportunity cost levels off and deviates substantially from the objective cost. In Experiment II, the change in price required to offset a fixed difference in frequency is determined which provides an estimate of the subjective-price function itself. This experiment demonstrates that subjective costs approximate objective ones when the time intervals involved are relatively long. The two experiments complemented each other: the first revealed the scalar range of the objective-subjective cost relationship while the second demonstrated where this relationship breaks down.

It has been implicitly assumed that the relation between objective and subjective costs approximate each other; these experiments showed that this is true but that the relationship breaks down at low costs. The function mapping objective costs into subjective ones (the "subjective-cost function") would prove useful because if the cost of a reward were to be used as a parameter that is manipulated in other experiments, it is important to choose a value of cost that the animal will accurately interpret.

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Finally, I am extremely grateful for my family: my parents, Ben and Jane, brother, Jonathan, and grandparents, Joshua and Dorothy Millman for their encouragement, love, and support.

DEDICATION

I dedicate this thesis to my loving parents: Ben and Jane Solomon.

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Glossary

ALT frequency: The frequency of the train triggered by the ALT lever. In Experiment I, the ALT frequency changes from trial to trial in a session.

ALT lever: Alternate lever; the lever that triggers the ALT frequency.

ALT price: The price of the ALT train measured in seconds.

BSR: Brain stimulation reward; refers to the phenomenon that animals will work to receive electrical stimulation through electrodes implanted in specific brain regions implicated in the perception of reward.

CP: Cross-point; when the rat allocates equal time to pressing both levers, the frequency (Experiment I) or price (Experiment II) of the train triggered by the ALT lever is denoted by the CP. On the graphs of time allocation as a function of ALT frequency or ALT price, the CP is the blue dot denoting the intersection of the two curves, when time allocation to both levers is equal.

Dual-operant: An operant task in which the subject has the choice between two alternatives to engage in, in the present experiments, the rat has the choice between two levers to press.

Effort cost: The cost of the reward expressed in how much effort the animal must exert, such as the amount of energy it expends, or the number of bar presses it must make to obtain a reward.

FCHT: Fixed Cumulative Handling Time schedule; the subject reaps the reward after holding down the lever for the cumulative amount of time required.

fVI: Free-Running Variable-Interval schedule; the lever is armed with the reward after a time interval, sampled from an exponential distribution, has elapsed. The rat must be holding the lever down at the expiry of the time interval in order to reap the reward.

Frequency: A property of the electrical stimulation that controls the strength of the stimulation; measured in Hz.

Leisure: All the activities the rat can engage in (in its operant box) when it is not working, such as grooming, sleeping, and exploring.

Objective price: The amount of time, as set by the experimenter, that the rat is required to press the lever in order to obtain the reward.

Opportunity cost: The cost of one option expressed as the foregone benefits of another. In an operant context, it is the amount of time the animal could have spent in leisure activities if it were not working for the reward. The objective opportunity cost is a value that everyone will agree on, expressed in monetary units or seconds, the subjective opportunity cost is a subject's internal representation of the objective component.

Reward intensity: The animal's subjective interpretation of the strength or magnitude of the reward.

STD frequency: The frequency of the train triggered by the STD lever. In Experiment I, the STD frequency stays constant throughout a session.

STD lever: Standard lever; the lever that triggers the STD frequency.

STD price: The price of the STD train measured in seconds.

Subjective price: The rat's own interpretation of the objective price.

Time allocation: The ratio of the time the animal spends working to the total amount of time available.

Train: A brief electrical signal introduced into the medial forebrain bundle, a brain area implicated in reward perception.

***Work*:** The act of engaging in the operant task such as pressing the lever in order to obtain the reward.

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Psychophysical functions

The goal of psychophysics is to develop functions that transform the objective, physical domain into the subjective, psychological domain. For example, the strength of a psychological construct such as a sensation can be scaled in relation to the scale of physical intensity. A common example is that of the perception of brightness. The subject is presented with a series of stimuli of varying intensities and is asked to estimate the magnitudes of the stimuli. After several trials, a psychophysical function of brightness can be developed such that perceived brightness is plotted as a function of the physical intensity of light (lumens).

Often, the psychophysical functions of many sensations are not linear which is also true for the psychophysical relationship for brightness. As the physical intensity of a flash of light increases, an individual's subjective interpretation of its brightness initially increases as well but eventually, further increases in physical intensity will fail to cause corresponding increases in subjective impact. At this point, the function reaches a plateau. Therefore, a change such as a doubling, in the physical intensity of brightness at low lumens will produce a meaningful change in the subjective intensity, whereas that same absolute change in physical intensity at higher lumens (where the function is at a plateau) will not produce a change in the subjective intensity.

In psychophysical experiments on operant tasks, psychophysical functions have been proposed to transform the objective strength of a reinforcer into its subjective value.

For example, the matching law has been used to tie subjective reward value, which refers to a subject's interpretation of how rewarding a stimulus is, to the concentration of a sucrose solution in rats (Heyman & Monaghan, 1994). As is the case in the psychophysical transformation of light intensity, the psychophysical function translating sucrose concentration into reward value eventually saturates. A doubling of sucrose concentration will cause a large increment in subjective reward value when the solution is dilute but not when it is highly concentrated.

Psychophysical experiments on operant tasks, however, seem less developed. In the case of natural reinforcers (Heyman & Monaghan, 1994) and brain stimulation reward (BSR) (Hamilton, Stellar, & Hart, 1985; Gallistel & Leon, 1991; Leon & Gallistel 1992; Mark & Gallistel, 1993; Simmons & Gallistel 1994), the function for subjective reward intensity has been measured, but the function describing the animal's interpretation of the cost of the reward, a variable related to the imposed schedule of reinforcement, has not. Specifically, the cost of a reinforcer can be defined in terms of what the animal is required to do in order to obtain the reward such as the number of bar presses it must make or the amount of time it must engage in a task. The corresponding subjective variable is the animal's interpretation of the experimenter-set cost. Could the animal's interpretation of the cost differ from that which the experimenter is actually imposing? In other words, is the cost function nonlinear as is the case for many psychophysical functions? The experiments described in this thesis were carried out in an attempt to extend psychophysical scaling beyond the area of sensation to the realm of motivation and decision-making. This work challenges the assumption that objective and subjective costs are always equivalent, but supports this assumption above a certain threshold.

Opportunity cost

The cost of a reward can be looked at in terms of "opportunity cost" which is a term used in economics to refer to the benefits that would have arisen from a forgone opportunity. Specifically, opportunity cost refers to the cost of one option expressed as the forgone benefits of another. For example, if an individual were to buy a car, the opportunity cost would be the benefits that might have arisen if the money were used in another way, such as keeping the money in the bank in order to receive interest.

The notion of opportunity cost can be separated into objective and subjective components. The objective opportunity cost is defined as the quantifiable benefits arising from a foregone opportunity such as the interest an individual would receive by keeping the money in the bank. The objective component is a matter that everyone will agree on, the actual numerical value of the money (e.g., five dollars). In contrast, the subjective opportunity cost is the subject's own interpretation of the benefits arising from a forgone opportunity. In the case of receiving interest, the subjective opportunity cost takes into account the personal significance of the amount of interest received. For instance, a return of five dollars may be regarded as negligible by one investor but significant to another. This subjective component is the internal representation of the objective one.

In the context of an operant experiment, the objective opportunity cost is the time required for the animal to work for a reward at the expense of the time it could spend engaging in "leisure" activities such as sleeping, grooming, and exploring when it is not engaging in the operant task, which can be referred to as "working". The objective opportunity cost is the actual (measurable) time that the rat could spend engaging in other activities, a value that everyone would agree on. The subjective opportunity cost is the rat's estimate of the cost, taking into account the personal significance of the potential time that could be spent engaging in other activities. The benefits arising from the potential time that the rat could be engaged in leisure activities is analogous to the benefits arising from the invested money that could have been used in another way. Just as a small amount of money could be regarded as negligible to one individual but not to another, the benefits arising from a very small amount of time could be considered as negligible to one animal, but not to another. The subjective component of opportunity cost in an operant context is the rat's internal representation of the objective one.

Schedules of reinforcement and cost

In a foraging context, the cost the animal has to pay to obtain a reward such as food is often looked at in terms of both the time and effort the animal spends locating, handling, procuring, and consuming the food. Thus, there are multiple components to the cost of a reward: opportunity cost, the forgone benefits arising from not foraging, often expressed as the amount of time that would be available for other activities, and effort cost which refers to the amount of effort the animal exerts to obtain the reward such as the energy the animal expends in order to attain its prey.

In an operant context, these two components of cost can be defined: effort cost refers to the amount of effort the animal must exert in order to obtain the reward, such as a required number of bar presses or a required distance it must run; opportunity cost as described in the previous section, refers to the amount of time the animal forgoes alternate activities in order to be engaged in the task. It is possible to control effort cost with a ratio schedule: on a ratio schedule, the subject must emit the experimenter-set response such as a required number of bar presses (amount of effort) in order to earn a reward. Ratio schedules, however, do not control opportunity cost.

The second traditional schedule used in operant experiments is an interval schedule in which a minimum inter-reward interval is set which limits the maximum rate at which rewards can be earned. Interval schedules do not control effort costs. Although interval schedules involve time, an aspect central to opportunity costs, Shizgal and Conover (2005) argue that traditional interval schedules do not control opportunity cost in operant experiments; what is manipulated is not the amount of time the animal must work in order to obtain the reward. For example, on an FI 5 s schedule, the reward is delivered on the first response after at least 5 s, however, the animal is not required to engage in the task for the entire length of the interval. The typical response pattern is to start engaging in the task such as bar pressing closer to the time of delivery of reward. Therefore, the cost of the reward to the animal is not 5 s because the animal is not required to work for the entire length of the 5 s interval to obtain the reward. Rather, the animal's requirement is to make a response after at least 5 s has elapsed. During the 5 s interval, the animal can be engaging in activities other than the operant task such as resting or exploring and does not actually invest a total of 5 s.

This scenario is also true for variable interval (VI) schedules of reinforcement in which the delivery of the reward is unpredictable throughout the session. For instance, on a VI schedule set to 5 s, on average the reward is delivered every 5 s, some trials can be less than 5 s and some can be greater than 5 s. It is important to note that on these interval schedules, after the interval has timed out, the reward typically remains available for the animal until it makes a response. For instance, if the subject does not respond during the interval of 5 s, the next response it makes, which may occur long after the end of the set-interval, the subject will be rewarded. Therefore, the subject could learn the average interval and only engage in the task towards the end of the interval or even beyond and still harvest most of the available rewards; it need not be engaged in the operant task throughout the experimenter-set interval and can obtain a large return by working only during a small proportion of the time. Therefore, the animal in a way is controlling the cost, the amount of time it must work, which is considerably less than the experimenter-set interval. What is actually being set by the experimenter is not the required time the animal must engage in the operant task to obtain the reward. Rather, it is a minimal inter-reward interval that is set by the experimenter (i.e. at least 5 s between rewards on average) and during this time, the subject cannot obtain the reward.

Shizgal and Conover (2005) have developed a schedule of reinforcement that provides tight control of opportunity cost (the amount of time the animal must engage in the task) compared to traditional schedules of reinforcement. Shizgal and Conover's schedule, the free-running VI (fVI) requires the subject to be holding down the lever at the end of an unpredictable time interval in order to obtain the reward. On the fVI, the reward is only available to the subject the moment the time interval has elapsed whereas on the VI schedule, the reward is available at any time after the time interval has elapsed, on the first response it makes. This new schedule establishes a fixed proportionality between work and return: the proportion of rewards harvested equals, on average, the proportion of time worked. In contrast, on the traditional interval schedule, the proportion of rewards harvested is greater, on average, than the proportion of time worked.

Price

In an operant context, I will refer to the objective opportunity cost as the "objective price" which is defined as the amount of time the subject must work in order to obtain the reward as set by the experimenter. The subjective opportunity cost is referred to as the "subjective price" and it is the animal's interpretation of the objective price that is set by the experimenter. The function relating objective and subjective prices is referred to as the subjective-price function.

Reward

An understanding of the types of rewards in an operant task is important because the reward is implicated in the definition of cost. In operant tasks, often, the reward is food and its magnitude is manipulated by varying the size or number of pellets delivered. An alternative that has long been used in studies of operant performance is the rewarding effect of electrical brain stimulation, which will be called "brain stimulation reward" (BSR). The use of this reward in an operant paradigm has many advantages because the effects of physiological feedback (such as satiation) and the response-reward delays that degrade conventional rewards are avoided. The strength of the rewarding effect of BSR is powerful and is easily manipulated by changing the parameters of the stimulation such as the frequency and current.

Payoff

A widely held assumption (made in this thesis too) is that the price and magnitude of a reward are combined by the animal to estimate the payoff, how worthwhile it is for it to work for the reward. It is this evaluation that the animal makes that is fundamental to deriving the subjective-price function in the present experiments. Therefore, an appreciation of the definition of payoff is essential. The subject's estimation of payoff can be used to derive the subjective-price function and will be elaborated on later.

In a foraging situation, the payoff (or how profitable or worthwhile it is for an animal to search for food) is often defined as the benefits arising from the food (such as the caloric value) in relation to the costs the animal has to pay to obtain the food (such as the time the animal spends working to obtain the food: searching, traveling, handling, procuring, and consuming) (Stephens & Krebs, 1986). In operant responding, Herrnstein's matching law (1961) uses a variation of the definition of payoff in natural circumstances in which payoff is defined as the product of the magnitude and rate of reinforcement.

$$\text{Payoff} = \frac{\text{Benefits}}{\text{Cost}} \quad \text{(simplified definition in a foraging context)}$$

$$\text{Payoff} = \text{Rate of Reinforcement} \times \text{Magnitude of Reinforcement} \qquad \text{(Herrnstein, 1961)}$$

The magnitude of the reinforcement is manipulated by the experimenter by varying the number or size of food pellets the animal receives. The rate of reinforcement is experimenter-set and refers to how often the animal can receive the reward (for example, 5 rewards every minute). Therefore, the benefit arising from the food in the foraging situation is roughly analogous to the magnitude of reinforcement in a laboratory setting. The cost required to obtain the food in foraging circumstances is roughly comparable to the reciprocal of the rate of reinforcement (rewards/min, or rewards/s) according to Herrnstein. Cost and reinforcement rate are referred to as being only roughly comparable because the subject must spend all of its time working for the experimenter-controlled reward in order for cost and reinforcement rate to be exact reciprocals of each other. A cost of 15 s in a foraging situation is therefore roughly analogous to a rate of reinforcement that would be set to 4 rewards/1 min.

Conover and Shizgal (2005) have developed a variation of Herrnstein's definition of payoff in operant tasks. In their definition, payoff is equal to the ratio of the reward intensity of the electrical stimulation (how rewarding the animal interprets this stimulation) to the subjective price.

$$\text{Payoff} = \frac{\text{Reward Intensity}}{\text{Subjective Price}} \qquad \text{(Conover \& Shizgal, 2005)}$$

Reward intensity is manipulated by the frequency of stimulation, subjective price is manipulated by the objective price. Herrnstein's definition of payoff and Shizgal and Conover's definition are closely related because if the subject works continuously on a VI schedule, the price is the inverse of the rate of reinforcement. For example, if the rate of reinforcement is set to 2 rewards/min (1 reward/30s), this implies that the price would be the reciprocal, 30 s required to work to obtain the reinforcer. The difference between these two accounts of payoff is that the rat's internal representation of both the reward and price is central to Shizgal and Conover's definition as opposed to the corresponding objective variables that characterizes Herrnstein's definition.

Proposed relation between subjective and objective prices

As stated, earlier, it has been assumed tacitly in analyses of operant behaviour that objective and subjective prices are equivalent. The proposal in the present experiments is that the assumption that objective and subjective prices are always equivalent may not be true. There is reason to believe that the relation may break down when prices are small. For example, prices of 0.1 s and 0.2 s may be interpreted by the animal as equivalent opportunity costs because reducing the price from 0.2 to 0.1 s does not allow it to perform additional alternate activities of any significance. In effect, the subjective opportunity costs associated with very low objective prices are predicted to be the same.

Conceptual links to the present experiments from studies on the estimation of time

Although not a lot of work has been done on the function relating subjective and objective costs, there is a vast literature on the estimation of time intervals. Because the price the subject pays is time, the subjective time function is relevant to developing the subjective-price function.

Countless studies since the beginning of psychology have been conducted to determine how accurately objective time is perceived. Early studies by Vieordt and the Wundtians (Boring, 1942) attempted to find an indifference-point, an interval with an absolute duration which would always be available to the mind as a standard, the time interval that is most accurately estimated. Various indifference points were reported but varied depending on the methods and eventually the idea of an absolute point was abandoned (Woodrow, 1930). Instead, studies focused on developing the actual function relating objective time to subjective time. Steven's power law (1957) relates the psychological variable to a physical variable, the intensity of the stimulus in the following way:

$$S = KI^a$$

or

$$\log S = a \log I + \log K$$

S is the sensation magnitude, I is stimulus intensity, K is a constant, and a is the power exponent that depends on the modality. Modalities such as brightness have an exponent of less than 1 which indicates that a person will underestimate the strength of stimuli as their intensity increases. A modality with an exponent greater than 1 implies that a person will overestimate the sensation of a stimulus as the stimulus intensity increases. An exponent of 1 indicates that a person is accurate at mapping objective stimulus intensity into subjective sensation.

Steven's power law has been used to describe the psychophysical function for time. Eisler (1976) compiled exponents of subjective duration experiments in humans from over one hundred studies using various methods and concluded that generally, the exponent for time perception is close to 0.9. The nature of the function, however, may depend significantly on the methods employed to measure the perception of time intervals. For instance, Allan (1979) proposed that a linear function between subjective and objective time may be a better representation of the data.

The difficulty in describing the psychophysical function of time is that the nature of the function varies depending on the methodology. However, most studies concerned with subjective estimates of time agree that the psychophysical function is not veridical. For instance, although close to an exponent of 1, Eisler's (1976) conclusion was that the exponent for the psychophysical function was approximately 0.9 for humans. Also, SET, scalar expectancy theory (Gibbon, 1977), presently one of the leading models of timing behaviour shows that subjects may underestimate or overestimate the time of expected reward. The ratios of the expectancies to the objective time intervals vary in direct proportion with each other over a range of time intervals.

SET is more in line with the present experiments because the rat is working on an FI schedule in order to obtain the reward. However, animal timing data for intervals less than 1 or 2 s have generally not been obtained (Gibbon, 1977)

Relating the psychophysical function of timing to the psychophysical function of price

The function relating objective and subjective time can help to build the function relating objective and subjective prices. Because objective prices are times, a function can be developed that translates objective prices into subjective times. The following notation describes the relation between subjective times and objective prices:

$$\mathrm{st} = f(\mathrm{op})$$

st = the subjective time estimate

op: objective price

f = the subjective time function

The rat estimates the experimenter-set time interval (op). Objective price is equivalent to objective time because price is defined in terms of the amount of time the animal must spend working. The literature on the estimation of time intervals describes different possible timing functions that vary depending on the type of schedule, task, and subjects used as discussed above. For now, the interval timing function will simply be called *f*, and its form will not be specified.

It is important to understand that an estimate of subjective time is not equivalent to an estimate of subjective price. As explained before, in the context of working for the reward, small time intervals such as 0.1 s and 0.2 s may be meaningless to the animal in terms of time required to engage in a task to earn a reward. Nonetheless, the animal may still be able to discriminate between these small time intervals but may simply not care that a difference exists because the benefits arising from the alternate activities (leisure) may be equivalent at these very small time intervals. Although time is used as the input of the subjective price function, the present experiments look at the animal's interpretation of price in the context of an operant task rather than the simple discrimination between intervals of time.

The subjective price function takes into account the subjective time function. Subjective time is transformed into subjective price by a second function, *g*.

$$sp = g(st)$$

$$sp = g(f(op))$$

where $st = f(op)$

sp = the subjective price estimate, and

g = the function that translates subjective times into subjective prices

To represent the embedding of f in g, a new function h can be defined.

$$sp = g(f(op))$$

$$sp = h(op)$$

The function h corresponds to the definition of a psychophysical function. It translates an objective quantity (op) into a subjective one (sp). This function takes into account both the translation of objective time intervals into subjective time intervals (f) and the subjective time intervals into subjective prices (g). Function h will be called the "subjective-price function".

The proposed subjective-price function

The proposed subjective-price function is illustrated in Figure 1. Initially, it was proposed that the objective-subjective price relation would break down when objective prices were small (Mullett, 2005). The flat part of the curve implies that prices less than a certain value are interpreted as being the same. The relation between objective and

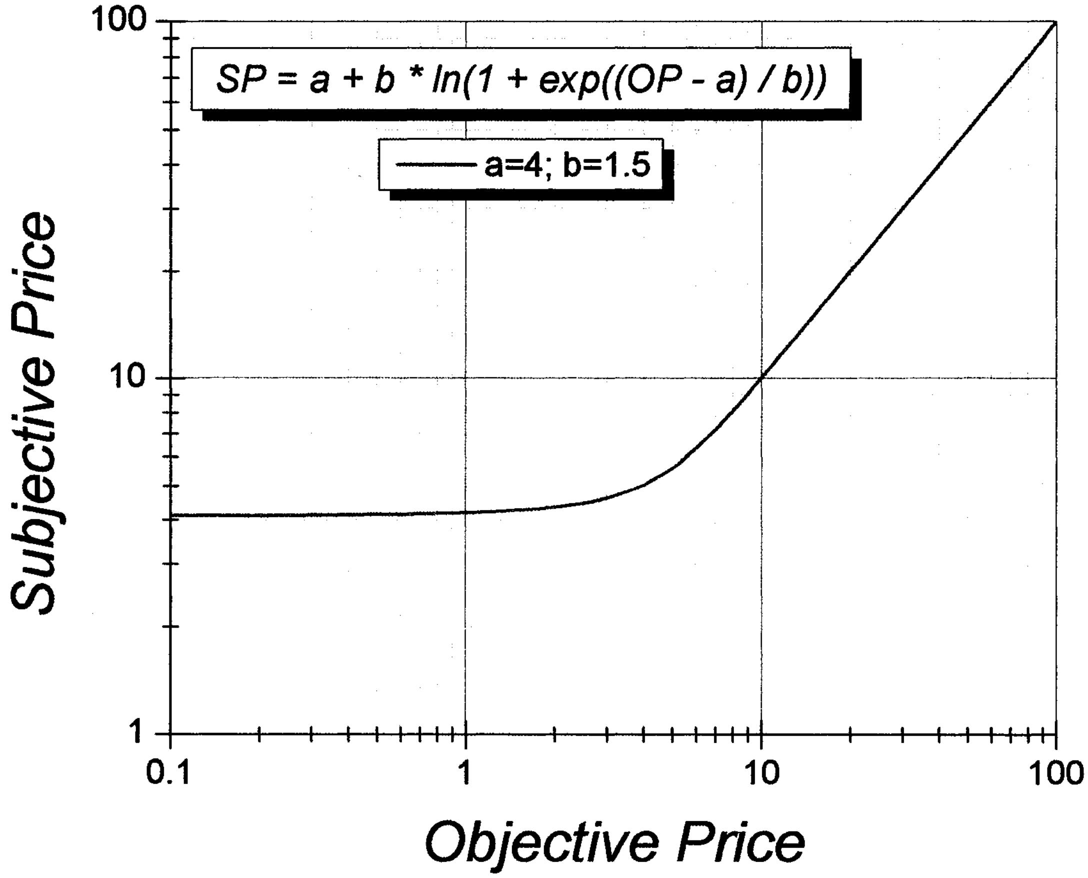


Figure 1. The proposed relation between subjective and objective price. At low objective prices, the function is flat because low objective prices are considered to be subjectively the same to the animal. In this example, the function starts to bend at around 1 s indicating that objective prices are beginning to be interpreted as being different from each other. At high prices, after 10 s, the function becomes scalar, such that the slope is constant (1 in this case) implying that the subjective and objective prices vary in direct proportion. Each rat is expected to have its own subjective-price function, although the shape will be similar.

subjective prices at higher prices is represented by the growth part of the subjective-price curve. At these prices, objective price is thought to be equal to subjective price, this relation is said to be scalar. A scalar relation implies that objective and subjective prices vary in direct proportion with each other. That is, if the ratio of the objective price and subjective price were 1 (scalar = 1), a 10 s objective price would be equal to a 10 s subjective price and a 15 s objective price would equal a 15 s subjective price. Similarly, if the proportion between the objective and subjective prices were 2, a 10 s objective price would be equal to a 20 s subjective price and a 15 s objective price would be equal to a 30 s subjective price. It is likely that the scalar is close to 1 s, because from an evolutionary perspective it is not advantageous to the animal to have a clock twice as fast or twice as slow as the objective time in a foraging situation, although it has been reported that the scalar may deviate slightly from 1 as mentioned above. This assumption of direct proportional variation is thought to no longer hold true at low objective prices, where the subjective-price function is thought to break down. The present experiments tested the assumption that over at a high range of prices, the relationship between objective and subjective price is scalar, but that this relation breaks down at low prices.

This relation between subjective price and objective price can also be represented by the first derivative of the subjective-price function (Figure 2). The derivative of the subjective-price function is the rate at which the subjective price changes in response to a change in the objective price. At low prices, when prices are thought to be interpreted as equivalent to each other, the derivative is close to 0 because subjective price changes very little with increases in objective price along this range. After a certain price, around

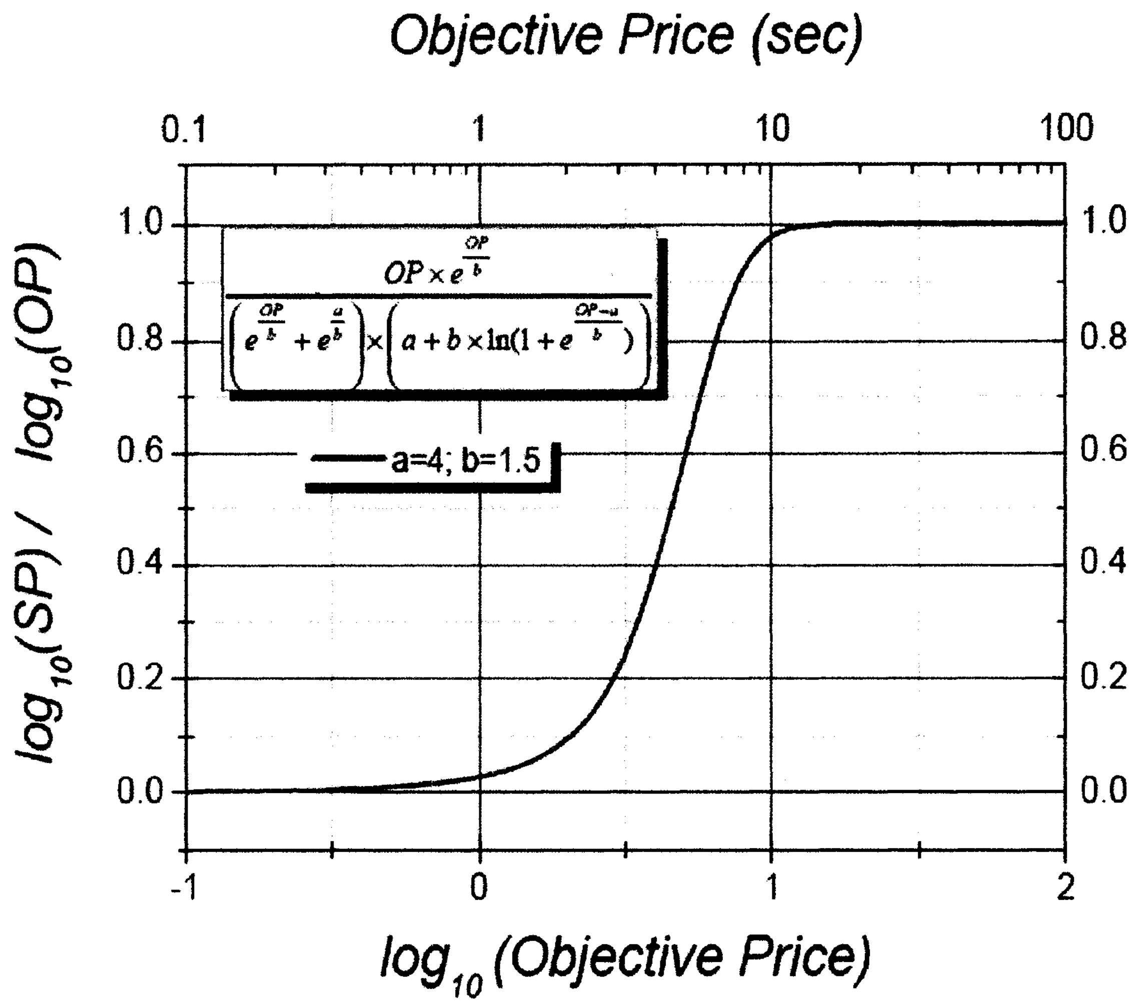


Figure 2. The prediction that very low objective prices are equal to each other is illustrated by the first derivative of the subjective-price function that is shown in Figure 1. The derivative of the subjective-price function is the rate at which the subjective price changes in response to a change in the objective price. The rate of change is 0 at very low objective prices because a change in very low objective prices does not change the value of the subjective prices. At very high prices, past 10 s, the rate is constant which indicates the scalar relationship. The growth part of the curve can be considered the transition phase in which objective prices are beginning to gradually be interpreted as being different from each other, located in between the two flat regions of the function.

1 s in this example, there is a transition phase in which the rate of change of subjective prices increases. The transition phase of the first derivative of the subjective-price function (Figure 2) corresponds to the range of prices on the subjective-price function (Figure 1) that lie on the bent part of the curve in which the price relation is not yet scalar, when objective prices begin to be interpreted as slightly different from each other. Finally, at a higher price (around 10 s in this example), the function levels off again which implies that the rate of change is constant. That is, for every change in subjective price, there is an equal change in objective price implying that this range is scalar. Experimentally this function can be estimated, it is roughly analogous to the proportional change in frequency of electrical stimulation required to compensate for a change in price as a function of objective price (Figure 3). The first goal of the present experiment was to estimate the function analogous to the first derivative of the subjective- price function.

Experiment I: Indirectly estimating the subjective-price function

The definition of payoff (the ratio of reward intensity to subjective price) is the fundamental assumption in the derivation of the subjective-price function in the present experiments. Reward intensity is known to increase with increasing strength (frequency) of stimulation (Simmons & Gallistel, 1994). Therefore, reward magnitude can be controlled in the above formulation by manipulating the stimulation frequency. The subjective price can be controlled by manipulating the objective price. Given the definition of payoff as the ratio of subjective reward intensity and subjective price, and because subjective reward intensity and subjective price can be controlled by varying the objective strength and price of the stimulation, it should be possible to offset changes in

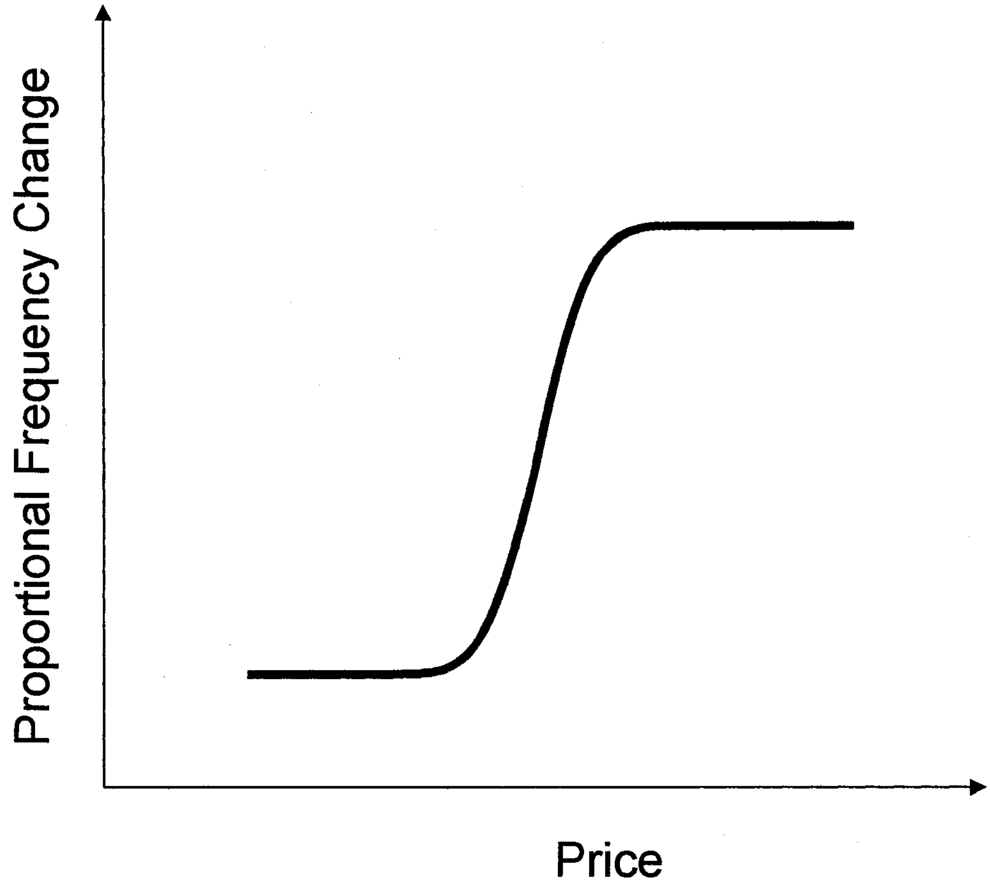


Figure 3. The derivative of the subjective-price function can be estimated experimentally. The derivative of the subjective-price function is roughly analogous to the proportional frequency change required to compensate for a change in price.

objective price with compensatory changes in frequency. For simplicity, assume in the following example that the reward-growth function and subjective-price function are scalar (although in reality they are not). The ratios of stimulation frequency (Hz) to price (s) such as 30:10, 60:20, 120:40 all have equivalent payoffs, 3Hz/1s. Therefore, if the price is reduced by a given amount, the reduction in stimulation frequency required to compensate for this price change (so that the payoffs remain equal) can be determined. In a choice paradigm, the following was measured: the proportional decrease in frequency required to compensate for a halving of prices so that the payoffs of the two choices, a cheaper, less rewarding reinforcer in comparison to an expensive, more rewarding reinforcer, remained the same.

In the present experiments, the task is to hold the lever for an experimenter-set amount of time (objective price) in order to obtain electrical stimulation of the medial forebrain bundle. Work is defined as the amount of time the rat spends holding the lever. Leisure is defined as the amount of time the rat spends engaged in activities other than work such as sleeping or grooming.

In order to estimate the derivative of the subjective-price function, it was necessary to obtain a series of changes in stimulation frequencies that compensate for a series of price changes. A dual-operant paradigm was used in which the subject has a choice between two levers (Figure 4). In the dual-operant paradigm used in this study, the alternate (ALT) lever delivers a train of electrical stimulation in which the pulse frequency varies from trial to trial. The frequency of the stimulation train triggered by the ALT lever is referred to as ALT frequency. The preference for the levers is reflected in the mean time allocation, the proportion of time the subject spends pressing the lever

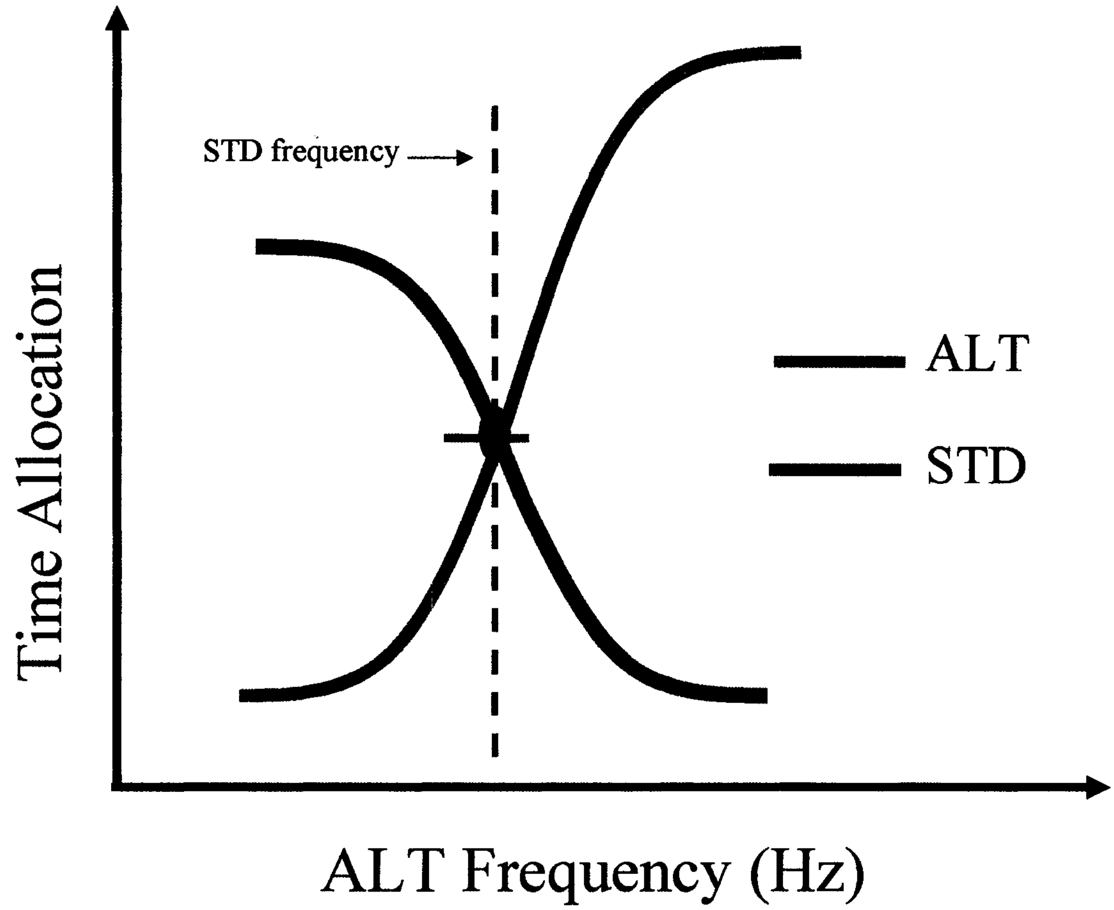


Figure 4. In a dual-operant paradigm, the animal is offered a choice between two levers. In the dual-operant paradigm used in this study, the standard (STD) lever delivers a fixed-frequency train of electrical stimulation. The alternate (ALT) lever delivers a train of electrical stimulation in which the pulse frequency varies from trial to trial. Here, the prices on both levers are equal. When the rat allocates equal time to pressing both levers, the ALT frequency (experimentally derived) is represented by the blue dot or cross-point (CP).

relative to the amount of time available. Time allocation as a function of ALT frequency is represented by the red curve. The standard (STD) lever delivers a fixed frequency-train of electrical stimulation with the frequency set midway between the highest and lowest values of the ALT frequencies. The frequency of the stimulation train triggered by the STD lever is referred to as STD frequency. The STD frequency value is denoted by the vertical dotted line on the graph. Time allocation at the STD lever as a function of ALT frequency is represented by the green curve. Given equal prices of the train on the two levers, the mean time allocation on both levers should be the same when the ALT frequency equals the STD frequency (i.e. payoffs are equal) as illustrated by the cross-point (CP) on the graph. To the left of the CP, ALT frequency values are less than the STD frequency values and the animal will spend more time attending to the STD lever than the ALT lever, thus it is inferred that the payoff of working at the STD lever is greater than the payoff for working at the ALT lever. To the right of the CP, ALT frequency values are greater than the STD frequency and the subject spends more time at the ALT lever, thus, the payoff of working at the ALT lever is greater than the payoff from working at the STD lever.

The CP represents the value of the ALT frequency when the rat spends equivalent time pressing the ALT and STD levers. Time spent working on one lever relative to the amount of time available reflects preference and is therefore thought to reflect the ratio of the two payoffs (ratio of reward intensity to subjective price). Therefore, it is assumed that the (CP) represents the value of the ALT frequency when equivalent payoffs are provided by the STD and ALT rewards. When prices are equivalent as in the case of Figure 4, the CP occurs when the frequency value of the ALT is equal to the frequency value of the STD. This makes intuitive sense, if the STD frequency is set to 120 Hz, for example, and the price of the STD and ALT rewards are the same, then the value of the ALT frequency that produces payoff equal to the value of the STD frequency will be the same as the STD frequency value, 120 Hz. In other words, the rat will spend the same amount of time working at the STD lever as he does at the ALT lever when stimulation frequencies and prices are equivalent. Therefore, the concept of payoff can be looked at in this paradigm as follows:

$$\frac{\text{Reward Intensity}_{\text{STD}}}{\text{Subjective Price}_{\text{STD}}} = \frac{\text{Reward Intensity}_{\text{ALT}}}{\text{Subjective Price}_{\text{ALT}}}$$

When the subjective prices of the stimulation triggered by the STD and ALT levers differ, the frequency of the ALT train at the CP must differ from the frequency of the STD train. If we raise the subjective price of both the STD and ALT by the same proportion in the above example, then by definition, the CP should remain the same according to the equation. However, if the prices of the STD and ALT differ, then the values of the stimulation frequencies will differ so as to produce equal payoffs. For example, if the subjective price of the STD train is raised, then in order to keep the payoffs offered by the STD and ALT lever equal to each other, the subjective reward value of the ALT train must be decreased by the same proportion.

$$\frac{\text{Reward Intensity}_{STD}}{\text{Subjective Price}_{STD}\uparrow} = \frac{\text{Reward Intensity}_{\text{ALT}}\downarrow}{\text{Subjective Price}_{\text{ALT}}}$$

Because it is known that reward intensity increases as the strength of the frequency of stimulation increases (Simmons & Gallistel, 1994) (Figure 5), the required decrease in reward value can be produced by lowering the frequency: In Experiment I the change in frequency required to offset a constant proportional change in price was determined. In theory, this provides an estimate of the first derivative of the subjective-price function. In Experiment II, the change in price required to offset a fixed change in frequency was determined. In theory, this provides an estimate of the subjective-price function itself.

Experiment I: Frequency scaling

Throughout this experiment, the STD price was always twice the ALT price, and the STD ranged from 0.25 s and 8 s. Figure 6 illustrates the procedure and predictions of the experiment. In the first condition (Figure 6 A), the STD is set to 8 s and the price of the ALT is halved, set to 4 s. According to the definition of payoff, if the subjective price of the STD is greater than the price of the ALT, in order to compensate for this difference, the reward value of the ALT must be reduced. This reduction of ALT reward value translates into a reduction of ALT stimulation frequency and is represented by a leftward shift of the ALT curve. For example, an 8 s, 120 Hz STD train will now produce an equivalent payoff as a 4 s, ALT train, with frequency lower than that of the STD, thus, the CP will lie to the left of the STD frequency denoted by the dotted vertical line. The compensatory frequency change is then measured: the ratio of the STD frequency value (represented by the dotted vertical line) to the ALT frequency value of the CP. This proportional change is the frequency required to offset a halving of an 8 s STD price. Next, a pair of lower prices is used to again obtain the proportional change in frequency

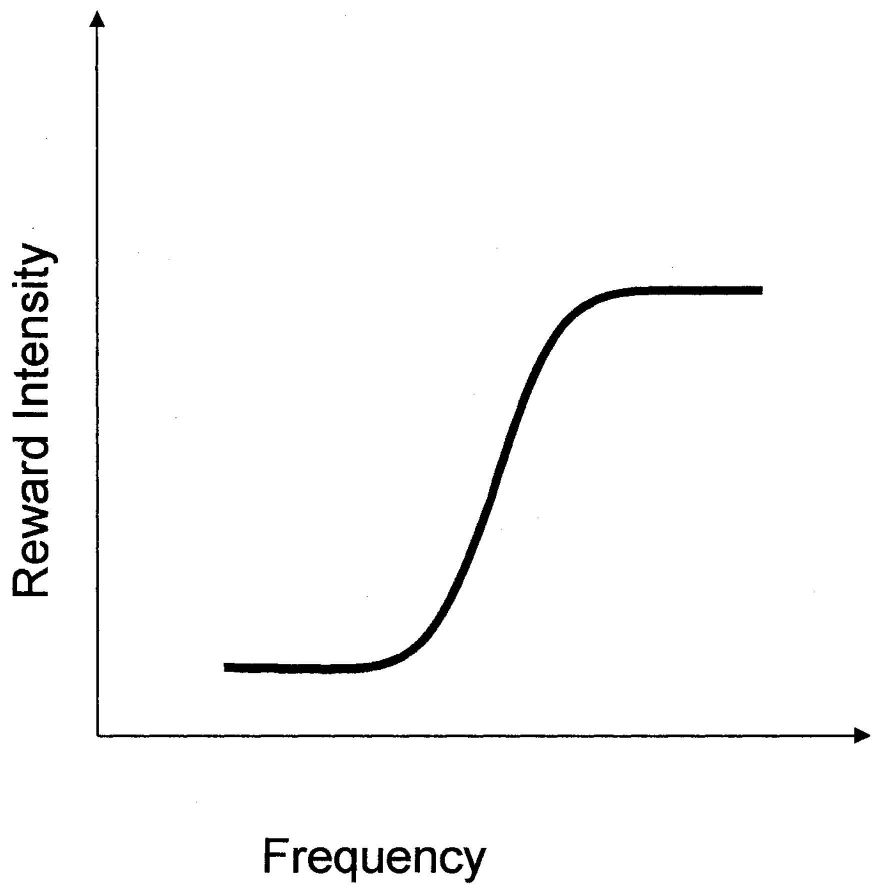


Figure 5. Reward intensity grows then saturates with increasing frequency of electrical stimulation.

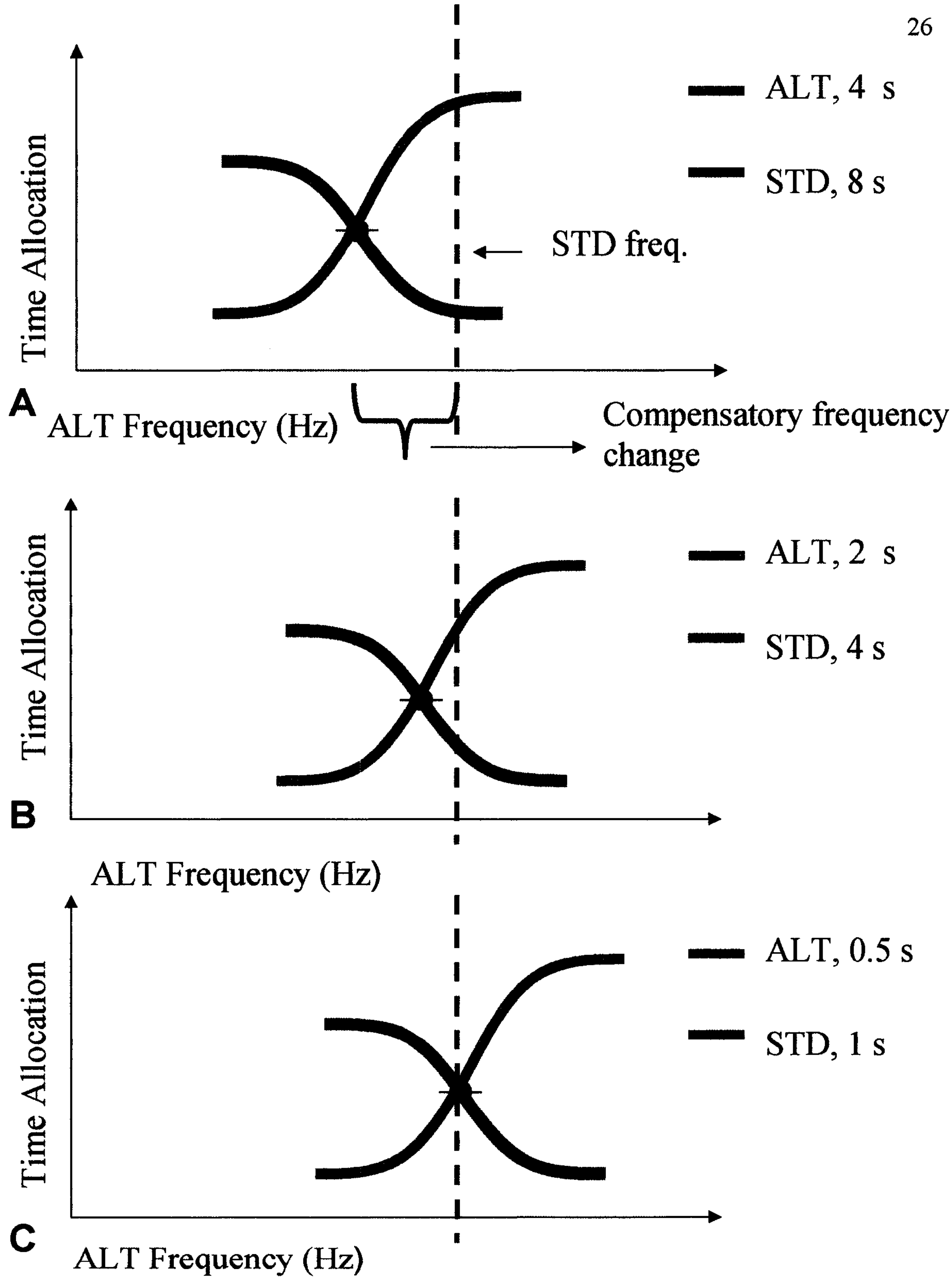


Figure 6. In this example, the ratio of the STD and ALT prices is 2. Condition A and Condition B have differing frequency changes implying that the derivative of the subjective-price function is still not scalar at a price of less than ~ 4 s. In order to find the scalar range, higher prices need to be tested to find the ranges in which equal compensatory frequency changes occur. In Condition C, no compensatory frequency change is required because the two low prices are subjectively equal.

that offsets the two-fold ratio of prices. In Figure 6 B, a STD price of 4 s and ALT price of 2 s are used. Here the compensatory frequency change is less than what was seen in the first condition. This reduction in compensatory frequency change indicates that subjective price now deviates from the objective price. Both price pairs of 8 s and 4 s, and 4 s and 2 s vary by a proportion of 2, and if the rats interpreted both of these sets of prices as a doubling, then the compensatory frequency change should be equivalent. However if the difference between 4 s and 2 s is not interpreted as the same as the difference between 8 s and 4 s, then the compensatory frequency change of the two pairs of prices would be different. If the subjective difference between 2 s and 4 s is interpreted as less than the difference between 4 s and 8 s, the compensatory frequency change would be less in the 2 vs. 4 than the 4 vs. 8 case. This subjective interpretation of a smaller change between pairs of prices that vary by the same price proportion would be attributable to the shape of the proposed subjective-objective price function, namely, that the rate of change of the subjective price is starting to decline as the objective price is lowered. In other words, if 4 s and 2 s are interpreted as being subjectively very close to each other while 8 s and 4 s are interpreted by the rat as being very different from each other, then it makes sense that the frequency change required to offset these prices changes would differ.

In Figure 6 C, the STD is 1 s and again the ALT is halved to 0.5 s. In this example no compensatory frequency change is required, which suggests that prices 0.5 s and 1 s are interpreted by the rat as being subjectively equivalent. In Figure 6 C, the ratio of the STD to ALT prices is still 2, and if (contrary to the depiction in Figure 6C) the rat interpreted the difference between 0.5 s and 1 s the same as it did for 8 s and 4 s, then the compensatory frequency change would be equivalent to the frequency change in the 8 vs. 4 s condition.

There are two different flat parts of the derivative function; that is, when the derivative is 0 and when its value is 1. These frequency differences would be found on the second flat part of the derivative function when its value is 1, indicating the rate of change for these pairs of prices is constant. An example of equivalent frequency changes along all the pairs of prices is illustrated in Figure 7A. However, because (in the illustration given in Figure 6C) there is no compensatory change required when the STD price is 1 s and the ALT price is 0.5 s, this implies that this range of prices are along the flat part of the derivative of subjective-price function in which the frequency difference is 0 (location C in Figure 7 B).

The first experiment entailed measuring the frequency changes that offset a two-fold ratio of STD to ALT prices. Predicted results are illustrated in Figures 2, 7B and 7C: when the prices are low, no compensatory change in frequency is required, and thus the derivative equals zero. When the prices are high, the magnitude of compensatory changes is constant, and thus the derivative equals one. Over the intermediate range of prices, the size of the required compensatory change in frequency grows, and the derivative increases accordingly. In the above examples, it is impossible to know whether the frequency change for 4 s vs. 8 s condition is on the flat part of the derivative of the subjective price function without testing higher prices because determining the flat part of the function requires having at least 2 frequency changes that are equal. In the above example, the frequency change for the 2 s vs. 4 s condition and 4 s vs. 8 s condition are not equal, therefore one can conclude that the 2 s vs. 4 s condition is not on the flat part,

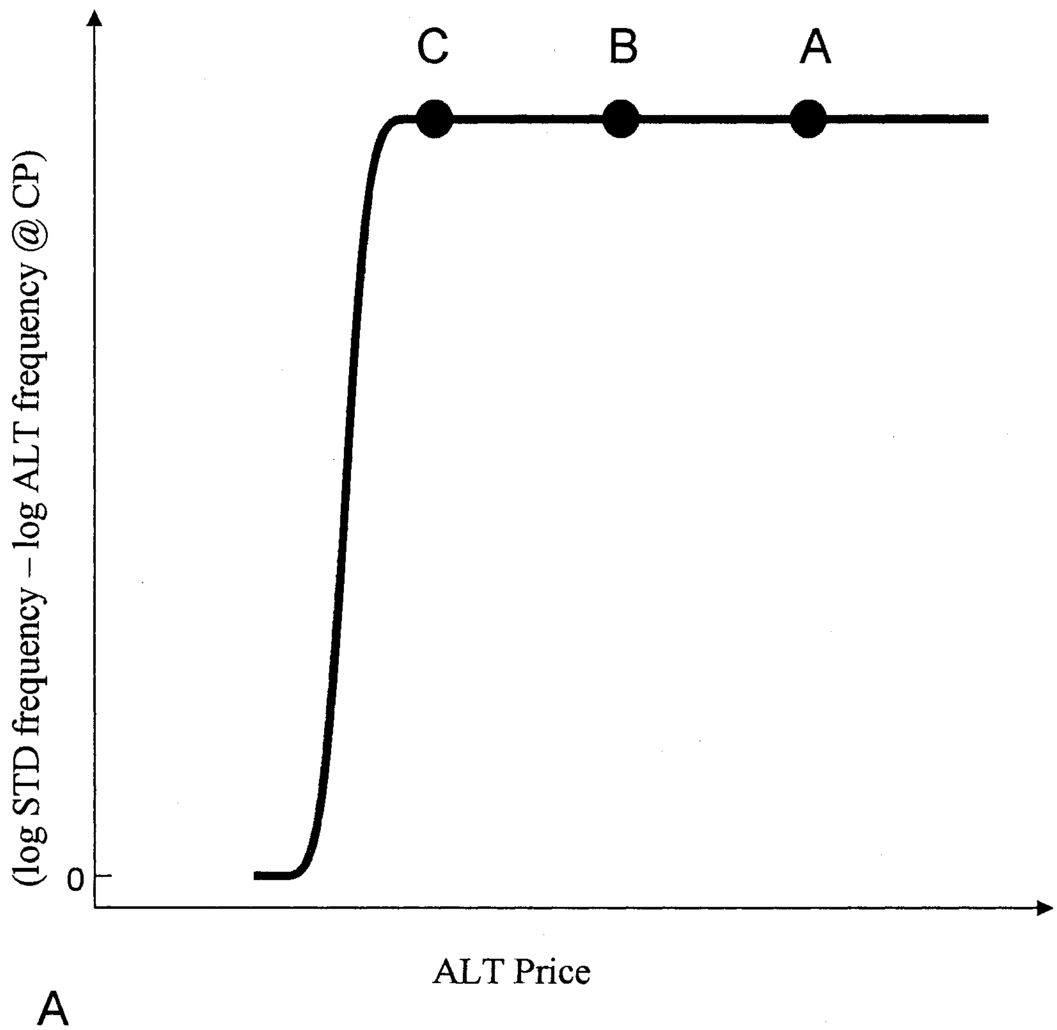


Figure 7A. The derivative of the subjective-price function is roughly analogous to the frequency change required to compensate for a change in price. If the frequency changes for all three conditions in the example illustrated in Figure 6 were equivalent, then all three points that denote the conditions would be on the flat part of the function, representing the scalar range.

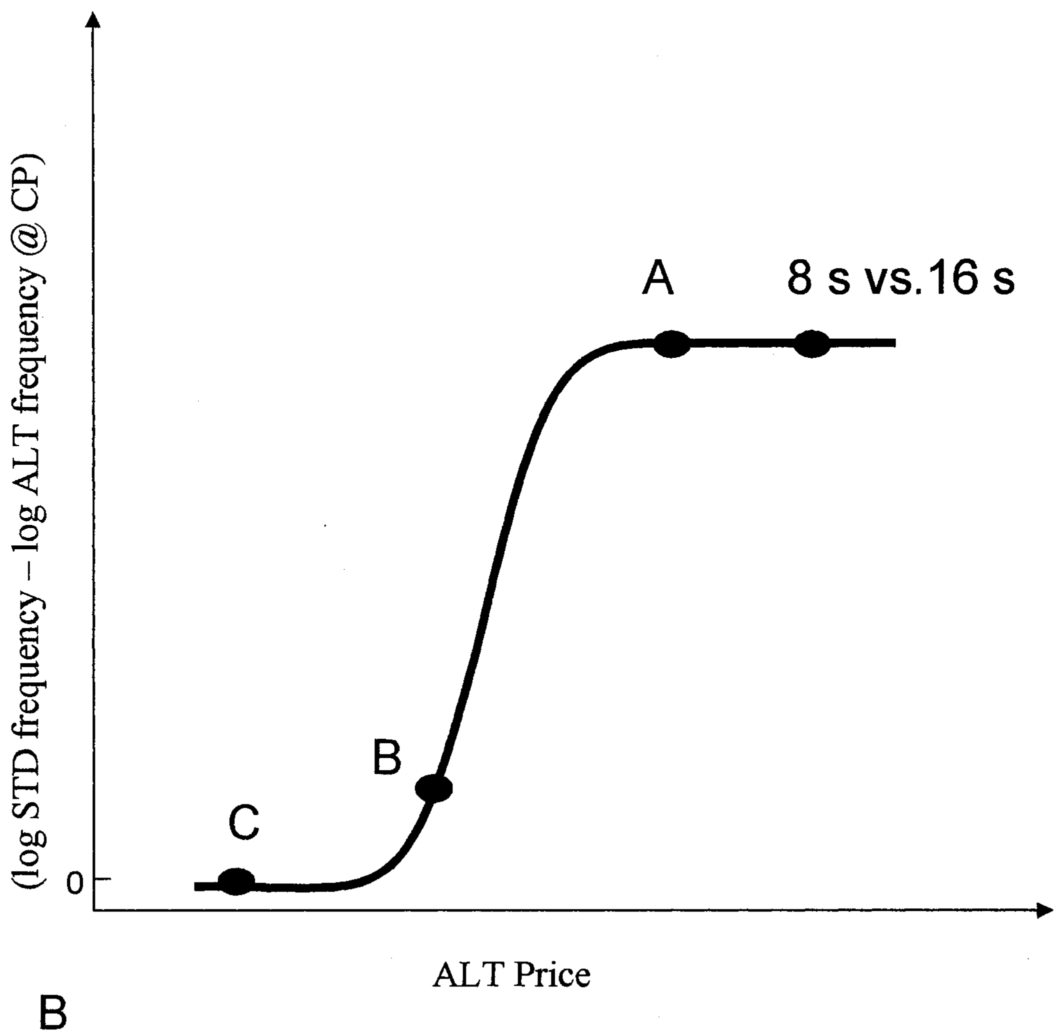


Figure 7B. Here, Condition A (4 s vs. 8 s) is on the flat part of the curve (2nd flat region) if the next condition, 8 s vs. 16 s has an equivalent frequency change. Condition B (2 s vs. 4 s) is on the growth part of the curve because the frequency changes in condition B and Condition A differ (rate of change is not constant). Condition C (0.5 s vs. 1 s) shows no frequency change and is therefore at a frequency change of 0 on the curve.

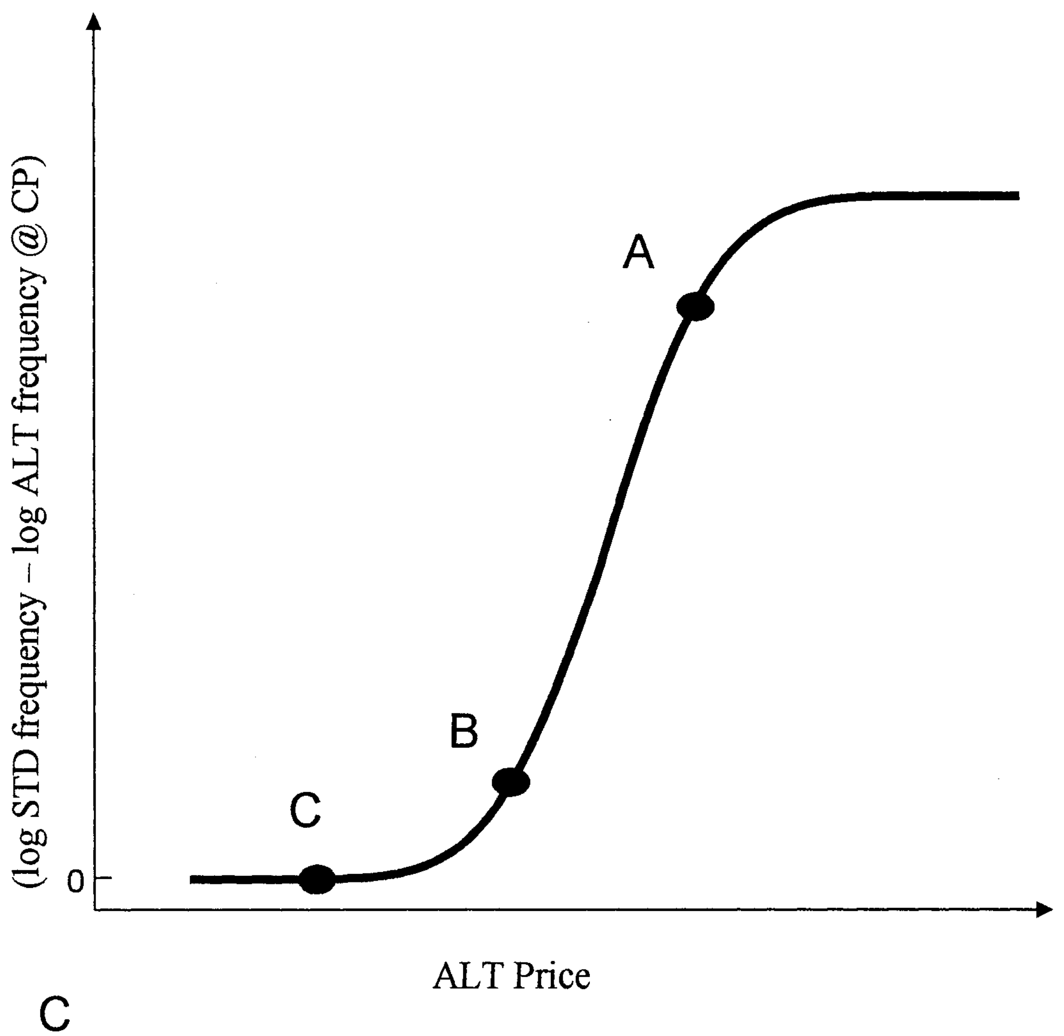


Figure 7C. Here, Condition A (4 s vs. 8 s) is on growth part of the curve if the next condition 8 s vs. 16 s has a greater frequency change. Condition B (2 s vs. 4 s) is on the growth part of the curve because the frequency change in Condition B is less than that of Condition A. Condition C (0.5 s vs. 1 s) shows no frequency change and is therefore at a frequency change of 0 on the curve. The 8 s vs. 16 s condition could either be on the growth part or flat part (2nd flat region) of the curve depending on the frequency difference in the next condition at even higher prices.

but on the growth part of the curve. The 4 s vs. 8 s condition would be on the flat part of the curve (Figure 7B) if another condition (8 vs. 16) were found to have the same frequency difference. If the frequency difference in the 8 s vs. 16 s condition were larger than the 4 s vs. 8 s condition, then the 4 s vs. 8 s frequency change would be on the growth part of the function (Figure 7C).

A limitation of the above experiment is that compensatory frequency changes as a function of price changes is only roughly analogous to the derivative of the subjective-objective price function. As stated previously, payoff is equivalent to the ratio of the reward intensity of the electrical stimulation to the price of the stimulation train. According to the definition of payoff, the rate of change of subjective price given a change in objective price can be estimated by obtaining the reward intensity required to compensate for differing prices of the rewards presented by the two levers. In this experiment, frequency rather than reward intensity was measured. Over a wide range, increasing the frequency increases reward intensity. However, the psychophysical mapping function is sigmoidal in shape and thus a given ratio of frequencies does not generally correspond to the same ratio of subjective reward intensities. To get around this problem, the reward-growth function relating reward intensity and stimulation frequency for each rat would have to be measured. This function has previously been estimated (Hamilton, Stellar, & Hart, 1985; Mark & Gallistel, 1993; Arvanitogiannis, 1997; Mullett, 2005) but in the present experiment, the reward-growth function was not measured because deriving both the subjective-price function and reward-growth function is lengthy and the lifespan of a rat is short. Therefore, these compensatory frequency changes obtained in this experiment are not directly equivalent to compensatory reward intensity changes.

Experiment II: Directly estimating the subjective-price function using conjoint measurement

One way around the problem of not having the function that translates stimulation frequencies into reward intensity is to use a more direct approach such as conjoint measurement. Conjoint measurement is concerned with the ordinal properties of the variables rather than their measurement along a ratio-scale. Thus, the actual quantitative association between reward intensity and frequency of stimulation need not be known and the only aspect required here is knowing that a given high frequency is more rewarding than a given low frequency. This ordinal scale is then used to mark off equal increments on another scale. These equal increments are then used to measure numerically the variable of interest. The power of this measurement strategy is that it converts ordinal evaluations into interval scaled output. Specifically, the present experiment uses a fixed ratio of subjective reward values to mark off equal increments of subjective price which are then used to measure the corresponding increments of objective price along a range prices. The use of conjoint measurement will become clear as the methods and rationale behind this experiment are laid out.

The goal of the second experiment was to directly estimate the subjective-price function, rather than the derivative of the function. A dual-operant paradigm was used, but the method employed was a variation of the first experiment. The first experiment measured the frequency changes that compensate for given price changes, whereas this experiment measured price changes that compensate for a given frequency change. Both of these experiments are conducted under the assumption that payoff equals the ratio of reward value to subjective price. The second experiment complements the first because the compensatory frequency changes and compensatory price changes are measured in the same rats. Developing this function in two ways allows us to compare the reliability of the methods.

In this paradigm, the ALT lever presents a series of prices, and the STD lever presents a price that does not change throughout the session. The STD frequency of stimulation is set to the STD frequency used in the previous experiment, and the ALT frequency is always set to a given value greater than the STD frequency (e.g. 0.1 common logarithmic units greater) throughout the experiment (Figure 8). The same ALT and STD frequency values are used in all conditions of this experiment. The CP denotes the ALT price at which the animal spends equal time pressing both levers.

It is crucial to note that the two frequencies delivered by the ALT and STD levers, respectively, do not vary across the different conditions of the experiment. Each of these frequencies is expected to produce a reward of a given intensity. These same two frequencies across conditions imply that the same two reward intensities are used. According to the definition of payoff (reward value: subjective price), the animal can compensate for this difference between two reward intensities in order for the payoffs on the two levers to remain equal by trading off the subjective price it pays. The central idea is that because the two differing reward values are always presented, the subject will always subjectively make the same proportional change in subjective price to compensate for the differing reward intensities no matter what price range is being tested. Therefore,

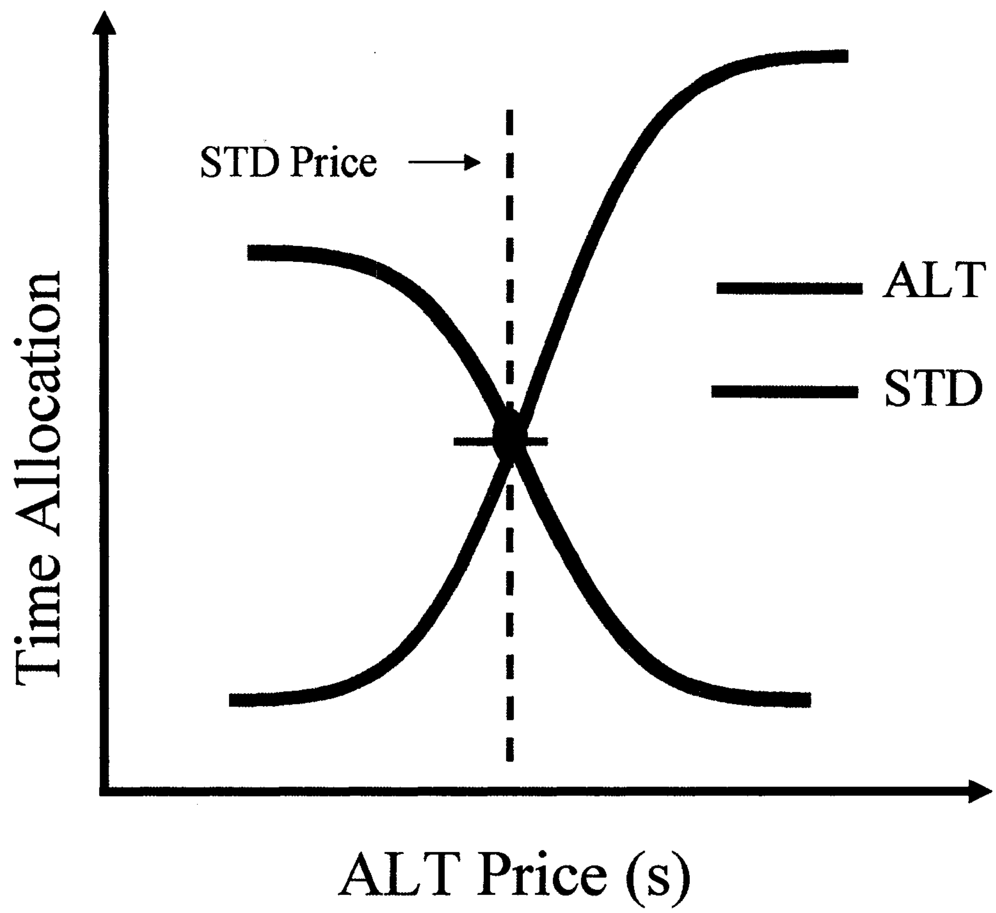


Figure 8. In a dual-operant paradigm, the animal is offered a choice between two levers. The standard (STD) lever delivers a train of electrical stimulation that is set to a price that does not change throughout the session.. The alternate (ALT) lever presents a series of prices that vary from trial to trial. The ALT frequency and STD frequency remain constant throughout the experiment such that the ALT frequency is set to a given amount (0.1 log units) greater than the STD frequency. When the rat allocates equal time to pressing both levers, the ALT price (experimentally derived) is represented by the blue dot or cross-point (CP).

it does not matter what the value is of the subjective price change, (nor can it be measured directly because it is an internal variable). The important idea is that the subjective proportional price changes are always the same. On the other hand, the objective price changes the animal uses to compensate for the differing reward intensities are thought to vary throughout the tested price range because the objective-subjective price relation is thought not to be scalar across the whole range, namely, at low prices.

In the following example, the ratio of the two frequencies is 0.1 common logarithmic units. These frequencies are then translated into the rat's subjective reward intensity by its internal reward-growth function represented by RG. The actual values of the reward intensity are not needed because they are constant throughout all conditions of the experiment. The subjective price, the rat's internal value of the price set by the experimenter, is denoted as h(x seconds) where h is the function translating subjective price into objective price and x is the objective price. The goal is to empirically determine x inside the function $h(\text{x seconds})_{\text{ALT}}$, the objective price of the ALT train regarded by the animal as the value required for the payoffs of both levers to be equal. The two frequencies and the price of the train triggered by the STD lever (2 s in this example) are set by the experimenter.

$$\frac{\text{Reward Intensity}_{STD}}{\text{Subjective Price}_{STD}} = \frac{\text{Reward Intensity}_{\text{ALT}}}{\text{Subjective Price}_{\text{ALT}}}$$

$$\frac{\text{RG(50 Hz)}_{STD}}{h(2\text{ s})_{STD}} = \frac{\text{RG(63 Hz)}_{\text{ALT}}}{h(\text{x s})_{\text{ALT}}}$$

$$\text{x} = h(4\text{ s})$$

objective proportional price change = 2

subjective proportional price change = z

In this case, in order for equivalent payoffs to occur on both levers, the objective price of the train triggered by the ALT lever is 4 s, thus the proportional objective price change has doubled. Because the same reward intensities are always presented throughout the experiment, the subject will always subjectively make the same proportional change in subjective price to compensate for the difference in reward intensity no matter what price range is tested. This subjective proportional price change can be referred to as z.

At an objective price of 8 s, the same subjective proportional price change will occur if the two reward intensities remain the same as the first condition. The same objective proportional price change will occur as above if the subjective-objective price relationship is scalar along the tested range (and the same two frequencies are used).

$$\frac{\text{RG}(50\text{ Hz})_{STD}}{h(8\text{ s})_{STD}} = \frac{\text{RG}(63\text{ Hz})_{\text{ALT}}}{h(\text{x s})_{\text{ALT}}}$$

x = 16 s

objective proportional change = 2

subjective proportional change = z

The objective price of the train triggered by the ALT lever at payoff is 16 s, thus producing an objective proportional change of a doubling.

What happens along the non-scalar range of prices? In the following example the STD price is set to 0.25 s, and the reward intensities remain the same as above.

$$\frac{\text{RG(50 Hz)}_{STD}}{h(0.25\text{ s})_{STD}} = \frac{\text{RG(63 Hz)}_{\text{ALT}}}{h(\text{x s})_{\text{ALT}}}$$

x = 4 s

objective proportional change = 16

subjective proportional change = z

Here the objective proportional change is found to be 16. It is important to remember that although the objective proportional change differed from what was determined in the previous examples, the subjective proportional change is still the same (z) because the reward intensities are the same. The above example illustrates that different ratios of objective prices can translate into the same ratio of subjective prices. Even though the subject is always making the same subjective proportional change, differing objective proportional changes occur due to the breakdown of the scalar price relationship.

To summarize, the present experiment measures the objective proportional changes along a range of prices that correspond to equal subjective proportional changes. The corresponding objective proportional price changes will not generally be equivalent to each other because objective prices may not always be equivalent to subjective prices (remembering the main hypothesis, when objective prices are very low the subjective-price function is thought not to be scalar). The following sections describes in more detail the methods used to obtain the compensatory objective price changes over a considerable price range, 0.25 s to approximately 20 s.

Experiment II: Obtaining the objective compensatory price changes

As stated earlier, the variables in the definition of payoff, reward value and subjective price are internal. It is important to remember that the reward value is manipulated by the frequency of stimulation; the subjective price is manipulated by setting the objective price.

In the first condition, the STD objective price is set to 0.25 s. The frequency of the train triggered by the ALT lever is set to a value (i.e. 0.1 log units) greater than that of the STD lever. The CP is the ALT price at which the subject spends equal time pressing both levers. Preference for either of the levers reflects payoff, therefore, equal preference on both levers reflects equal payoff:

$$\frac{\text{Reward Intensity}_{STD}}{\text{Subjective Price}_{STD}} = \frac{\text{Reward Intensity}_{\text{ALT}}}{\text{Subjective Price}_{\text{ALT}}}$$

It is the ALT price at the CP that is experimentally derived because the frequencies presented on the two levers and the price of the STD train are set by the experimenter. It is predicted that there will be a rightward shift of the CP. This shift indicates the proportional increase in the objective price required to compensate for a given stimulation frequency ratio. For example, if the STD frequency value is set to 50 Hz and price of 0.25 s and the ALT is 63 Hz, the objective price of the ALT required to compensate for the 0.1 log unit frequency difference can be determined experimentally by finding the point of equipreference (CP). The required compensatory proportional change is the ratio of the price of the ALT train at the CP to the price of the STD. Because we know that the ALT frequency is greater than the STD frequency, the directional effects can be predicted: in order to keep payoffs constant, the price of the ALT would be raised as well, thus, producing a rightward shift:

$$\frac{RG(50\text{ Hz})_{STD}}{h(0.25\text{ s})_{STD}} = \frac{RG(63\text{ Hz})_{\mathrm{ALT}}}{h(\text{x s})_{\mathrm{ALT}}}$$

Here, in order for payoffs to be equal, the price of the train triggered by the ALT lever would be greater than 0.25 s.

A less rewarding (controlled by manipulating frequency), subjectively cheaper (controlled by manipulating the objective price) train of stimulation has the same payoff as a more rewarding more expensive train of stimulation. The objective is to determine the price of the more rewarding stimulation (ALT) that makes its payoff equal to that of the STD.

To summarize, the first step is to measure the compensatory price change required by the rat in order for payoffs of the ALT and STD levers to be equal. It is assumed that the payoffs are equal when the rat spends equal time holding down the STD and ALT levers (this occurs at the values of the CP). The experimenter sets the frequencies triggered by the ALT and STD lever, and the price of the train triggered by the STD lever. The ALT price at the CP is then empirically determined. The proportional price required to offset the frequency difference can be determined by calculating the ratio of the experimentally derived ALT price at CP to the experimenter-set STD price.

In the next conditions of the experiment, the STD price is set to the ALT price at the CP determined in the preceding condition and a compensatory proportional price change is measured as above. Setting the STD price to the ALT price at the CP experimentally derived in the pervious condition allows for the objective intervals to be measured continuously along a range of prices (0.25 s to about 20 s) in steps that all correspond to the same increments of subjective price. The next conditions of the experiment are done in the way described above, setting the price of the STD to the price of the ALT at the CP in the previous condition until the STD is about 20 s. This method measures the size of the objective proportional changes spanning from very low to high prices that correspond to equal increments of subjective proportional changes. Exactly how the subjective-price function is derived will be elaborated on later. The method for this experiment is illustrated in Figure 9. The predictions for this experiment compared to the first are described below.

Experiment II: Directly estimating the subjective-price function: predictions

Two major predictions were made in Experiment II. First, it is predicted that at low prices, the compensatory price shifts for a given frequency ratio will be greater than at high prices. This prediction is similar to that of the first experiment in which the compensatory frequency change is measured. In the first experiment, at low prices, the proportional frequency change is predicted to be small because rats presumably will not interpret very small prices as significantly different and therefore will not need a large compensatory frequency change. In the second experiment, a large compensatory price shift is predicted at low prices as compared to high prices, for the same reason: low subjective prices are thought to be equivalent to each other as illustrated by the flat part of the proposed subjective-price function in Figure 1. This flat region demonstrates that low objective prices (0.1 to approximately 1 s in Figure 1) are all equal to the same

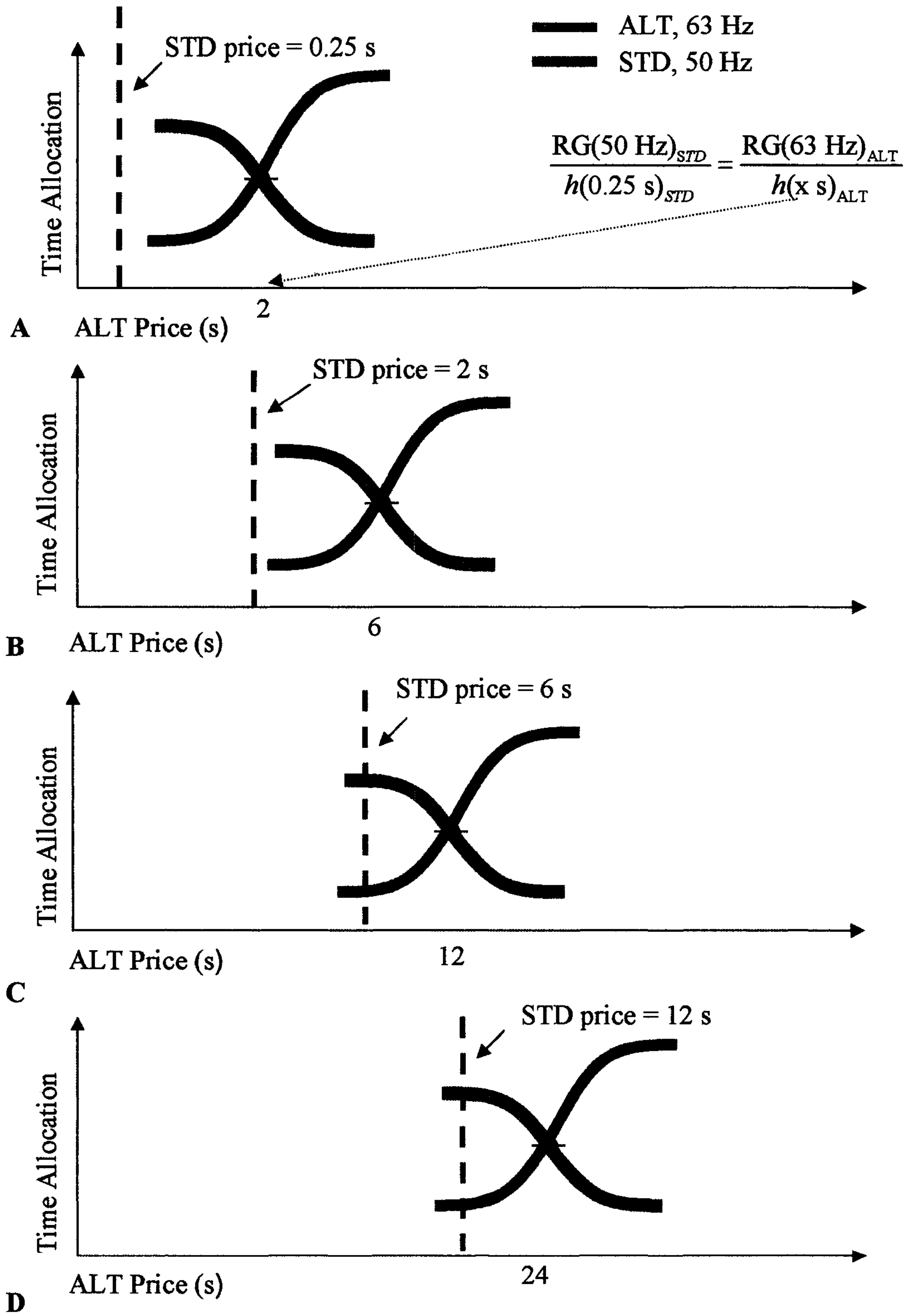


Figure 9. In the first condition (A), the STD price is set to 0.25 s and the rat makes a compensatory price change reflected in the shift of the CP, the ALT price at CP is 2 s (an 8-fold objective price change). In the second condition (B) the STD price is set to the previously derived CP, 2 s, and the new ALT price at CP is 6 s (3-fold objective price difference). In the third condition (C), the STD price is set to 6 s, and the new ALT price at CP is 12 s (2-fold difference). In the fourth condition (D), the STD price is set to 12 s and the new ALT price at CP is 24 s (again a 2-fold difference).

subjective price, therefore these low objective prices are considered to be equivalent to each other. The rat will only interpret a price change as meaningful at higher prices where the function begins to become non-flat (or grow) as illustrated by the bent region of the subjective-price function in Figure 1 that occurs from approximately 1 s to 10 s. In other words, at higher prices, a compensatory objective change such as an objective doubling corresponding to a subjective price change, z, will not be the same objective change seen at low prices even though the rat is always subjectively making the same subjective price change, z. Instead, the objective price change required to make a subjective price change, z, will be larger at low prices because low objective prices are thought to be subjectively equal each other (represented by the flat region of the function). Consequently, an objective doubling at these low prices is not interpreted by the animal as a change.

The following is a concrete example of the prediction above. If the STD price is 5 s and the rat makes a compensatory change such that the ALT price at CP is 10 s, an objective price doubling has occurred. An objective doubling, a STD price set to 0.25 s, producing an ALT price at CP of 0.5 s is not what is expected at low prices. This objective doubling at low prices would probably not occur because it is predicted that 0.25 s and 0.5 s are considered to be equal to the animal. To the subject, an objective price change of 0.25 s to 0.5 s is not considered a subjective change because 0.25 s and 0.5 s lie on the flat region of the subjective-price function in Figure 1 and are therefore interpreted as the same. The animal will only perceive an objective price change along the range of objective prices that are out of the flat region of the subjective-price curve, when objective prices begin to be interpreted differently from each other. In Figure 1, the function begins to bend at around 1 s, perhaps an objective price change of 0.25 s to 2 s (in which 2 s lies on the bent region) would be subjectively equal to a doubling seen at higher prices.

The second prediction is that past a certain price along the high range of prices, the objective compensatory price changes offsetting the constant ratio of reward intensities will be equivalent to each other. This equivalent objective compensatory price change occurs along the range of prices in which subjective and objective prices change at the same rate (scalar relationship). The same subjective compensatory price offsets the two differing reward values, therefore, along the scalar range, the corresponding objective price changes are thought to be equivalent as well. Equal compensatory price changes will not occur when the relation between objective and subjective prices is not scalar as described above. This prediction is analogous to the prediction in the first experiment, that along the range of high prices, the compensatory frequency change will be equivalent because the objective-subjective function is scalar, and therefore the same proportional frequency change would be required to compensate for equivalent proportional changes in price.

A simulated subjective-price function derived by these methods is plotted in Figure 10. Figure 9 shows hypothetical experimental conditions for a subject. In the first condition (A), the STD price is set to 0.25 s and the rat makes a compensatory price change reflected in the shift of the CP, the ALT price at CP is 2 s (there is an 8-fold objective price change). In the second condition (B) the STD price is set to the previously derived CP, 2 s, and the new ALT price at CP is 6 s (3-fold objective price difference). In the third condition (C), the STD price is set to 6 s, and the new ALT price

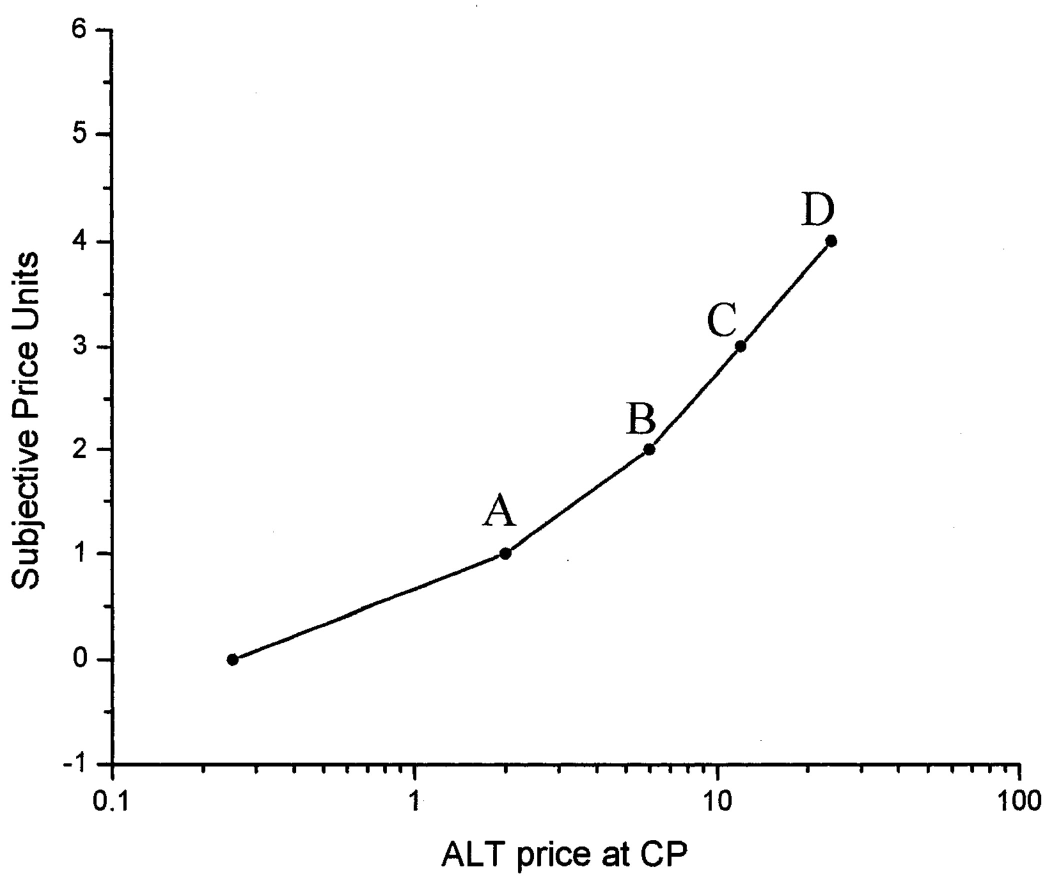


Figure 10. The analogue of the subjective-price function. The subjective price units are equally spaced, and are plotted as a function of the log ALT price at the CP. In this example, the relation between objective and subjective price becomes scalar after 6 s. That is, equal compensatory price changes occur after 6 s. Before 6 s, the increments of objective price are unequal to each other, and therefore the relation between subjective and objective price is not scalar at these low prices. The letters denote the ALT price at CP to their corresponding conditions in Figure 9.

at CP is 12 s (2-fold difference). In the fourth condition (D), the STD price is set to 12 s and the new ALT price at CP is 24 s (again a 2-fold difference). Figure 10 plots the results of this experiment. Plotted on the y-axis of the function are the "subjective price units". The actual values of these subjective price units are arbitrary. The key idea is that these units are equally spaced on the graph because they all correspond to the same difference in subjective price that offsets the ratio of reward intensities produced by the ALT and STD trains. Plotted on the x-axis are the corresponding objective prices, specifically, the ALT price at the CP in each of the four conditions of the experiment. The first point is not experimentally derived, it is 0.25 s, arbitrarily set to 0. The second point on the curve is the first experimentally derived CP in Condition A, 2 s which corresponds to subjective price unit 1. The third point is the CP in Condition B, 6 s which corresponds to subjective price unit 2. The fourth point is the ALT price at CP in Condition C, 12 s which corresponds to subjective price unit 3. The fifth point is the ALT price at CP in Condition D, 24 s which corresponds to subjective price unit 4. A scalar relation between subjective price units and objective price (represented as the ALT price at CP) occurs after 6 s because equal proportional price changes, from one ALT price at CP to the next ALT price at CP occurs after this price (as seen as an equivalent proportional price difference in Condition C and D, a doubling).

The function described above illustrates the use of conjoint measurement in the present experiment, and its rationale will be further elaborated on in the Results section. Conjoint measurement uses an interval on one scale to mark off equal increments on another. Here, a fixed ratio of subjective reward values is used to mark off equal increments of subjective price units. These subjective price units are then used to measure the corresponding objective price changes.

An important advantage of using this method for estimating the subjective-price function in this experiment compared to Experiment I is that the frequency values triggered by the ALT and STD levers remain the same throughout all conditions of the experiments. The definition of payoff involves reward value and not the frequency of stimulation. It is incorrect to assume that the frequency of stimulation directly translates directly into reward value as discussed above. However, because only two frequencies of stimulation are used, it is correct to make the claim that two differing reward values are presented. The actual magnitudes of these reward values do not matter because they are always constant in the equation for payoff. The calculation of the compensatory price change does not take into account the actual reward magnitudes: it is defined as the ratio of the two prices on both levers at the CP. Therefore, the important feature in this experiment is that only two frequencies are presented which implies that only two reward intensities are presented.

The above methods allowed us to see where the relation between objective and subjective price breaks down. Experiment I and Experiment II enabled the development of the analogue of the subjective-price function in two complementary ways.

Method

Subjects

The subjects were 6 male Long Evans rats that weighed between 300g and 400g and ranged from 4 to 5 months at the time of surgery. They were housed individually in plastic 'shoebox' cages and had unlimited access to food and water. A reverse light cycle was in effect.

Apparatus and materials

The test boxes have the following dimensions: 34 cm x 23 cm x 60 cm. The boxes had three Plexiglass walls with a hinged Plexiglass door on the front of the box. Two retractable levers (1.5 cm x 5 cm) were located in the center of the right and left walls, 10 cm above the wire-mesh floor.

Stimulating electrodes were constructed from 000 stainless steel insect pins. The insect pins were insulated with Formvar to within 0.5 mm of the tip. The electrode assembly consisted of the attachment of the end of the insect pin to a male Amphenol pin; the blunt end was soldered to a male Amphenol connector. The Amphenol pins of 2 electrodes were inserted into an externally threaded, nine-pin connector and cemented with dental acrylic to 6 jeweller's screws embedded in the skull. The skull screws served as the anode. Three female Amphenol pins inserted into a 9 pin plug, attached to a cable were inserted into the male amphenol pins. This cable was attached to a receptacle which was connected to the stimulator.

Surgical procedure

A subcutaneous injection of 0.05 mg of atropine sulfate was given prior to surgery in order to reduce bronchial secretions. Ten minutes later, the rats were anesthetized by means of an intraperitoneal injection of 65 mg/kg of sodium pentobarbital or administration of isofluorane. To confirm that the level of anesthesia was sufficiently deep, the tail was pinched 15 min after the sodium pentobarbital was injected or 5 min after isofluorane was given. Once the rat no longer responded to pinching, the surgery began. The rat was mounted into a stereotaxic frame to secure the head. An incision was made across the scalp, and the edges of the skin from the incision were retracted with hemostats. Pilot holes were drilled for the six jeweller's screws that served as anchors for the electrode assembly. Holes were drilled in the skull over the stimulation targets, which are 2.8 mm posteriour to bregma, 1.4 mm lateral to the midline and 8.3 mm ventral from the dura matter according to the Paxinos and Watson (1998) atlas. The stimulation electrodes were lowered into place using standard stereotaxic manipulators. Dental acrylic was used to secure the electrode and connector to the screw anchors and skull. Buprenorphine (0.17 ml/kg) was administered after surgery as an analgesic. Rats were given a 1 week recovery period after surgery to allow healing before preliminary testing began.

Experimental procedure

Experiment I: Frequency scaling

Screening: preliminary testing. The preliminary testing allowed the experimenter to determine whether the stimulation electrode was in the correct location. The subject was connected to the stimulator by a cable and could move freely around the test cage. Using manually operated stimulators, the rat was initially given a low-intensity train of electrical stimulation and the stimulation intensity was increased if the rat failed to approach the lever and no signs of aversion or motor-effects were observed. The rat was trained to press the lever using standard shaping techniques. Once the animal learned to press the bar, the current and pulse numbers were gradually increased to determine the parameters supporting maximal response rates for the rat.

Single-operant frequency sweeps. Once successfully shaped, subjects were transferred to an automated set-up. A single-operant frequency sweep implies that the subject is required to press a single lever (rather than having a choice of 2 as in the next conditions) in order to receive a stimulation train; the pulse frequency remains fixed within a trial but is decreased progressively from trial to trial. The frequency sweep was performed in order to find a range of frequencies that drove performance from its lower to its upper asymptotes. The schedule of reinforcement used was fVI 1 s.

One daily session (about 3 hours in duration) consisted of four identical determinations. Each determination consisted of 10 trials, 200 s each. The lever was extended at the beginning of the trial and was withdrawn for 2 s when the animal received a reward. In a determination, the frequency changed from trial to trial while the current was held constant; it was lowered in downward steps of initially 0.05 log units (e.g., 200 Hz, 178 Hz, 159 Hz, 142 Hz, 126, 112, 100, 89, 80 Hz). The log unit spacing was varied until the range of frequencies recorded consisted of several points from the lower asymptote, several along the rising portion of the function and several from the upper asymptote. The first of the ten trials in a determination was a "warm-up" trial, the frequency of the train in this trial was the same as the frequency of the train in the second trial. Data from the warm-up trial were discarded in the analysis.

After the frequency range was appropriately adjusted, animals were tested over 5 days in order to obtain 20 determinations (5 sessions x 4 determinations = 20 determinations for the single-operant frequency sweep condition). The behaviour plotted was time allocation as a function of frequency averaged over 5 sessions. Generally, a plot of the behaviour of a rat in a condition throughout the experiments consisted of the average of 20 determinations.

Dual-operant training. In the dual-operant task, the subject has the choice between 2 levers. The ALT lever delivers a frequency of a train that varies from trial to trial (termed the ALT frequency) while the STD lever always delivers a constant frequency that is halfway between the range of the highest and lowest frequencies presented on the ALT lever (termed the STD frequency).

Each daily session (approximately 3 h in duration) consisted of 4 determinations. One determination consisted of 9 trials, each trial lasting 240 s, in which the ALT frequency differed on every trial, while the STD frequency remained constant throughout the session. In order to avoid a side-bias, such that the rat would prefer one side of the box over the other, the ALT and STD levers switched midway throughout every trial. The range of frequencies presented on the ALT lever in this condition was roughly equivalent to the frequencies in the single-operant frequency sweeps condition. As before, each frequency in the frequency series of a determination was separated by a given log unit step. Frequencies were not presented in a descending order as in the Single-operant frequency sweeps condition but in a pseudo-random order in which a higher frequency trial was always between two lower frequency trials (e.g., 159 Hz, 126 Hz, 200 Hz , 112 Hz, 178 Hz, 89 Hz, 142 Hz, 100 Hz). Every determination in a session had a different pseudo-random order, but consisted of the same frequencies.

The STD and ALT lever were set to a fVI of 1 s. Both levers were extended at the beginning of the trial and were withdrawn for 2 s when the animal received a reward. Once stable data were obtained, the price of the stimulation was increased to 2 s. The structure of the sessions in subsequent conditions was equivalent to this session structure.

The animals were trained for several days in this condition; once stable behaviour was seen, data were averaged over 5 sessions. The behaviour plotted was time allocation on the ALT lever (red curve) and time allocation on the STD lever (green curve) as a function of the 8 different ALT frequencies (Figure 4) averaged over 5 sessions. The STD frequency does not correspond to the x-axis, it is a constant value that corresponds to the frequency value represented by the dotted vertical line. Similar plots were obtained for the next conditions of Experiment I.

4 s ALT vs. 4 s STD (4 vs. 4). Both the STD and ALT price were set to 4 s. This condition was a check to see if the rat has learned the task: if it learned the task under these settings, and performed without a significant side bias, the CP confidence interval should include the value of the frequency of the STD. That is, the rat should allocate equal time to working at the ALT and STD levers when the ALT frequency equals the STD frequency. After stable responding, five additional sessions were conducted and the data were averaged and plotted as above.

Condition A: 4 s ALT vs. 8 s STD (4 vs. 8). The ALT price was set to 4 s, and STD price was doubled to 8 s. The value of the STD frequency was raised from the value presented in the 4 s vs. 4 s condition. The new high STD frequency was chosen such that the rat preferred the STD lever when the ALT frequency was low (it was required that the time allocation to the STD lever was at least 0.5 when the ALT frequency was low) and the ALT lever when the ALT frequency was high. The STD frequency was raised because if the STD frequency were left the same as in the 4 s vs. 4 s condition, the rat would not work much for it at the higher price (because it is expensive and not that rewarding, the payoff is not great). In effect, the increase in STD frequency offset the increase in the STD price. This new STD frequency was used as the reference point for this condition and the remaining conditions of the experiment.

The data were averaged across five sessions and plotted as above. The deviation of the cross-point (CP) from the high frequency STD was measured thus indicating the decrease in ALT frequency that compensated for the fact that the price of the ALT trains was one half the price of the STD trains. This deviation was measured across all conditions.

Conditions B-F: The next conditions (B-F) were conducted in the same way as Condition A (4 s vs. 8 s). The pairs of prices presented are reduced by half in each subsequent condition: Condition B: 2 s vs. 4 s, Condition C: 1 s vs. 2 s, Condition D: 0.5 s vs. 1 s, Condition E: 0.25 s vs. 0.5 s, Condition F: 0.125 s vs. 0.25 s. The STD frequency was set to the same STD frequency as Condition A. After five sessions of consistent responding, the data were averaged and plotted as above.

Experiment II, Phase A: Price scaling

Price sweep training. The same subjects in Experiment I were used in Experiment II. A price sweep implies that the price of the ALT reward changes from trial to trial throughout the session.

The session structure in this condition (price sweep training) was equivalent to the session structure in the next conditions (Conditions A, B, C, D) of Experiment IIA. Each daily session (approximately 3 h in duration) consisted of 2 determinations. One determination consisted of 9 trials in which the price of the ALT train (ALT price) differed on every trial while the price of the STD train (STD price) remained constant throughout all trials. It is the STD price that differs throughout the conditions of Experiment II. In the series of ALT prices in one determination, each ALT price was separated by 0.2 log units. The range of prices was continually adjusted such that there would be 4 points above the CP and 4 points below the CP in the plot of time allocation to the STD lever and ALT lever as a function of the 8 different ALT prices across the averaged sessions. In each determination, the ALT prices were in a pseudo-random order such that a higher-price trial was always between two lower-price trials. The first trial of a determination was always a "warm-up" trial in which the ALT price was identical to the ALT price of the second trial. Data from the warm-up trial was discarded in the analysis.

The trial times in a determination were increased with the increasing ALT price because the animals require a long trial duration at high prices in order to have enough opportunities to experience the distribution of prices it encounters in the trial so that it can estimate the average price (the trial length could vary from about 60 s to about 2000 s). In a determination, the series of trial times were separated by 0.1 log units. The 0.1 log unit spacing of trials times was chosen in order for there to be a sufficient amount of time for 2 determinations.

In this condition, the ALT prices ranged from 2 s to 20 s. The STD price was set to 4 s (5 s for 2 rats); it was chosen such that it would be midway of the range of ALT prices. The STD and ALT frequency were equivalent and set to the same STD frequency used for Conditions A-F in Experiment I.

Once the rat's performance had stabilized (by visual inspection of the data), 10 additional sessions were conducted (20 determinations in total). The behaviour plotted was mean time allocation to the ALT lever (red curve) and STD lever (green curve) as a function of the 8 different ALT prices (Figure 8) averaged over 10 sessions. The STD price is represented by the dotted vertical line.

This condition was conducted with the aim of training the rat to estimate the ALT prices that changed throughout the session; it was also used as a test to determine whether the animal had learned the task: if the rat had learned the task under these parameters, and performs without a significant side bias, then the CP confidence interval should include the STD price (the dotted vertical line). That is, the rat should allocate equal time to working at the ALT and STD levers when the ALT price equals STD price and when the ALT frequency equals the STD frequency.

Condition A: Price sweep at STD price of 0.25 s. The session structure for this condition and the subsequent conditions in Experiment II was similar to that of the price sweep training condition. The main difference was that the ALT frequency was set to 0.2 log units greater than the STD frequency. The STD frequency was set to the same STD frequency in Condition A (which is the STD frequency used in Experiment I). (For 2 subjects, the ALT frequency in this experiment was set to that of the STD frequency in Experiment I and the STD frequency in this experiment was set to 0.2 log units less than the ALT frequency. The important idea is that the ALT price was always 0.2 log units greater than the STD price.)

The STD price was set to 0.25 s. The range of ALT prices was chosen and adjusted such that there would be 4 points above the CP and 4 points below the CP in the plot of time allocation to the STD lever and ALT lever as a function of the 8 different ALT prices across the averaged sessions.

After stable responding was seen and the ALT prices were adjusted appropriately, 10 additional sessions were conducted (20 determinations in total) and the behaviour was plotted as time allocation as a function of ALT prices. A rightward shift of the CP was predicted.

Condition B. The ALT and STD frequency were set to the same values as in Condition A. The STD price was set to the CP (the ALT price at which time allocation to the ALT and STD levers is equal) in Condition A. The session structure was equivalent to the one above. After 10 sessions of stable responding, the data were averaged and plotted as in Condition A.

Condition C. The ALT and STD frequency were set to the same values as in Condition A. The STD price was set to the CP in Condition B. The session structure was equivalent to the one above. After 10 sessions of stable responding, the data were averaged and plotted as in Condition A.

Condition D. The ALT and STD frequency were set to the same values as in Condition A. The STD price was set to the CP in Condition C. The session structure was equivalent to the one above. After 10 sessions of stable responding, the data were averaged and plotted as above. Not all subjects reached this condition because for some subjects, the prices were too high to support reasonable allocation to the lever.

Experiment II, Phase B: Price scaling

This experiment was identical to that of Experiment IIA except that the ALT frequency was set to 0.1 log units greater than the STD frequency (instead of 0.2 log units). Again, in this experiment, the STD price was always set to the CP from the previous condition.

Experiment III

A new subject was added to this experiment. This experiment was identical to that of Experiment IIA but differed in the schedule and the number of encounters the subject had with the reward. These changes were made to facilitate learning the ALT price and discriminating between it and the STD price. A fixed cumulative handling time (FCHT) schedule was used in which the subject was rewarded after holding down the lever for the cumulative amount of time required. That is, if the FCHT was set to 8 s, then the subject would be required to hold down the lever for a cumulative time of 8 s to obtain the reward. For example, if the subject held the lever for 2 s, released for 1 s, held again for 4 s, released and responded on the other lever, came back to the lever and held again for 2 s, the reward would be delivered because the total amount of time holding the lever since delivery of the previous reward had reached 8 s. The spacing between trial times was 0.15 log units instead of 0.1 log units in order for there to be longer trial times in the high-priced trials (longer than the previous use of 0.1 log unit spacing) so that the animal would be able to earn more reward (~ 20 rewards) at the higher prices, thus basing the estimates of time allocation on more data.

Results

Raw data

The raw data obtained were the distribution of "holds" (intervals when the lever was depressed by the rat) and "releases" (periods when the lever was extended but not depressed by the rat) during the trials. The times during the trial the animal held and released the levers and the duration of these holds and releases were recorded. A release of the lever for at least 1 s was defined as "leisure"; shorter releases were classified as a brief tap and not considered to be representative of leisure because these brief intervals are too short for the animal to be engaged in leisure activities (such grooming or exploring). During these very brief interruptions of a hold, the rat is usually standing with its paw over the lever, not engaged in other activities. Therefore, a correction was made to the data such that these very short releases were quantified as work. A hold of the lever and a release of less than 1 s was considered as "work", a release of more than 1 s was considered as leisure. The total length of time the subject held either of the levers was summed across a single trial. These cumulative hold times were then converted into proportions referred to as "time allocation" such that the amount of time the animal held either lever during one trial was divided by the total trial time. For example, if on one trial the subject held the STD lever for a total of 50 s and the trial duration was 240 s, then the proportion of time allocation for the STD lever on this trial would be 0.21 (50 divided by 240). These calculations were carried out using RS/1 (Chelmsford, MA, 1999).

The trials differed from each other in terms of the prices or pulse frequencies of the STD and ALT trains (depending on the experiment). For each condition, time allocations as a function of the 8 stimulation frequencies (Experiment I) or 8 prices (Experiment II) were averaged across 20 determinations and plotted. In other words, in a plot of the time allocation as function of frequency or price for a given condition (e.g. 1 s vs. 2 s condition), a given point represents the average time allocation across the session (20 observations) for the corresponding frequency or price.

Statistical analyses: fitting the model

After 20 determinations had been collected for each condition and after the tapping correction had been applied and time allocation had been calculated, the data were transferred to Matlab (Natick, MA, version 2006a). This program was used to fit functions to the data sets consisting of time allocation for both ALT and STD levers as a function of stimulation frequency (Experiment I) or price (Experiment II). The goal of fitting a model to the data set was to be able to derive the CP. Specifically, spline functions, functions formed by joining polynomials together at knots (interval endpoints, specifically the x-value that joins two functions) were fit to the data. These functions are useful because they offer enough flexibility to adapt to a given data set while minimizing the correlation between parameter estimates. In this case, the spline function captures the asymmetrical curvatures of the function which were thought to better represent the data than what has been used most often in the past, continuous symmetrical sigmoids. Specifically, a spline function consisting of two quadratic functions and two straight line segments (one denoting the maximum y-value and one denoting the minimum y-value) joined together by knots was fit to a curve representing responding on the STD lever (green curve) and a curve representing responding on the ALT lever (red curve).

Therefore, each curve was divided into four domains. The parameters consisted of the growth constant for each quadratic function, a set of knot values and two straight line segments for each curve. For each spline function (curve), there are 3 knots (one that joins the lower asymptote to the first quadratic function, one that joins the two quadratic functions, and one that joins the second quadratic function with the upper asymptote).

In total, there were 14 parameters in the model of time allocation to the STD and ALT levers as a function of frequency (Experiment I) or price (Experiment II) which are illustrated in Figure 11: the STD left straight line segment, the STD right straight line segment, 3 STD knots, STD growth constant 1, STD growth constant 2, the ALT left straight line segment, the ALT right straight line segment, 3 ALT knots, ALT growth constant 1, ALT growth constant 2. (In the model, 2 out of the total 6 knots are fitted parameters, ALT knot 1 and STD knot 1, the other knots are derived parameters; they are determined when the other parameters are known). The x-value and y-value of the CP was the outcome of the model, calculated after the best fitting parameters (by the method of least squares) were determined for the data set. Figure 11 displays these parameters in a plot of time allocation as a function of frequency but the same parameters were used to fit the model for time allocation as a function of price. Appendix B describes the equations for the functions. (For rats B7 and B9, a slight variation of the model above was used. A third quadratic function for the ALT curve was added because at high ALT frequencies, the function turned down slightly instead of reaching an asymptotic value as was the case for the other rats. The function turned down at high frequencies due to the aversive or inhibitory side-effects of the stimulation.)

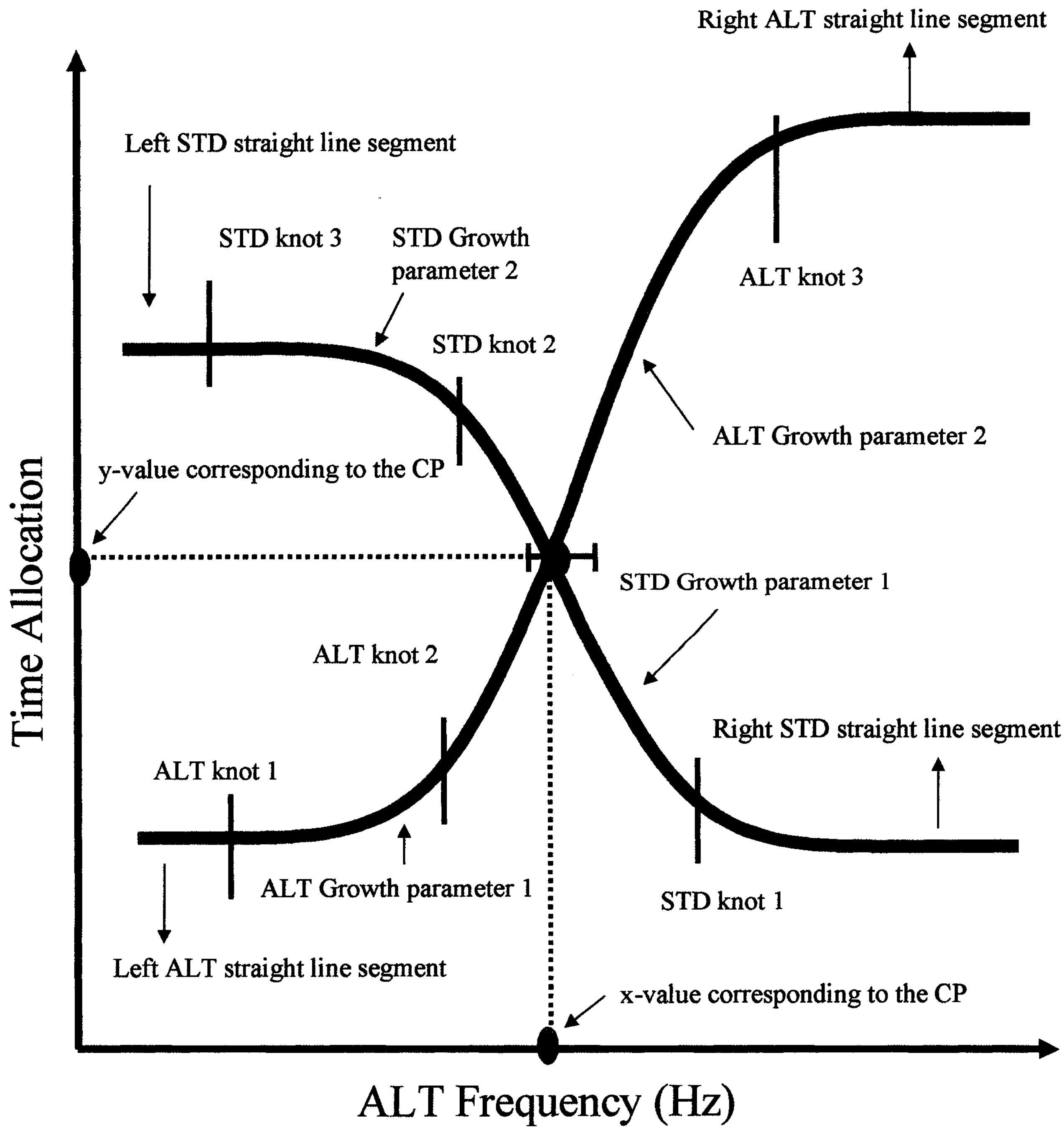


Figure 11. The 14 parameters of the model and the most important values derived from the curve-fitting procedure, the x-value and y-value of the CP.

The functions were fit to the resampled data point means (time allocation as a function of frequency or price). The bootstrap method was used because the raw data, consisting of the 20 observations corresponding to a single frequency (Experiment I) or price (Experiment II)), were not normally distributed and therefore simply averaging the data did not provide a reliable estimate of the position parameter. The data sets did not have a normal distribution because the dependent variable, time allocation, is constrained from 0 to 1. Therefore, in certain cases such as for higher frequencies, the distribution would be skewed to the left because time allocation cannot be greater than 1. The use of the bootstrap method did not require assumptions to be made about the data distributions and provided needed flexibility. For instance, this method allowed for heterogeneity of variance (heteroscedasticity) as well as asymmetrical confidence intervals which can capture the skew of distributions. Specifically, the data point means were calculated by resampling the means with replacement 1000 times and then calculating the 95 % confidence interval around the means. The best fitting parameters of the resampled data points were determined by fitting the spline functions to each set of the resampled means 1000 times and calculating the median of the parameters. The plotted functions were based on the median values parameter values because the distribution was bimodal for some of the parameters and it was thought that the median values would be a better representation of the data. Grubb's test (extreme studentized deviate) was used to detect outliers before resampling. The weighted outliers were included in the resampling routine with the use of Tukey's bisquare weighting method. (It was thought that the outliers were too numerous (therefore affecting the quality of the fit) when they were equal to or greater than 20% of the data for an individual observation (frequency or price) of a condition. In order to normalize the data and thus reduce the outliers, the raw data were altered such that time allocation at a given frequency or price was collapsed over the determinations. For example, time allocation of two observations of a frequency of 20 Hz was now represented as one observation, calculated by adding the time the animal spends working in both observations and dividing by the sum of the two trial times. In some cases, numerous outliers may have occurred because it was thought that the rat needed a greater trial time to accurately estimate the price, therefore, collapsing the determinations was in a way a method of predicting what the time allocation would have been had trial times been longer.)

Confidence interval regions (bands) were plotted around the functions, and are represented by dashed lines (Figure 12). These confidence interval bands represent the 95% confidence interval region of the 1000 functions fit to the resampled data sets. These confidence interval bands imply that 95% of the time, the resampled functions lie in this region. These 95% confidence bands were computed by determining the predicted upper and lower limits for the 95% confidence intervals (the 97.5th and 2.5th percentile) along a high density of points on the x-axis. These predicted y-values were then joined together to form a confidence interval band. This method of plotting confidence interval bands was used in order to represent the reliability of this critical estimate. Similarly, around the CP, a 95% confidence region was plotted. This region was calculated by determining the predicted upper and lower 95% confidence interval regions along a high density of points that surround the CP.

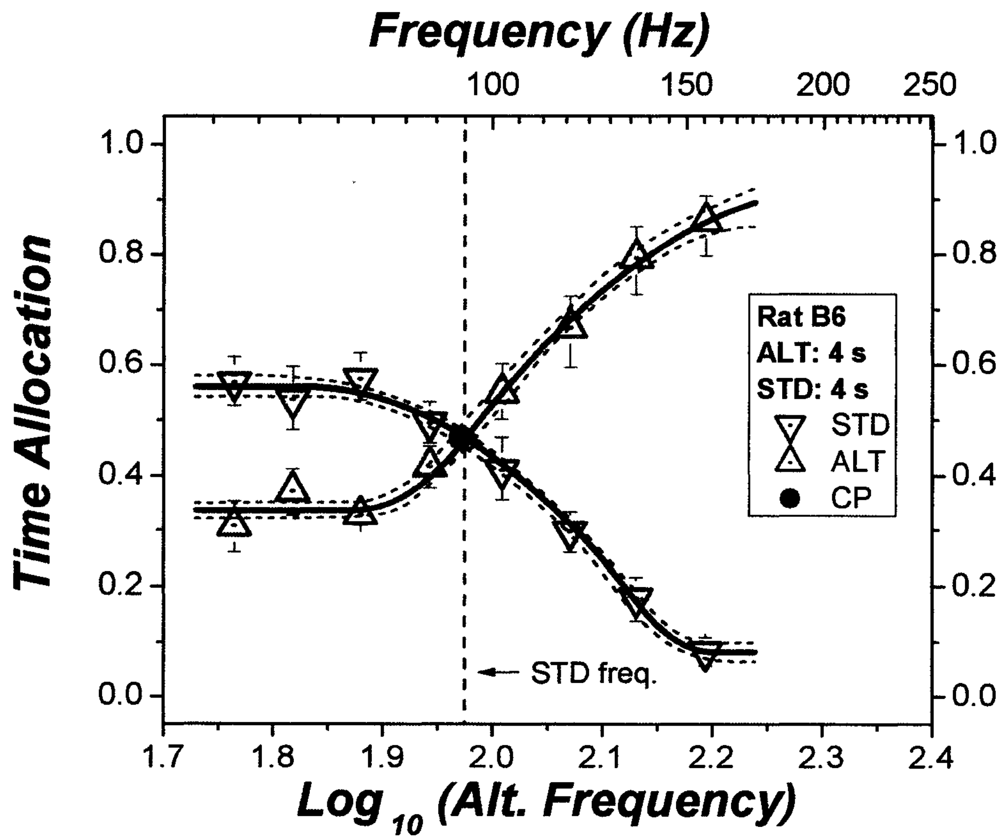


Figure 12. The 4 s vs. 4 s condition is a training condition and check to determine whether the rat had learned the task. The CP 95% CI includes the frequency value of the STD which implies that rat B6 had learned the task.

Experiment I: Individual frequency shifts

Data from 6 subjects were obtained in this condition. Five rats were tested in 6 experimental conditions (8 s vs. 4 s, 4 s vs. 2 s, 2 s vs. 1 s, 1 s vs. 0.5 s, 0.5 s vs. 0.25 s, 0.25 s vs. 0.125 s). Rat Y6 was tested in 5 conditions, all conditions except 0.25 s vs. 0.125 s. Before the first condition, the rat was trained in condition 4 s vs. 4 s in order to become familiar with the dual-operant frequency sweep paradigm at higher prices. This condition also verified whether the rat had learned the paradigm because if the price and frequency of the train triggered by the STD and ALT levers (referred to as ALT price, ALT frequency, etc.) are the same, then the rat should spend equal amounts of time on these levers. Therefore, the CP confidence interval (that denotes the ALT frequency when equal amount of time is spent on both levers) should include the frequency value of the curve for the STD lever. For 3 of the 6 rats, the CP confidence interval included the STD frequency. The CP confidence interval was very close to the STD frequency for the other 3 rats in which the confidence interval did not include the frequency value of the STD. A graph for this condition for one rat (B6) is presented in Figure 12; the graphs for the other rats in this condition are presented in Appendix A (Figure 31). Plotted in Figure 12 is the time allocated to the lever as a function of the stimulation frequency triggered by the ALT lever. The green curve corresponds to the proportion of time allotted to pressing the STD lever which delivers a frequency that is always constant (denoted by the vertical line) and the red curve corresponds to the proportion of time allotted to pressing the to the ALT lever that delivers a frequency that varies from trial to trial and is represented along the abscissa. The CP (blue dot) is the intersection of the two curves and denotes the ALT frequency value that offsets the price difference. The rat allocated equal proportions of its time to pressing the two levers levers when the ALT frequency was that of the CP. As the price pairs became smaller across conditions (Figure 13 A to E), the CP frequency shift (the displacement of the CP frequency from the STD frequency) became smaller. The CP frequency shift decreased as a function of price in all rats. The graphs for the other rats in these conditions are presented in Appendix A (Figures 32-36).

Experiment I: Frequency shift summaries

Plotted in Figures 14 to 19 are the summaries of the frequency shifts across the conditions for all of the rats in Experiment I. In theory, this function should be roughly analogous to the derivative of the subjective-price function because the frequency change that the rat makes to compensate for the differing prices is comparable to the rate at which subjective price changes in response to a change in objective price (the derivative). Plotted on the y-axis is the proportional change of the frequency of the CP with respect to the frequency of the STD. The x-axis represents the tested prices. In this experiment, two prices are used in each condition; the STD price is twice that of the ALT price. A logarithmic abscissa is used, and the models treat equal intervals along this axis as equivalent. Thus, the point plotted is the average of the two log values (geometric mean). For example, the price representing the 4 s vs. 8 s condition is ~ 5.7 s (the highest price on the x-axis). The error bars represent the 95% confidence interval around the CP data points as determined by resampling.

The first hypothesis was that as the prices decrease, the frequency changes would decrease. The data support this hypothesis: for all of the subjects, the frequency change

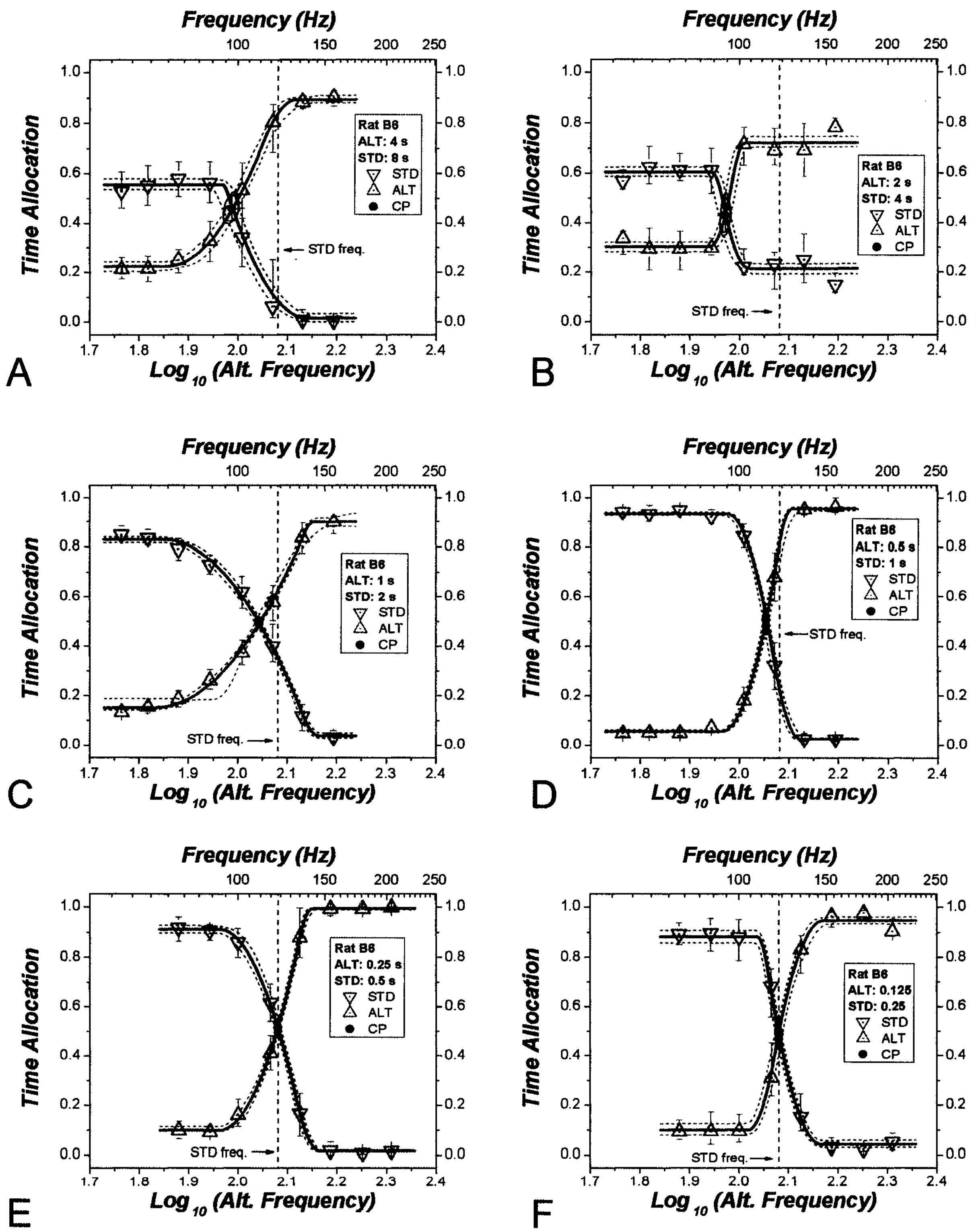


Figure 13. Graphs A-F are the results obtained for the experimental conditions. As the price pairs are decreased throughout the condition, the CP shift from the STD frequency diminishes which implies that the compensatory frequency change diminishes. This reduction in frequency occurs because small prices are thought to be subjectively similar and therefore less frequency is required to compensate for the price difference at smaller prices. Error bars represent 95% confidence intervals.

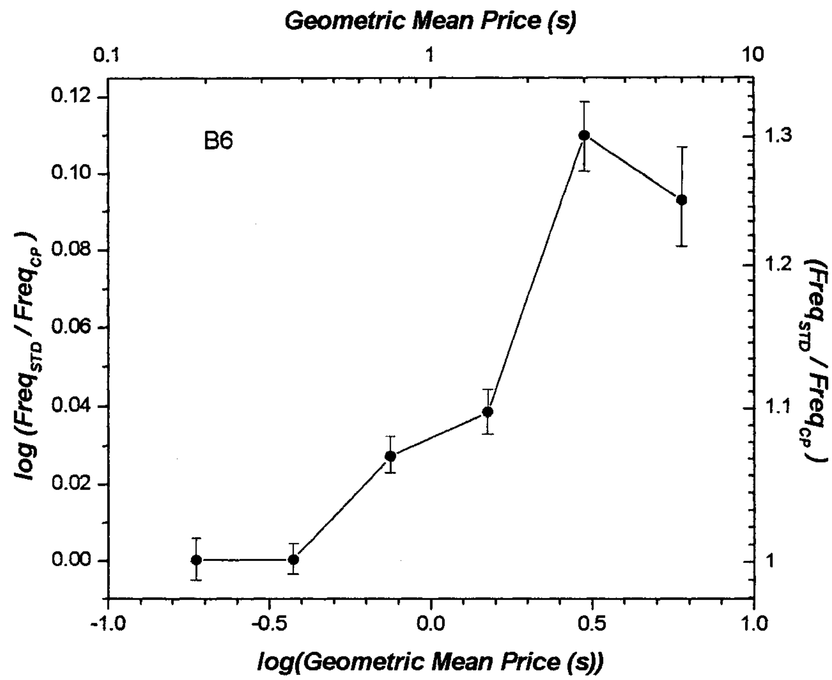


Figure 14. The compensatory frequency changes for rat B6. As prices are increased, the frequency changes increase and level-off after 2 s. Error bars represent 95% confidence intervals.

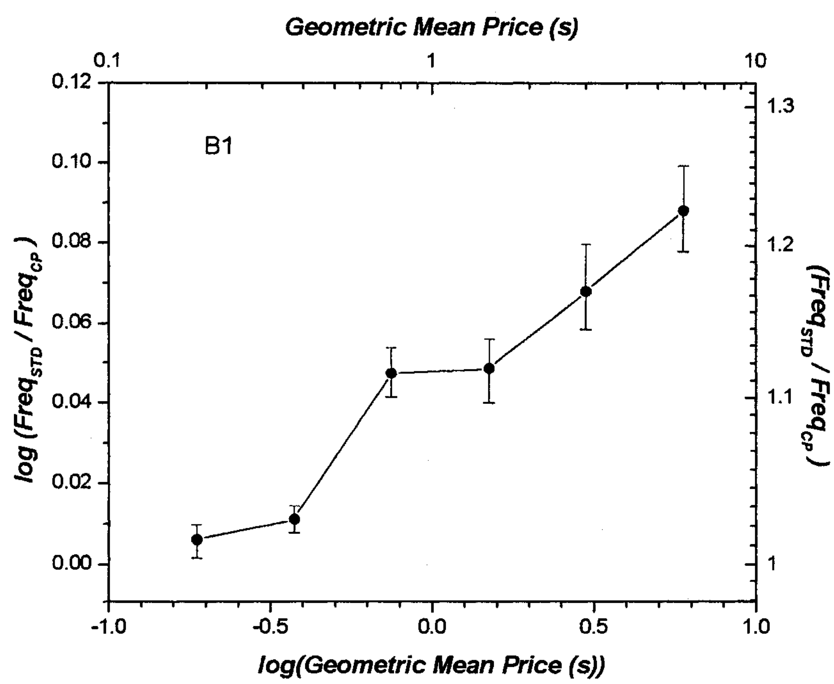


Figure 15. The compensatory frequency changes for rat B1. As prices are increased, the frequency changes increase and do not level-off. Error bars represent 95% confidence intervals.

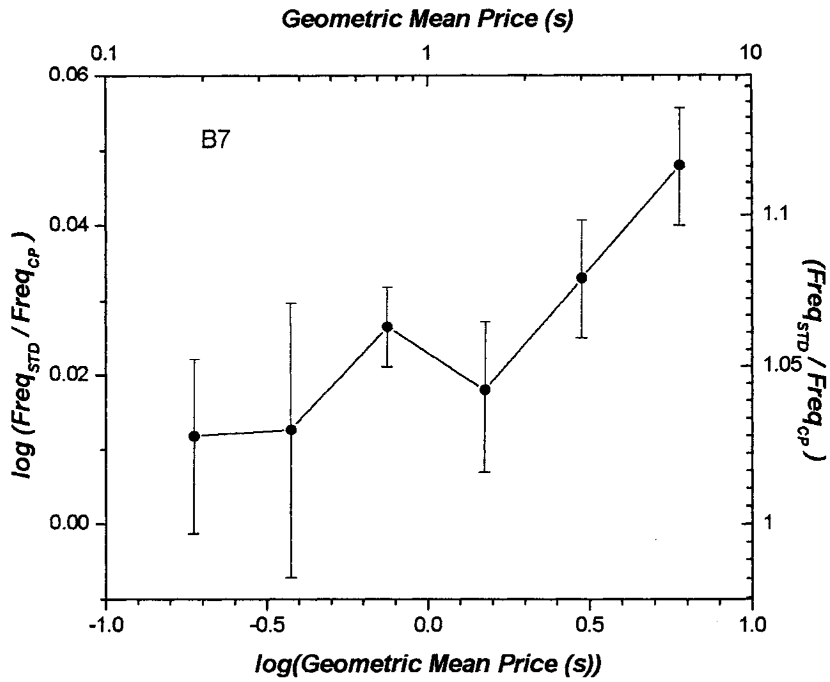


Figure 16. The compensatory frequency changes for rat B7. As prices are increased, the frequency changes increase and do not level-off. Error bars represent 95% confidence intervals.

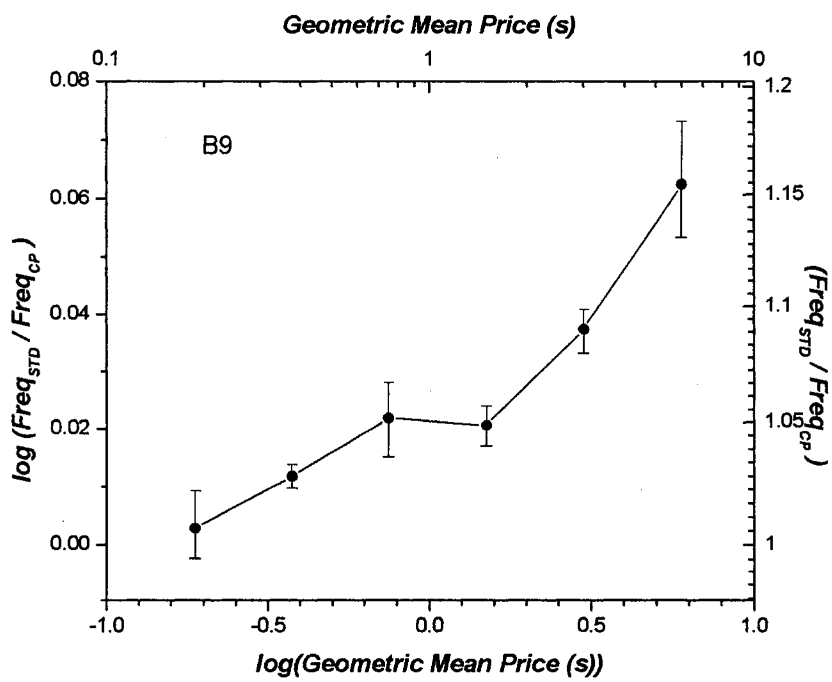


Figure 17. The compensatory frequency changes for rat B9. As prices are increased, the frequency changes increase and do not level-off. Error bars represent 95% confidence intervals.

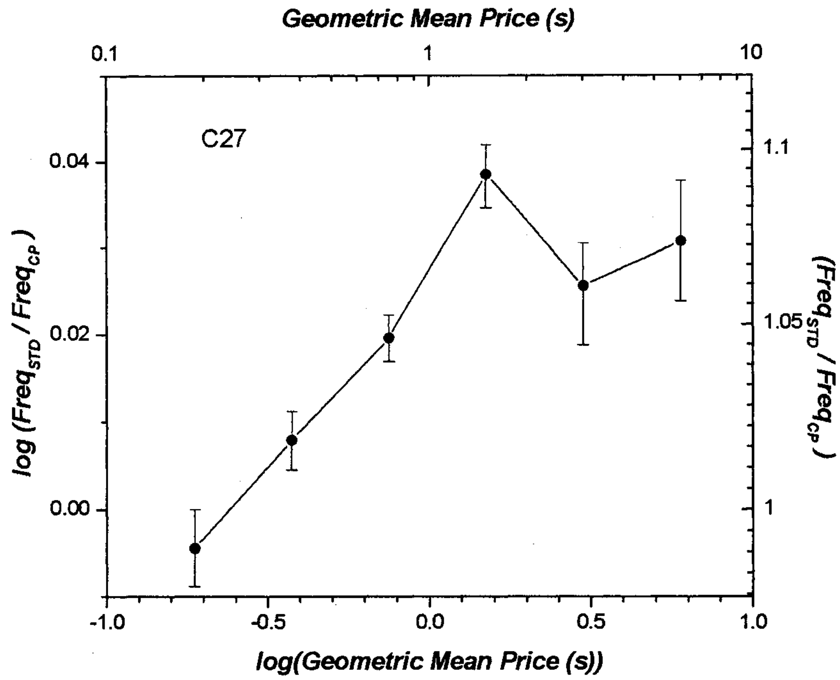


Figure 18. The compensatory frequency changes for rat C27. As prices are increased, the frequency changes increase. There is a decrease in the frequency change after about 1.5 s and then the frequency change appears to level-off after about 3 s. Error bars represent 95% confidence intervals.

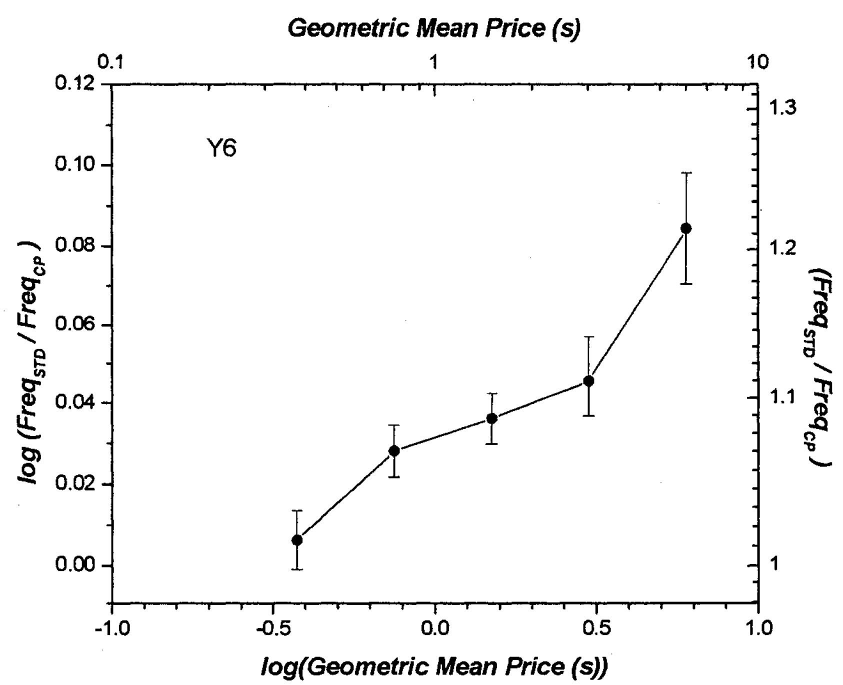


Figure 19. The compensatory frequency changes for rat Y6. As prices are increased, the frequency changes increase and do not level-off. Error bars represent 95% confidence intervals.

decreases as prices decrease. At the lowest price, ~ 0.18 s (representing 0.125 s vs. 0.25 s) the frequency change is 0 or very close to 0 for all rats. This frequency change of 0 implies that prices of 0.125 s and 0.25 s are considered to be subjectively equal to each other; no frequency change is required to compensate for a difference between these prices because subjectively to the rats, there is no subjective difference between prices this low. This function is roughly analogous to the derivative of the subjective price function, therefore, this would imply that the rate at which subjective price changes in response to a change in objective price is 0 at very low prices and increases as the prices are increased.

The second hypothesis was that as the prices increased from condition to condition, the frequency change would become constant at a certain price due to the proposed scalar relationship at higher prices. Such leveling off of the CP frequency shift was seen only in the case of one rat, B6, Figure 14. For this rat, the proportional difference is equivalent for ~ 2.8 s (2 s vs. 4 s condition) and ~ 5.7 s. For rat C27, Figure 18, the function appears to level-off after ~ 2.8 s as well, but at the ~ 1.4 s price (1 s vs. 2 s condition), the frequency difference is greater than the two higher prices. The odd results for rat C27 may be due to the very small frequency shifts in comparison to the other rats. For the other 4 rats, the frequency changes do not level-off at higher prices. Instead, the frequency changes continue to grow, they become larger as prices are increased over the tested range.

Experiment II: Individual price shifts

Data from 5 subjects were obtained in Experiment II. The same rats were used in this experiment as were used in Experiment I except for rat B1 who died after Experiment I. This experiment consisted of two phases: the first in which the frequencies delivered by both levers were separated by 0.1 log units, and the second in which the frequencies were separated by 0.2 log units. In the 0.2 log unit phase, the rats were tested in 4 conditions, and in the 0.1 log unit phase, the rats were tested in 4 to 6 conditions. In this experiment, the frequencies of the trains triggered by the ALT and STD levers remained constant while the price of the train triggered by the ALT lever (ALT price) varied from trial to trial and the STD price remained constant. The ALT price value at the CP was used as the STD price in the next condition; therefore, the price values of the STD lever are different for all rats.

Before the first experimental condition, the rats were trained in a condition in which the frequencies presented on the two levers were the same (in contrast to the 0.1 and 0.2 log unit separation in the experimental conditions) and the price of the ALT varied while the price of the STD was kept constant (4 s for most rats, 5.15 s for two rats). This condition was similar to the 4 s vs. 4 s condition in Experiment I because it was conducted so that the animal learned the paradigm of the differing prices from trial to trial. Plotted in Figure 20 is time allocation as a function of the price of the train presented on the ALT lever (ALT price). The green curve corresponds to the proportion of time allotted to pressing the STD lever for which price is always constant (denoted by the vertical line), and the red curve corresponds to the proportion of time allotted to pressing the ALT lever for which price varies from trial to trial. The CP (blue dot) is the intersection of the two curves and denotes the ALT price that offsets the frequency difference. The rat allocated equal proportions of its time to pressing the two levers when the ALT price is that of the CP. Whether the animal had learned the paradigm was verified by determining whether the 95% confidence interval (CI) surrounding the CP included the price of the STD. This inclusion of the STD price in the 95% CI implies that the animal spends equal time pressing both levers when the STD and ALT frequencies and prices are equivalent. For 3 of the rats, the CP 95% CI included the STD price, for the other 3 rats in which the STD price was outside the confidence interval, the deviation was small. Figure 20 shows the data for rat B6 for this condition in which the STD price is outside the CP 95% confidence interval (very small deviation). The graphs for the other subjects are shown in Appendix A (Figure 37).

Figures 21 and 22 present the data obtained from rat B6 for the experimental conditions. The individual price shift data for the other 4 rats are presented in Appendix A (Figures 38-45). The variable of interest is the ALT price required to offset the frequency difference of the trains triggered by the two levers which is represented by the ALT price value at the CP. Figures 21 A to D illustrate rat B6's behaviour in the 0.2 log unit phase. The CP price shift is initially large in Condition A, becomes smaller in Condition B, and then gets even smaller in Condition C, and stays almost the same in Condition D. The equivalent price shifts imply that the subjective-objective price relation is scalar along this range (after about 5 s in this case). Figure 21 A to G illustrates B6's behaviour in the 0.1 log unit phase. The CP price shift is initially large in Condition A, and as the prices increase, the shift gradually becomes smaller and appears to level off (subjective-price function is scalar) after Condition E (after about 5 s as well).

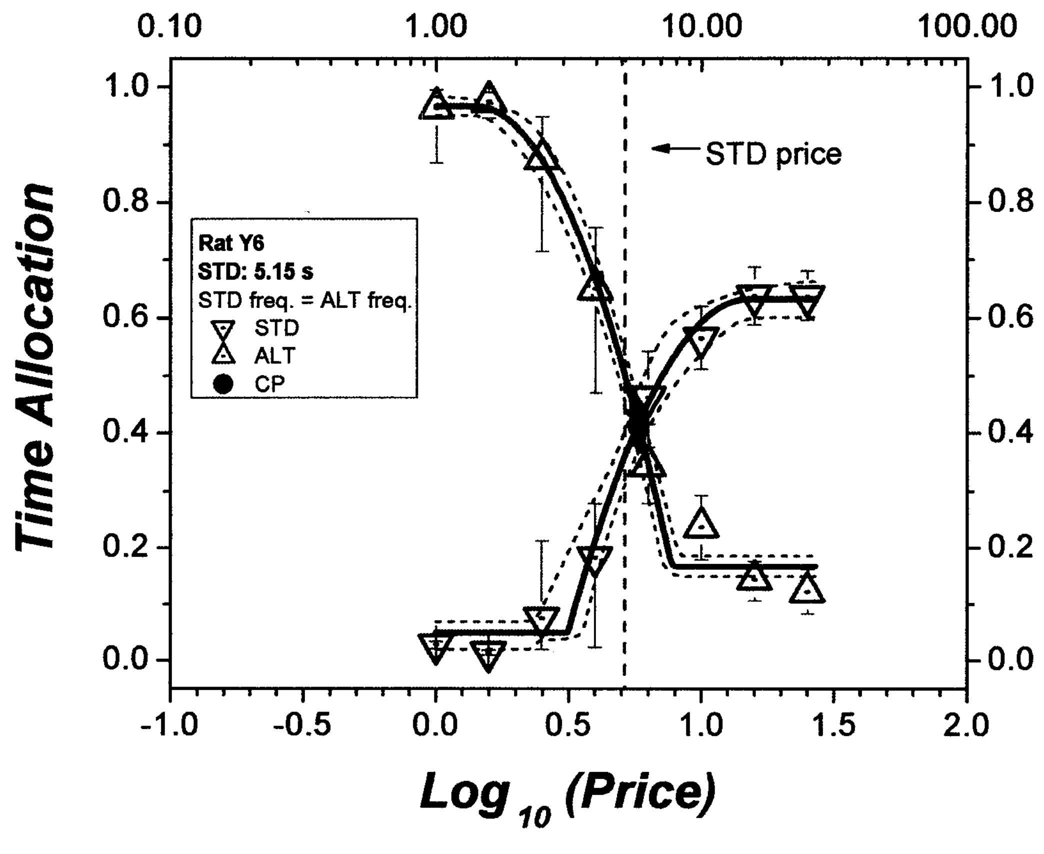


Figure 20. The price sweep phase in which the ALT frequency and STD frequency are equal is a training condition and check to determine whether the rat had learned the task. Inclusion of the STD price in the CP 95% CI implies that the rat had learned the task. Here the STD price is very close to the CP 95% CI, it can be inferred that the rat learned the task.

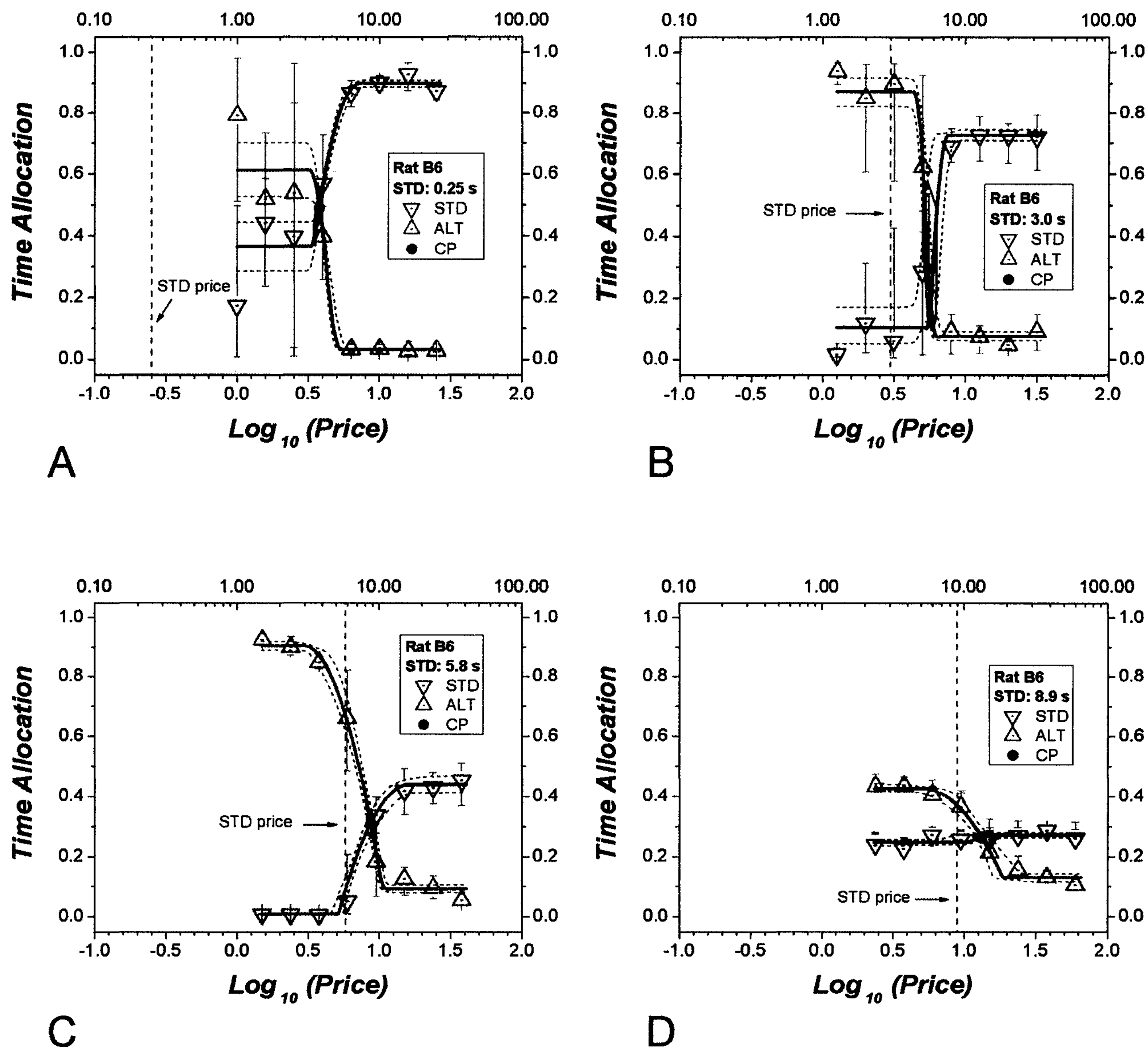
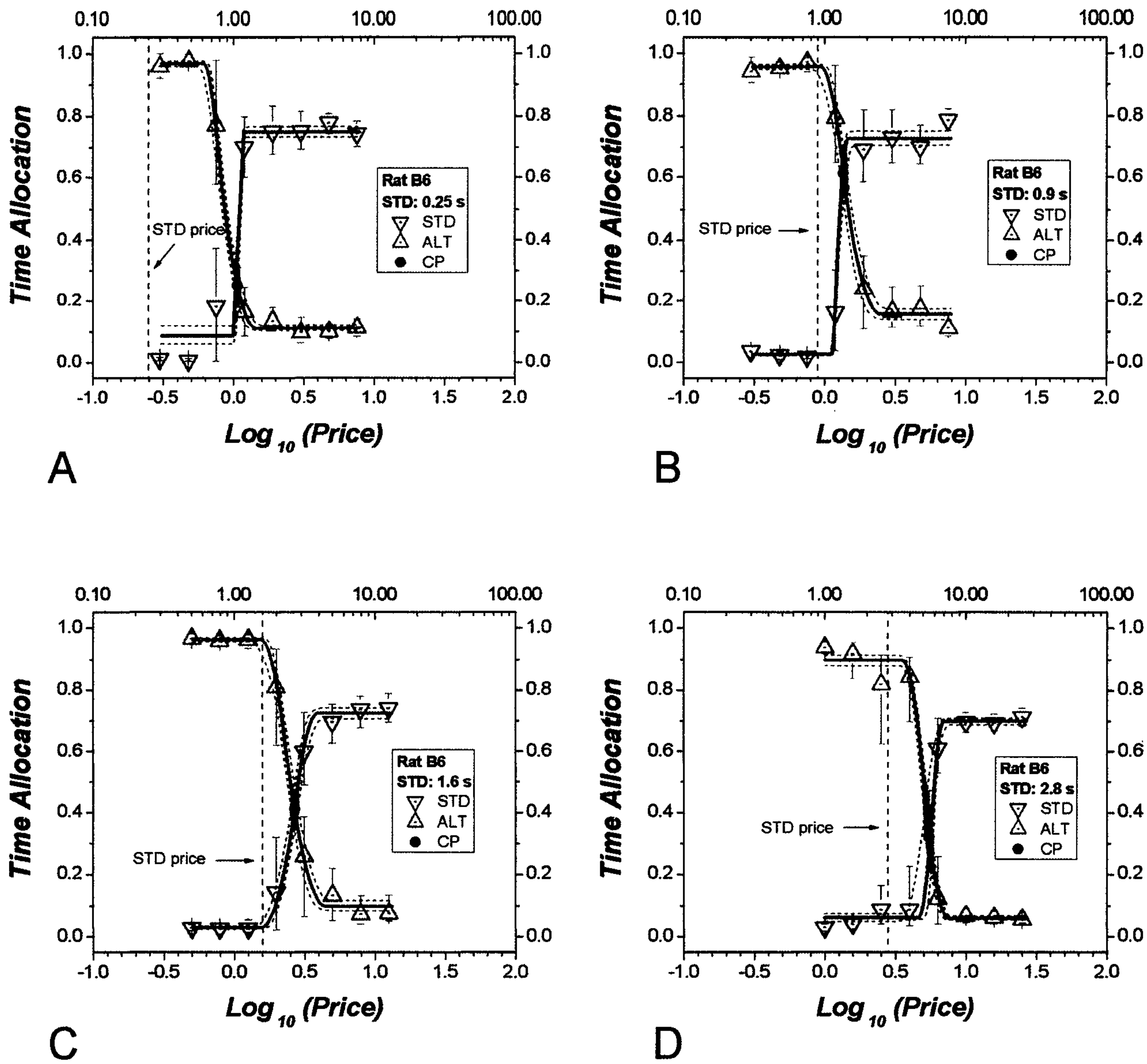


Figure 21. Graphs A to D illustrate time allocation as a function of ALT price when there is a 0.2 log unit spacing between the two frequencies for rat B6. The CP price shift is initially large in Condition A, becomes smaller in Condition B, and then gets even smaller in Condition C, and stays almost the same in Condition D as it did in Condition C.


Time Allocation
Log 10 (Price)
Rat B6
STD: 0.25 s
STD
ALT
CP
STD price
A
Rat B6
STD: 0.9 s
STD
ALT
CP
STD price
B
Rat B6
STD: 1.6 s
STD
ALT
CP
STD price
C
Rat B6
STD: 2.8 s
STD
ALT
CP
STD price
D

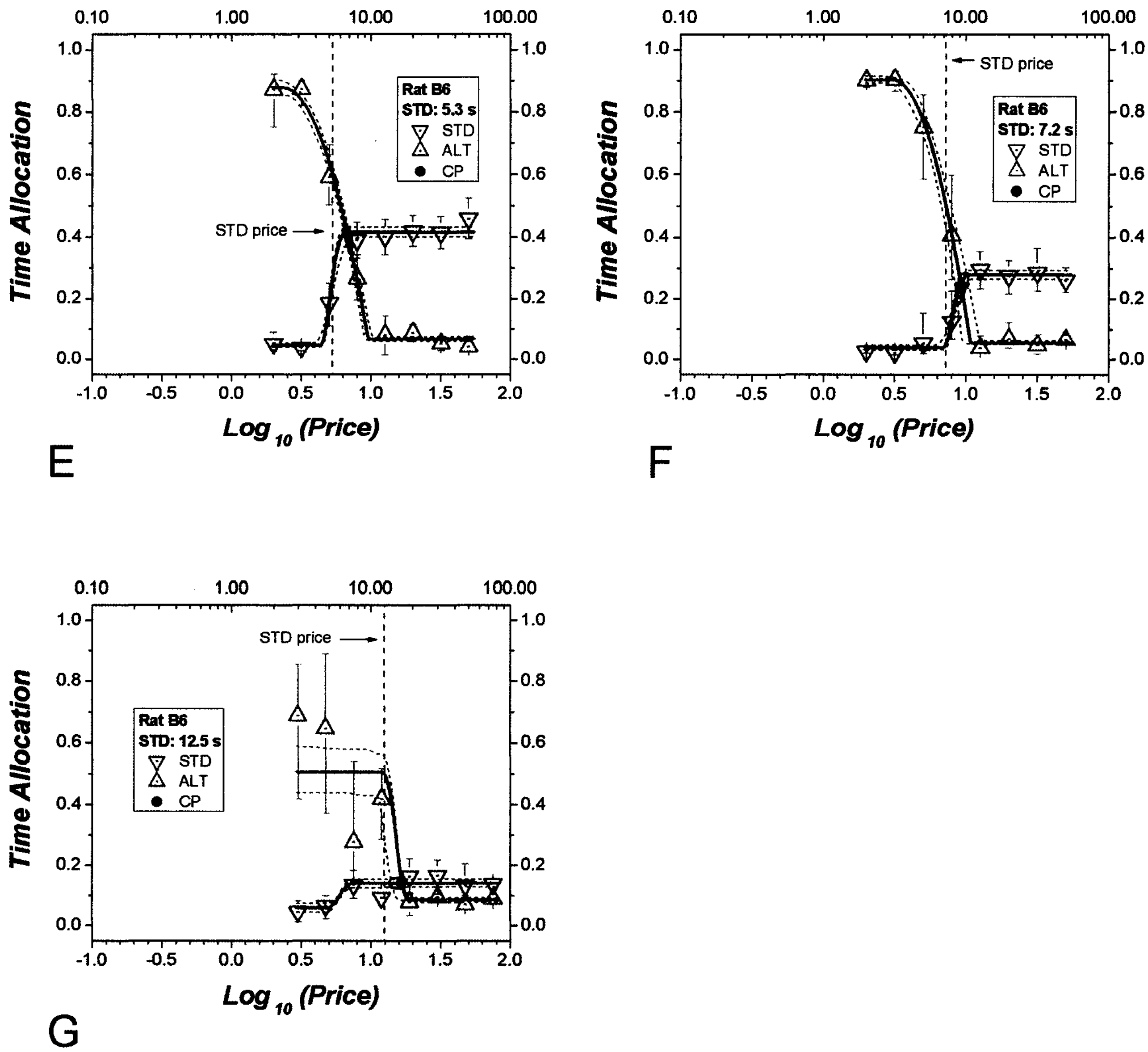


Figure 22. Graphs A to G illustrate time allocation as a function of ALT price when there is a 0.1 log unit spacing between the two frequencies for rat B6. The CP price shift is initially large in Condition A, and as the prices are increased, the shift gradually becomes smaller and appears to level off after Condition E.

Experiment II: Price shift summary

Plotted in Figures 23 to 27 are the price shift summaries of the CPs for all conditions for the 5 rats in Experiment II. This function estimates the subjective-price function. Plotted on y-axis are the arbitrary subjective price units which are equally spaced. These subjective price units are equally spaced because throughout all conditions of the experiment, the ALT frequency is held at one value and the STD is held at a lower value; thus, the shift in the CP always compensates for the same change in stimulation strength, and, by inference, in reward strength. The values of these subjective price units are not known nor are they important, they key point is that the units are equally spaced on a logarithmic axis. Plotted on the x-axis is the log of the CP. The CP values are analogous to the objective price in the subjective-price function. The first x-axis value is 0.25 s, which is not an experimentally derived CP, but is the value of the STD price (0.25 s) in the first condition which is set to correspond to a subjective price unit of 0. The subsequent subjective price units each correspond to the subsequent log CP values. For instance, the first derived CP value on the curve corresponds to subjective price unit 1, the second derived CP value corresponds to subjective price unit 2, and so on.

For most of the rats, two subjective-price functions were obtained: the first (A) shows the data when the frequencies of the trains triggered by the two levers were separated by 0.2 log units, and the second (B) when the frequencies were separated by 0.1 log units. Rat C27 only completed the first condition (STD lever price 0.25 s) of the 0.1 log unit phase and therefore there is only one graph (Figure 25) for this rat. Rat B9 did not complete the entire the 0.1 log unit phase, only reaching a CP price of 3 s.

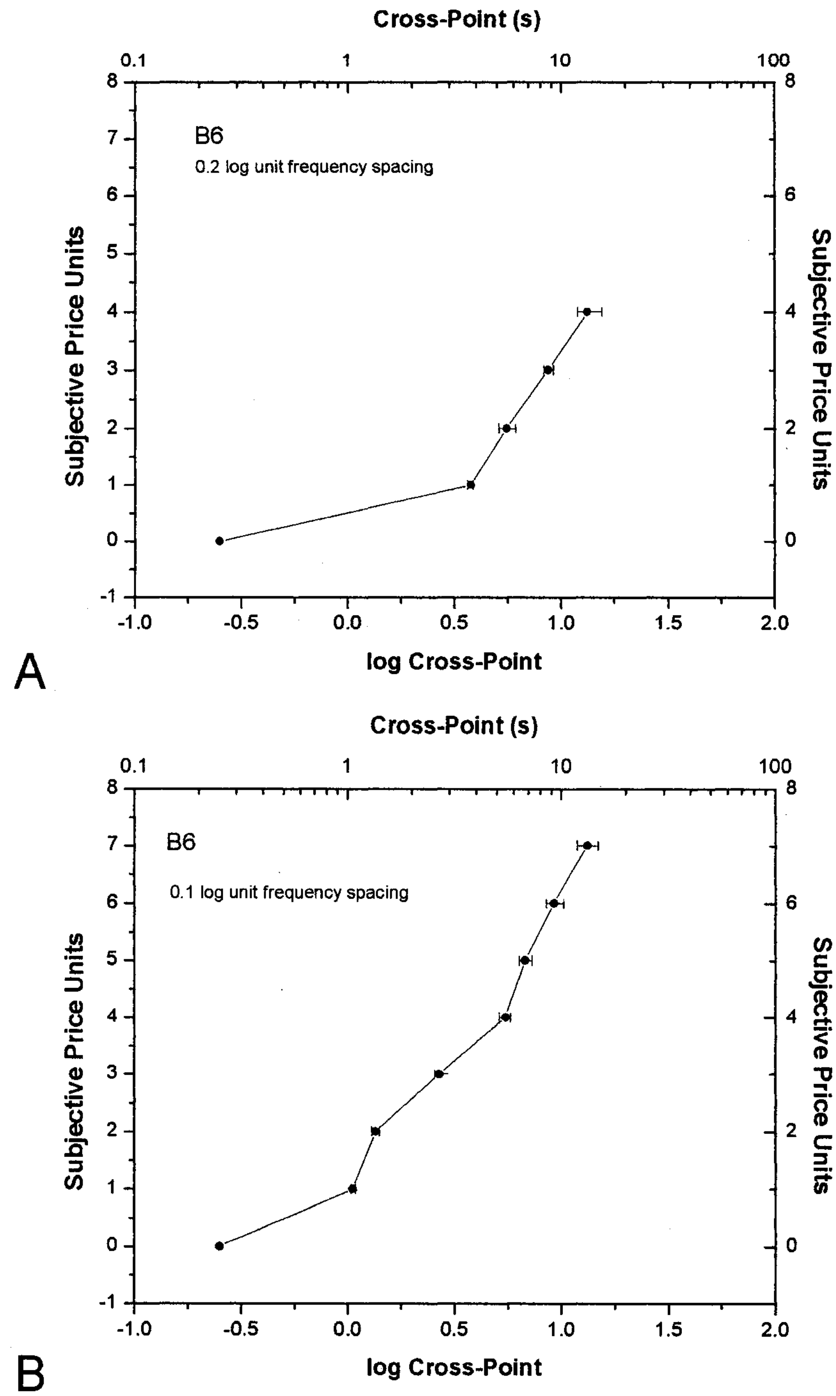


Figure 23. The subjective-price function plot for rat B6. "Cross-point" in these graphs and the following graphs refer to the ALT price at cross-point. Graph A is a plot of the equally spaced subjective price units that correspond to the CPs when the frequency difference of both trains is 0.2 log units. Graph B is a plot of the corresponding subjective price units and CPs when the frequency difference is 0.1 log units. The CP proportional differences at higher prices become equivalent to each other after about 3 s in Graph A and 5 s in Graph B.

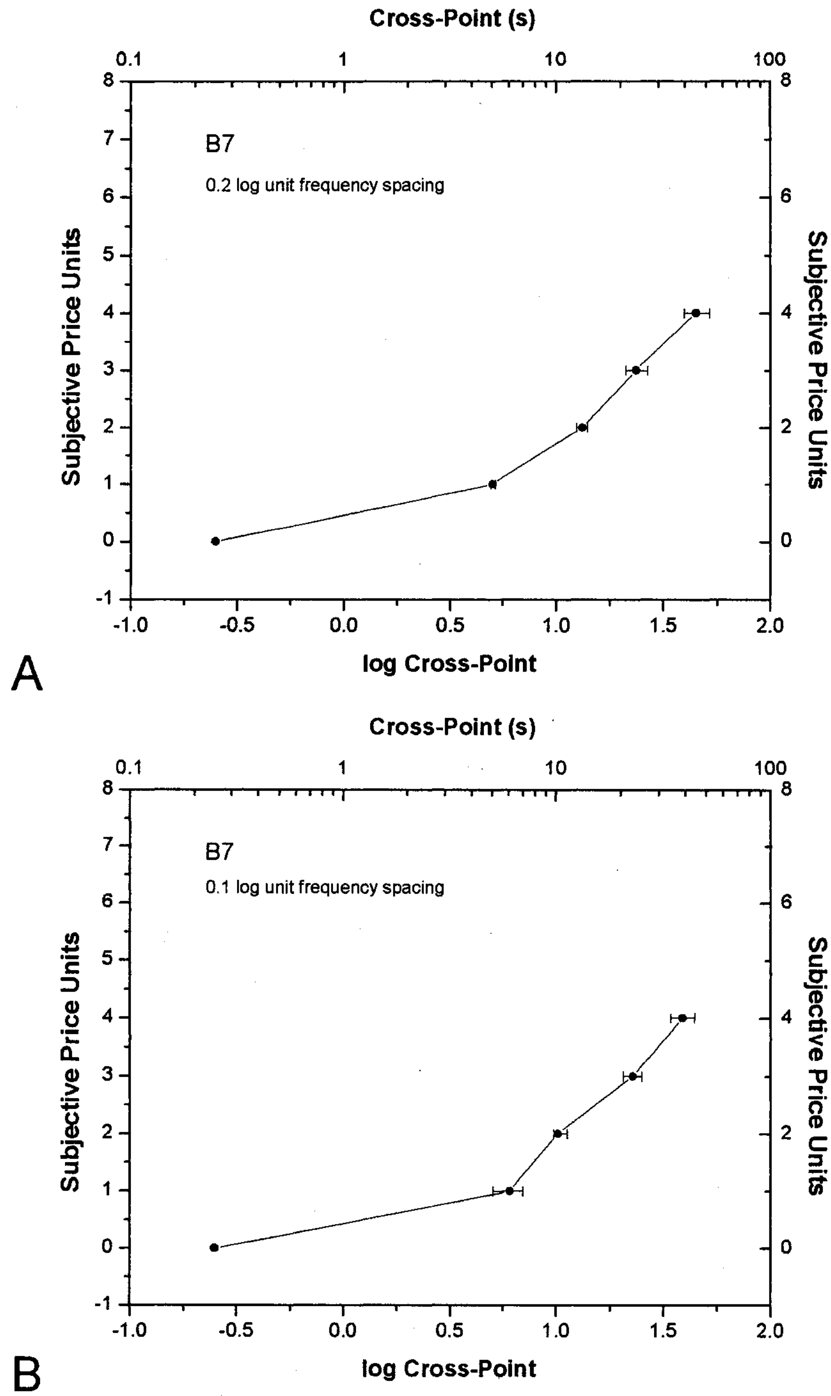
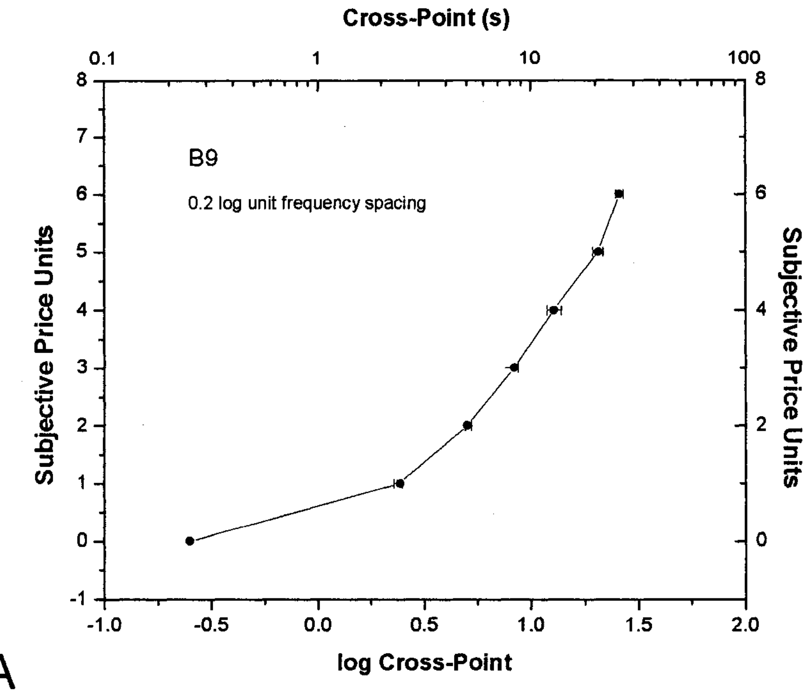
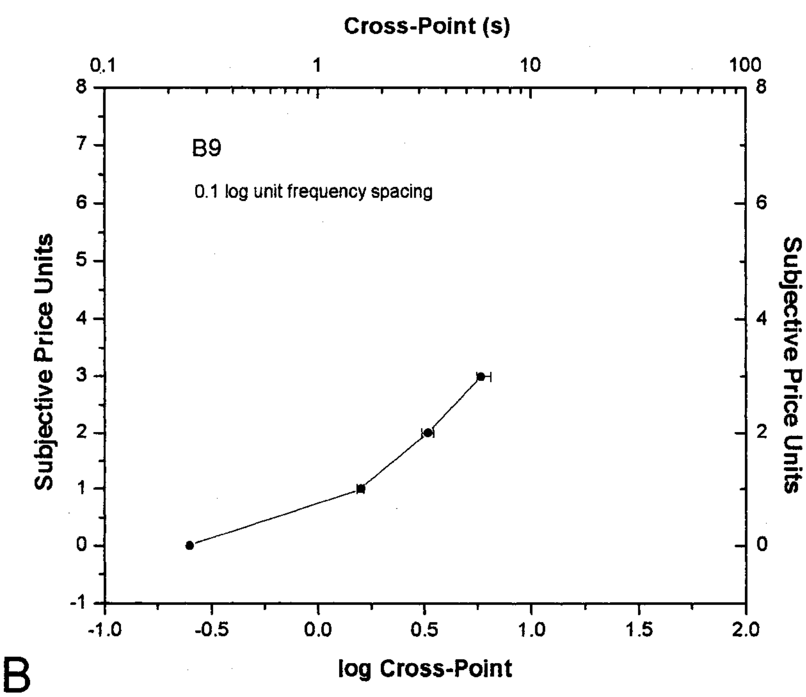


Figure 24. The subjective-price function plot for rat B7. Graph A is a plot of the equally spaced subjective price units that correspond to the CPs when the frequency difference of both trains is 0.2 log units. Graph B is a plot of the corresponding subjective price units and CPs when the frequency difference is 0.1 log units. The CP proportional differences at higher prices become equivalent to each other after about 5 s in both conditions.

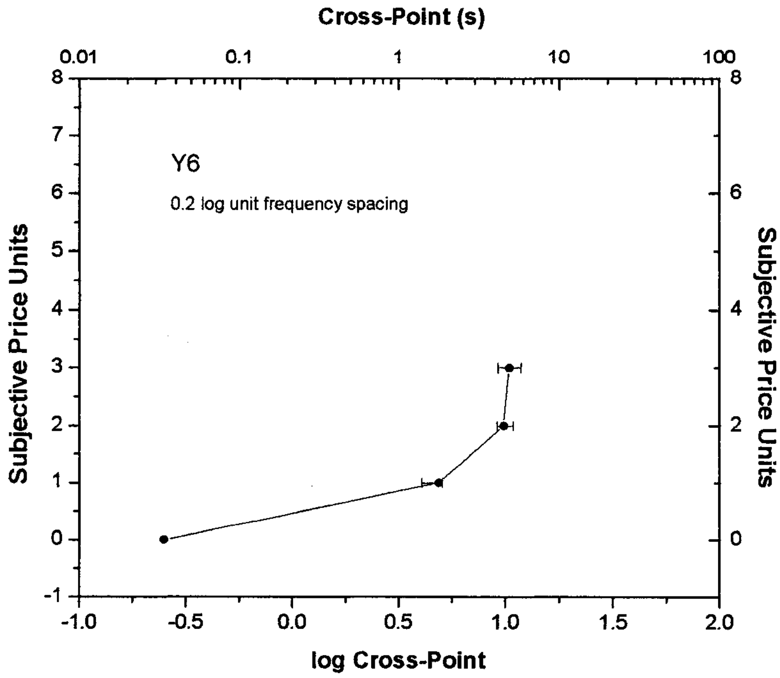


A

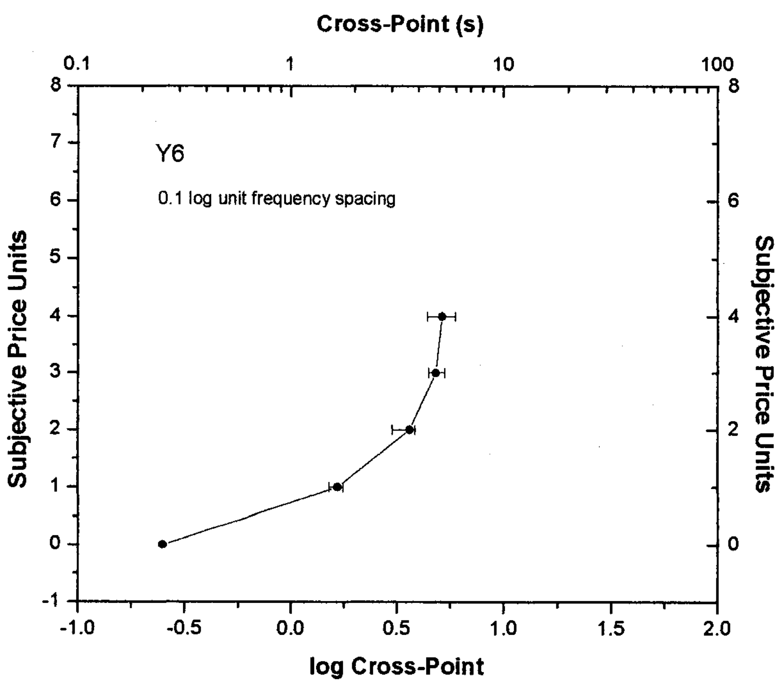


B

Figure 25. The subjective-price function plot for rat B9. Graph A is a plot of the equally spaced subjective price units that correspond to the CPs when the frequency difference of both trains is 0.2 log units. Graph B is a plot of the corresponding subjective price units and CPs when the frequency difference is 0.1 log units. The CP proportional differences at higher prices become equivalent to each other after about 5 s in Graph A, and after about 1 s in Graph B.



A



B

Figure 26. The subjective-price function plot for rat Y6. Graph A is a plot of the equally spaced subjective price units that correspond to the CPs when the frequency difference of both trains is 0.2 log units. Graph B is a plot of the corresponding subjective price units and CPs when the frequency difference is 0.1 log units. The CP proportional differences at higher prices do not appear to become equivalent to each other in Graph A or Graph B.

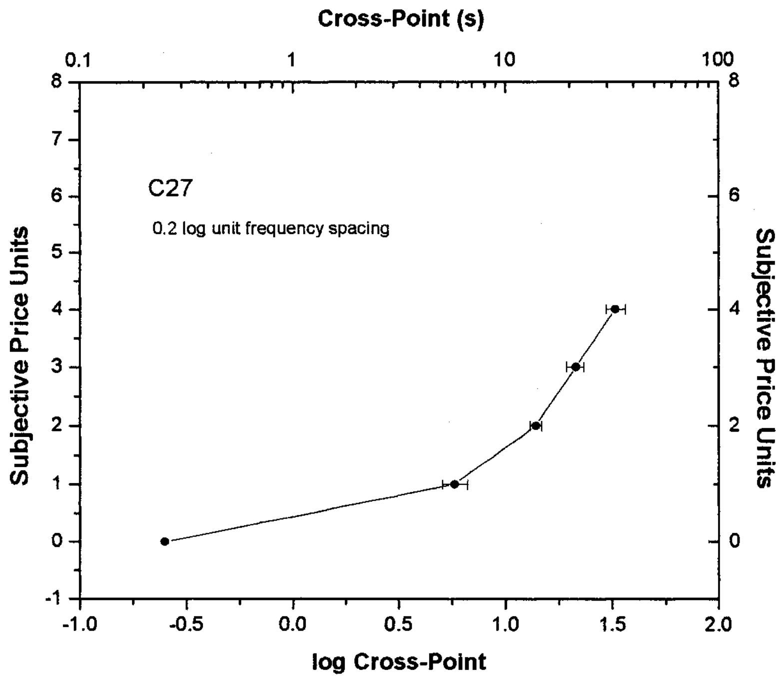
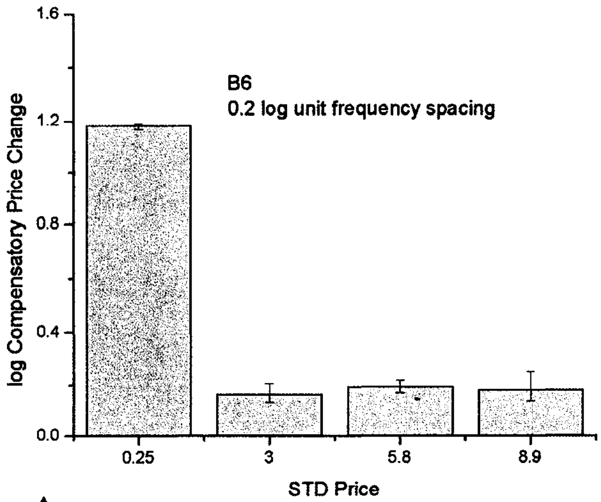


Figure 27. The subjective-price function plot for rat C27. This graph is a plot of the equally spaced subjective price units that correspond to the CPs when the frequency difference of both trains is 0.2 log units. The CP proportional differences at higher prices become equivalent to each other after about 14 s.

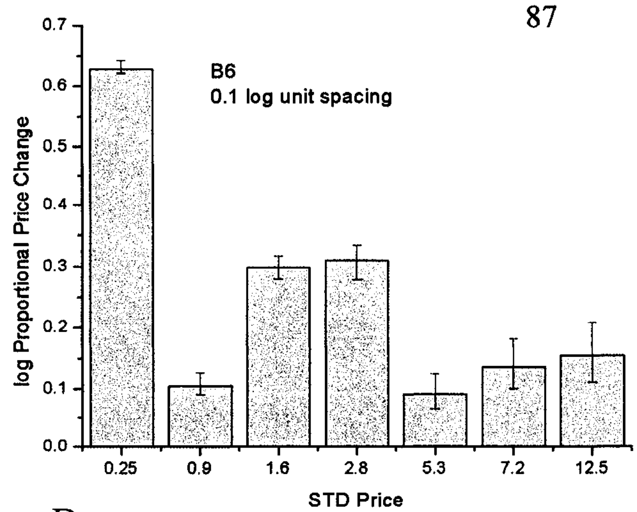
The variable of interest is the proportional difference between CPs. This proportional difference can be calculated by determining the ratio of the ALT price at the CP to the STD price. These proportional differences can then be compared across sessions. If these proportional differences are the same over a given range, then this suggests that over this range, the subjective-price function is scalar. In the Figures 23-27, the log of the CPs were plotted and joined. The log distances (or differences) between the CPs are actually the proportional price differences because the STD price in one condition was the estimated ALT price at the CP in the previous condition. As predicted, for almost all rats (except B7), the first CP shift (compensatory price change) was the largest. This large shift at low prices compared to higher prices supports the first hypothesis that low prices are subjectively equivalent to each other. The second hypothesis was that higher prices would be scalar. This scalar relationship is represented in the graph by an equal spacing between the log CPs (equivalent proportional CP differences). For rat B6 (Figure 23), roughly equal proportional distances (changes) occurred after about 3 s in the 0.2 log unit spacing phase and about 5 s in the 0.1 log unit spacing phase. For rat B7 (Figure 24) roughly equal proportional distances occurred after about 5 s in both frequency spacing phases. For rat B9 (Figure 25), equal proportional distances occurred after about 5 s in the 0.2 log unit spacing phase and about 1 s in the 0.1 log unit spacing phase. For rat Y6 (Figure 26), the proportional distances between CPs are very small, and the shape of the curve is odd: equivalent proportional price changes do not appear to occur in the 0.2 log unit or 0.1 log unit spacing phases. For rat C27 (Figure 27), equal proportional distances occurred after about 14 s in the 0.2 log unit phase.

Figure 28 displays another way of looking at Figures 23-27. For each rat, in both phases, histograms denote the magnitude of the proportional price change as a function of the STD price that offsets the difference in reward intensities. The error bars represent 95% confidence intervals. Overlapping error bars imply that the proportional price changes are not statistically significantly different. The magnitude of proportional price change is in effect the rate of change or derivative of the functions plotted in Figures 23-27, (specifically, the rate of change between two CPs). These graphs demonstrate at what price non significantly different price changes occur, as do Figures 23-27. These histograms offer a clearer representation of the proportional price changes because it is easier to visually compare magnitudes (price changes) that are vertically represented, rather than magnitudes that are horizontally represented as they are in Figures 22-26.

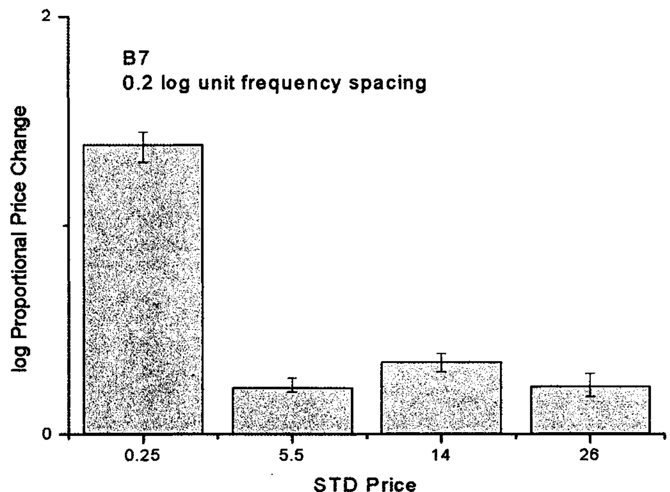
Comparing the curves in Figures 23-27 of the 0.2 log unit phase with the 0.1 log unit phase for each rat, the spacing between CPs was predicted to be smaller in the 0.1 log unit phase. This smaller spacing was expected because less of an objective and subjective proportional price compensatory difference is needed when the spacing of the two frequencies is small (separated by 0.1 log units) than when the spacing is larger (0.2 log units). Because the subjective proportional price difference is expected to be smaller in the 0.1 log unit frequency spacing phase, the corresponding objective price difference (the variable of interest) should be smaller as well. Comparing the curves (by visual inspection) of the 0.2 log unit phase with the 0.1 log unit phase, the spacing between CPs is smaller in the 0.1 log unit phase for rats B6 and B9. For B6, this smaller CP spacing in the 0.1 log unit frequency spacing phase is evident in the first condition (STD price = 0.25 s), and in the steeper slope of the curve (which reflects smaller proportional price


B6
0.2 log unit frequency spacing
log Compensatory Price Change
STD Price
1.6
1.2
0.8
0.4
0.0
0.25
3
5.8
8.9

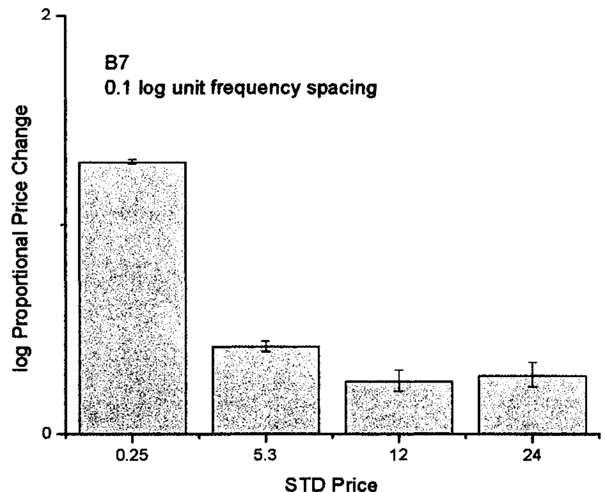
A


B6
0.1 log unit spacing
log Proportional Price Change
STD Price
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.25
0.9
1.6
2.8
5.3
7.2
12.5

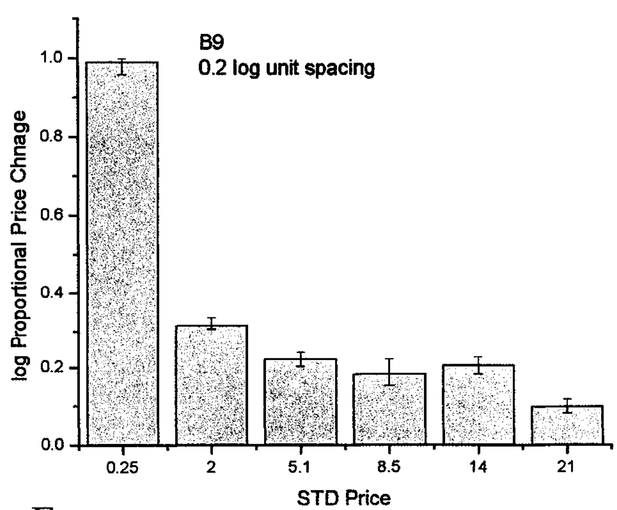
B


B7
0.2 log unit frequency spacing
log Proportional Price Change
STD Price
2
0
0.25
5.5
14
26

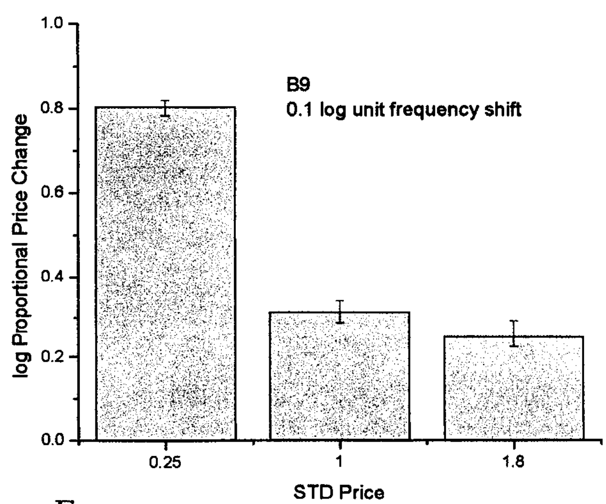
C


B7
0.1 log unit frequency spacing
log Proportional Price Change
STD Price
2
0
0.25
5.3
12
24

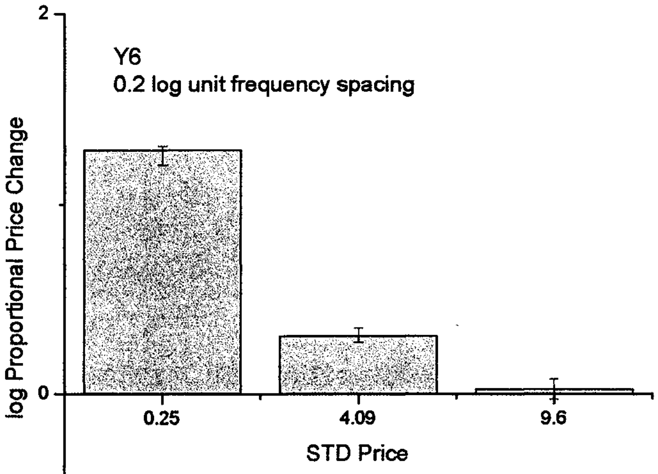
D


B9
0.2 log unit spacing
log Proportional Price Chnage
STD Price
1.0
0.8
0.6
0.4
0.2
0.0
0.25
2
5.1
8.5
14
21

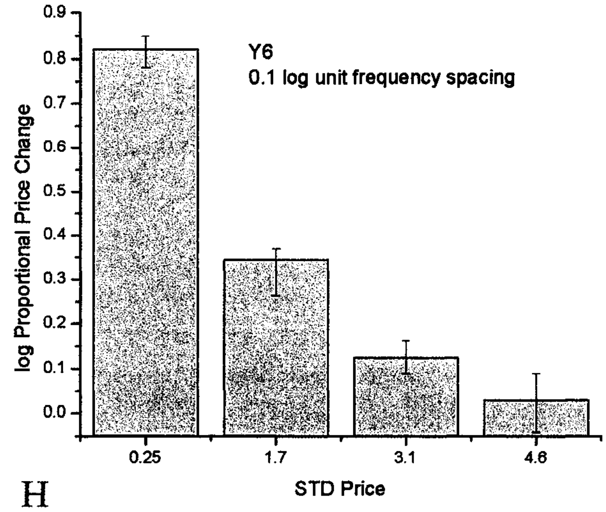
E


B9
0.1 log unit frequency shift
log Proportional Price Change
STD Price
1.0
0.8
0.6
0.4
0.2
0.0
0.25
1
1.8

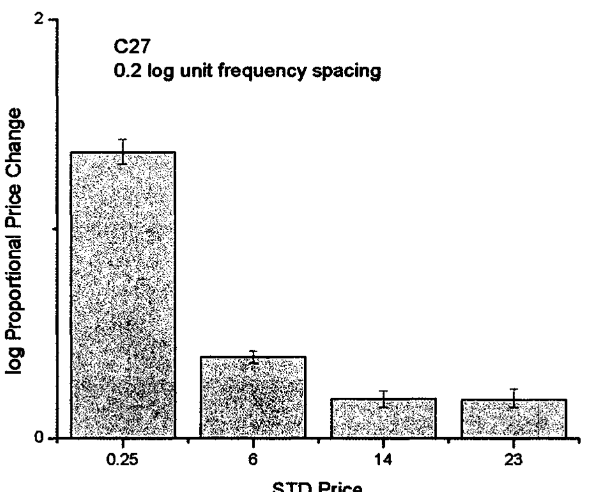
F



G



H



I

Figure 28. For each rat, histograms denote the magnitude of the proportional price change the rat makes in terms of the STD price in Phase A (0.2 log unit frequency spacing) and B (0.1 log unit frequency spacing). Error bars represent 95% confidence intervals. Overlapping error bars imply that the proportional price changes are not statistically significantly different. The magnitude of proportional price change is the rate of change or derivative of the functions (between adjacent CPs) plotted in Figures 22-26. For rat B6, non significantly different proportional price changes occur after about 3 s in Condition A (Graph A) and about 5 s in Condition B (Graph B). For rat B7, non significantly different proportional price changes occur after about 5 s in both conditions (Graph C and D). For rat B9, non significantly different proportional price changes occur after about 5 s in Condition A (Graph E) and about 2 s in Condition B (Graph F). For rat Y6, non significantly different proportional price changes do not occur in Condition A (Graph G) and appear to occur after about 3 s in Condition B (Graph H), however, this is difficult to interpret because the error bars for the last point are large. For rat C27, non significantly different proportional price changes occur after about 14 s for Condition A (Graph I).

changes) in the last few conditions of the 0.1 log unit frequency spacing phase compared to the 0.2 log unit frequency phase. For B9, this smaller spacing is evident in the first condition (STD price = 0.25 s), but there is not enough data points in the 0.1 log unit frequency spacing phase to compare the proportional price changes (the steepness of the curve) across both phases. This smaller price spacing in the 0.1 log unit phase did not occur for rat B7 who had equivalent log unit spacing across phases. It was difficult to make comparisons for rat Y6, but it is evident that that the spacing in the first condition (STD price of 0.25 s) is larger in the 0.2 log unit phase than the 0.1 log unit phase. Only the first phase was completed for rat C27, therefore it was not possible to make comparisons for this subject.

Experiment III: Compensatory price shifts using the FCHT schedule

One rat, B10, completed the 0.2 log unit phase of the price-shift experiment which was a replication of Experiment II with a few adjustments: a different schedule and an increase in trial times. Changes were made in this condition so as to facilitate learning the ALT price and discriminating between it and the STD price. Figure 29 displays the CP shift data for each condition. The quality of the data obtained in this condition was an improvement over Experiment II: the CP shifts are large suggesting that the animal can discriminate well between the STD and ALT prices.

Figure 29 displays time allocation as a function of ALT price in the 0.2 log unit frequency spacing phase. Figure 30A shows that similar to the other rats, the shift is largest for the first condition (STD price of 0.25 s). This function shows that equal proportional changes appear to occur after 2.87 s. Figure 30B is a histogram that shows

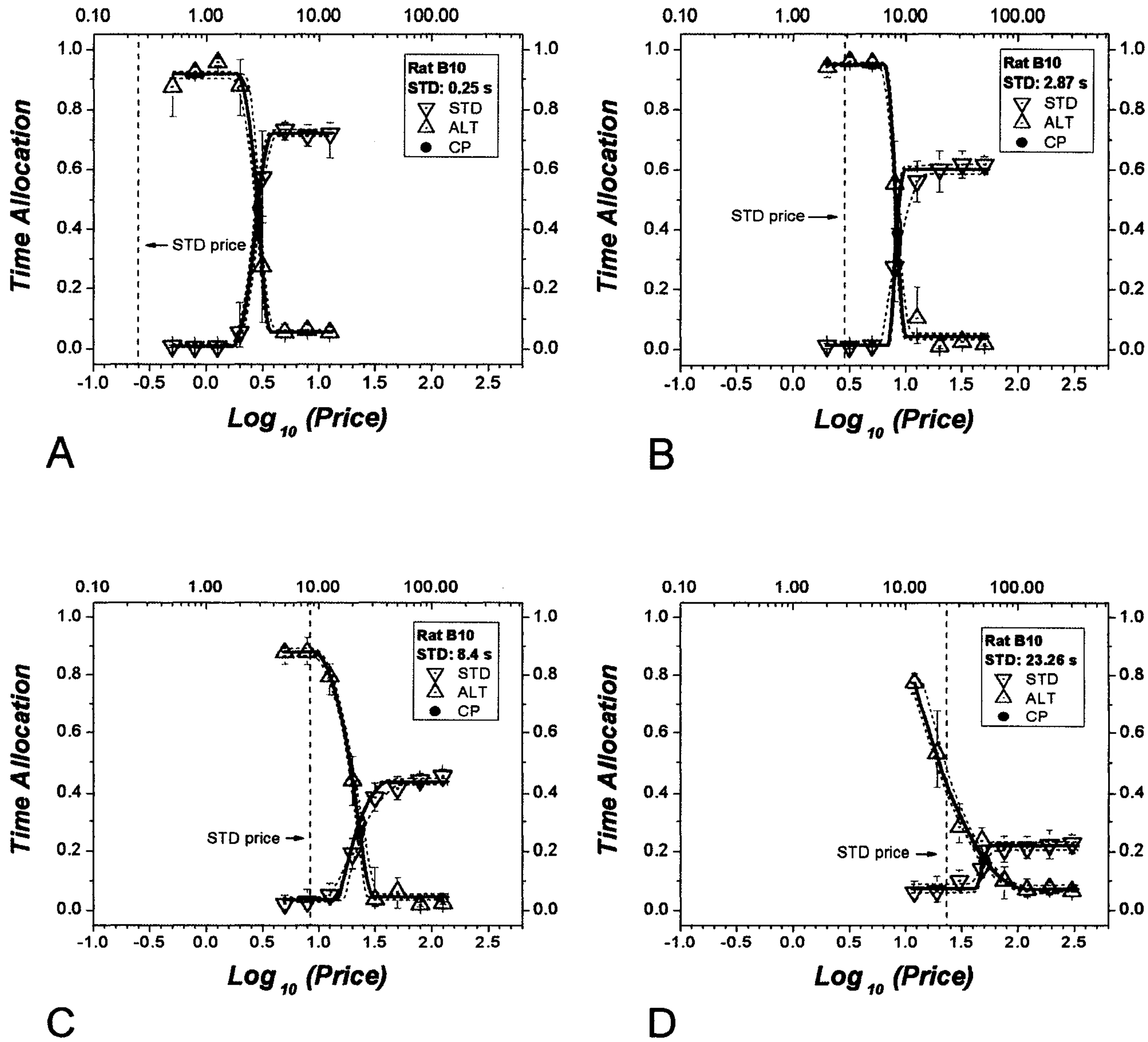
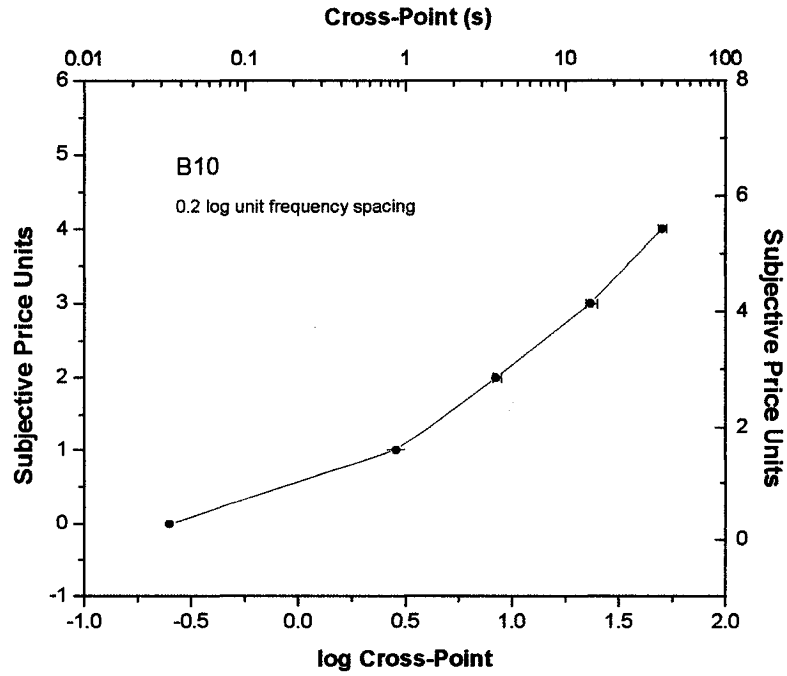
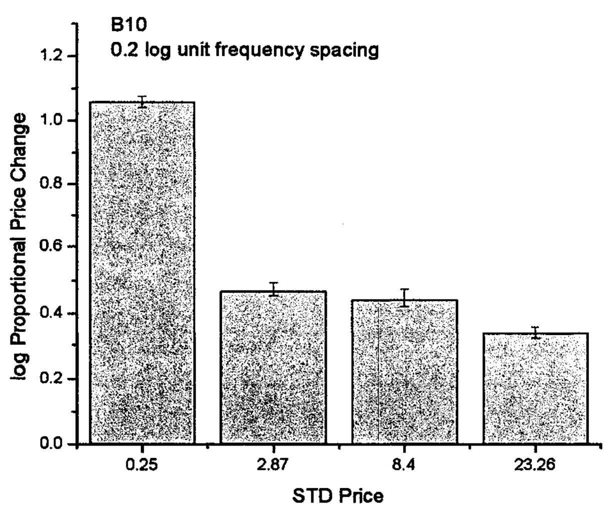


Figure 29. Graphs A to D illustrate time allocation as a function of ALT price when there is a 0.2 log unit spacing between the two frequencies for rat B10. The CP price shift is initially large in Condition A, becomes smaller and levels-off in Condition B and Condition C, and decreases slightly in Condition D.



A



B

Figure 30. Graph A displays time allocation as a function of ALT price in the 0.2 log unit frequency spacing condition. Graph B illustrates the proportional price change in terms of the STD price. Graph A shows that equal proportional price changes appear to occur after about 3 s. However, Graph B more clearly demonstrates that the proportional price change slightly decreases when the STD price is 23.26 s which corresponds to the price range past 23.26 s in Graph A.

the proportional price change in terms of the STD price which more clearly demonstrates, however, that the proportional price change somewhat decreases (the error bars do not overlap) when the STD is 23.26 s which corresponds to the price range past 23.26 s in Figure 30A.

Discussion

The present experiments have led to three main findings. First, Shizgal and Conover's (2005) proposed definition of payoff, the ratio of reward value to subjective price, is supported. The next two findings involve the subjective-price function that was proposed in this thesis, the function that maps objective prices into their subjective equivalents. The findings in the first experiment support the proposal that low prices are subjectively equivalent to each other; the findings in the second experiment further strengthens this proposal, and shows that the subjective-price function is scalar at higher prices.

The definition payoff is supported by consistent cross-point shifts

Shizgal and Conover (2005) proposed that payoff is the ratio of reward intensity to subjective price. The term "payoff" can be interpreted as an index of how worthwhile it is for the subject to engage in a task or activity in order to obtain a reward. In the present experiments, the required task is to hold the lever for an experimenter-set amount of time in order to obtain rewarding electrical stimulation. In a natural circumstance such as a foraging situation, how worthwhile it is for the animal to be engaged in a task is looked at in terms of a cost-benefit comparison in which the animal's payoff is assumed to be equal to the ratio of benefits derived from the reward (such as the energy content of a prey item) to the cost of the activity (such as time spent foraging). Thus, Shizgal and Conover's interpretation of payoff in a laboratory situation is close to that of the definition in the foraging literature. Reward intensity is analogous to the benefits derived from the natural reward, and subjective price is analogous to the opportunity cost of the reward. The results of both experiments in this thesis are consistent with the proposed definition of payoff. When the animal allocates its time equally to the STD and ALT levers, this indicates that the equivalent payoffs are obtained from pressing either lever. In the experiments, reward value is manipulated by adjusting the frequency of stimulation (Hz), and subjective price is controlled by setting the objective price (s), the time the rat must work in order to earn a reward. When the rat allocates equal time to pressing both levers, the objective price of the train or frequency of the train triggered by the ALT lever is denoted by the CP. At the frequency values to the left of the CP on the plot of time allocation as a function of frequency in Experiment I, the rat allocates more time to pressing the STD than the ALT lever which indicates that payoff offered by the STD lever is greater than the payoff offered by the ALT lever. Similarly, at the frequency values to the right of the CP, the rat allocates more time to pressing the ALT than the STD lever which indicates that the payoff offered by the ALT lever is greater than payoff offered by the STD lever. Assuming that the payoffs derived from pressing the STD and ALT levers are equal at the frequency values of the CP, then the equation below can be set up.

$$\frac{\text{Reward Intensity}_{\text{STD}}}{\text{Subjective Price}_{\text{STD}}} = \frac{\text{Reward Intensity}_{\text{ALT}}}{\text{Subjective Price}_{\text{ALT}}}$$

If three values in the above equation are held constant and the rat can choose the fourth value, the rat will choose the fourth value so that the payoffs remain equal. For instance, if the STD reward value, STD price, and ALT price are held constant such that

STD price is greater than that of the ALT price (e.g., STD price twice that of ALT price), the rat chooses the reward intensity that compensates for this price difference. Under the assumed definition of payoff, the chosen reward intensity of the ALT train must stand in the same proportion to the reward value of the STD train as the ratio of the ALT and STD prices (proportion of 2 in this example) in order for the payoffs of both levers to remain equal. The reward value the rat chooses to keep payoff constant is reflected in the CP, namely, the ALT frequency value of the CP, which is denoted by the position of the CP along the x-axis. Therefore, compared to a baseline condition in which reward intensity and subjective price of both trains are equivalent, by manipulating one value, such as the price of the ALT train in Experiment I, the compensatory frequency change is revealed by determining the size of the CP shift. For instance, referring back to the above example, if the STD price was set to twice the ALT price, then the compensatory frequency change that offsets the price difference would be a reduction (by half) of the reward intensity of the ALT. Therefore, the directional effects can be predicted. This lowering of the ALT reward intensity is reflected in the shifting of the CP to the left (to the lower frequencies). What Experiment I was measuring was just how much the CP shifted to the left, but the main idea here is that the CP shifted to the left for all animals. This supports the idea that payoff is combined in a multiplicative way (reward value: subjective price).

The definition of payoff was also supported in Experiment II. In this experiment, the reward intensity of the train triggered by the ALT lever was greater than that of the STD train, and the price of the STD train remained constant. The ALT price that offsets the greater reward intensity of the ALT train is then empirically determined by finding the x-value of the CP. The directional effects can be predicted: if the ALT reward intensity is greater than the STD reward intensity, then for the two payoff equations to remain constant (which is denoted on the graph by the CP), the ALT price the rat chooses is predicted to be greater than the STD price (Figures 21, 22). On a plot of time allocation as a function of ALT price, this increase in ALT price the rat would choose to keep payoffs equal is reflected in the ALT price at CP. Because an increase in ALT price is predicted, the CP was predicted to shift to the right. Such rightward shifts were seen in the data from all subjects, a finding consistent with the assumed definition of payoff.

The shifts of the cross-points in the predicted direction (under the proposed definition of payoff) suggest that the animals are computing payoff in the proposed way. However, the cross-points may have shifted in the predicted direction if the animal were making some other, similar computation of payoff. The most powerful support for the definition of payoff comes from the evidence of a scalar relationship between objective and subjective prices (Figures 23, 24, 25, 27, 29) inferred by equal proportional price changes (past a certain price) required to offset a frequency difference. These equal proportional price changes could not have occurred if the subject was not making a scalar combination of reward intensity and subjective price (ratio of reward intensity to subjective price). In other words, the subject must be making a scalar combination in order to obtain a scalar relationship.

Experiment I: Low prices are subjectively equivalent to each other

The second proposal that the present experiments supported is that low prices are subjectively equivalent to each other. Experiment I estimated the derivative of the subjective-price function based on the proposed definition of payoff. The proposed subjective-price function (Figure 1) is plotted as subjective price as a function of objective price. The derivative of this function is the rate at which subjective price changes in response to a change in objective price as a function of objective price (Figure 2). The y-axis of the derivative function is the slope (rate of change) of the subjective-price function. There are three phases of the derivative of the subjective-price function: the first flat part which corresponds to a derivative of 0, the middle part (transition phase) in which the derivative increases, and the second flat part that corresponds to a constant derivative of 1. A derivative of 0 indicates that subjective prices do not differ from each other (the slope is 0 or flat on the subjective-price function graph), a constant derivative indicates that the objective-subjective price relation is scalar (the slope of the subjective-price function is constant), and an increasing derivative over a range of prices indicates that the subjective prices are beginning to be interpreted as different from each other but the relationship is not yet scalar.

The function empirically derived is roughly analogous to the derivative function, it is plotted as the proportional change in frequency required to compensate for a proportional price difference as a function of the objective price. The proportional price increases were always a doubling and spanned a range extending from very low prices (0.125 s ALT to 0.25 s STD) to substantially higher ones (4 s ALT vs. 8 s STD). If the proportional change in subjective price always matched the proportional change in objective price, then this change would always be offset by the same proportional change in frequency. However, Experiment I revealed that at the lowest pairs of prices, there was no compensatory frequency change (Figures 14-19), which suggests that the derivative of the function is 0 or close to 0 for all rats at very low prices. This indicates, as predicted, that the subjective-price function is flat when the objective prices are very low.

The experiment also reveals the growth phase of the derivative of the function that occurs before the scalar region. If the rat begins to experience a greater subjective difference between increasing price pairs, for example 0.125 s vs. 0.25 s is interpreted as equivalent, 1 s vs. 2 s is interpreted as differing by a ratio of z, while 4 s vs. 8 s. is interpreted as differing by a ratio greater than z, then the proportional frequency difference should increase in order to compensate for this increasing subjective price difference. This was demonstrated: as the price pairs were increased, the frequency change increased as well. All of the subjects in Experiment I (Figures 14-19) showed no frequency change at very low prices, which is analogous to the first flat part in which the derivative is 0, and an increase in frequency as the prices were increased, which is analogous to the growth phase of the subjective-price function in which the derivative increases as prices increased, before the relation becomes scalar.

Experiment II: The subjective-price function is scalar over a range

The third proposal that was supported in these experiments is that the subjective-price function is scalar along a range of high prices. This scalar relationship implies that the objective and subjective prices vary in direct proportion with each other. In other words, along the scalar range, the ratio of objective price to subjective price is constant. If the scalar were 1, a 10 s objective price would equal a 10s subjective price, a 20 s objective price would equal a 20 s subjective price, etc.

Experiment II directly estimated the subjective-price function by measuring the objective compensatory price changes that correspond to a constant change in subjective price. It was predicted that past a certain price, the proportional compensatory price change required to offset two differing frequencies would become equal. In Experiment II, the derived the subjective-price function is plotted as subjective price units as a function of the ALT price at the CP (which can be referred to simply as the CP).

In order to understand the rationale for deriving the subjective-price function, let us first focus on the x-axis. Recall that the price change that offsets the difference in reward intensities is revealed by a CP shift and is measured as the ratio of the ALT price at CP to the STD price. It is this proportional compensatory price change that is needed to infer a scalar region. Therefore, if one wanted to compare the proportional price changes across conditions, (at differing prices of the STD) the ratio of the CP to the STD price would be compared. These ratios would be constant over the scalar range of prices. How can this be plotted? The key idea is that the STD price for each condition must be set to the CP derived in the previous condition. The first point on the x-axis initially starts at 0.25 s (which is the first STD price), but the rest of the points are the experimentally derived CPs. Therefore, what is actually plotted on the x-axis are the proportional price changes for each condition reflected by the distance between the common logarithms of the CPs. The spacing between the CPs in logarithmic space is the actual measure of the proportional price change because the STD price is set to the ALT price at CP derived in the previous condition.

The proportional price change can also be plotted (ALT price at CP divided by STD price) in a simpler way: a histogram that plots the proportional price changes in terms of the STD price. These histograms are shown in Figure 28. Equivalent proportional price changes are inferred from equality in the heights of the bars. However, by plotting the log of the CPs as described above, the subjective-price function can be developed. The y-axis of the derived subjective-price function consists of equally spaced subjective price units: these units are equally spaced because under the assumption of payoff the rat in its mind always requires the same subjective price change to compensate for the constant ratio of reward intensities produced by same two frequencies, throughout all conditions. The y-axis is plotted in a continuous manner, that is, subjective price units range in a systematic fashion, from 1 to about 5 (the range depends on the rat). Each of these subjective price units correspond to a point on the x-axis: subjective price unit 1 always corresponds to 0.25 s (the STD price), subjective price unit 2 corresponds to the next x-axis value (the first experimentally derived CP) and so on. Therefore, the points on the x-axis (the CPs) must be plotted in a continuous manner as well. Plotting the CPs in a continuous manner is achieved by always setting the STD price to that of the CP derived in the previous condition so that the CPs on the x-axis are contiguous.

One might think that the compensatory price changes can be measured (ratio of CP to STD price) if STD prices were chosen at random (instead of setting the STD price to the previously derived CP). Over a high price range, the compensatory price changes are predicted to be equal if the objective-subjective price relation is scalar. Therefore, the bar graphs would show heights (equal compensatory price changes) past a certain price. However, if STD prices were not set to that of the CP in the previous condition, the subjective-price units would no longer be concatenated, and it would be impossible to determine how they should overlap. An equal spacing of the CPs (scalar relationship) was seen in most of the rats past a given price that varied across subjects. In general, the relationship became scalar after about 5 s for most rats.

Individual rats

Because the present experiments are psychophysical, data from each individual subject are considered independently. Each rat will have a different subjective-price function as well as a different reward-growth function. The reward-growth function was not estimated in the present experiments (because deriving both the subjective-price function and reward-growth function is lengthy, and the lifespan of a rat is short), but its existence, to translate frequencies into reward intensities, is relevant because reward intensity is central to the definition of payoff. The functions, however, were predicted to be similar in shape across subjects. Comparing the subjective-price functions derived from several rats enables the estimation of the general form of the subjective price function, namely where the scalar relation between objective and subjective prices breaks down for most rats. The next sections focus on the similarities and differences in the rats' behaviours across experiments.

Limit to how many points can be experimentally derived on the subjective-price function

It is important to note that there is a limit as to how high the prices can be experimenter-set in the present experiments. Brain stimulation reward produces robust responding, but the rat's willingness to work decreases as the price increases. This willingness to work is reflected in the time allocation to the lever as illustrated by the graphs of the individual conditions on the y-axis (Figure 4). When the price is low (0.25

s) the rat will allocate a large amount of its time to work. As the price increases, the allocation of its time to working decreases. Eventually, when the price becomes too high for the rat, the rat will no longer work for the reward, and time allocation to the lever will be 0 or close to 0. When the animal is not working at the lever, he is engaged in leisure activities such as grooming and exploring. In relation to the concept of payoff, when the price is very high, the animal will spend more of its time engaged in leisure activities than engaged in working, therefore at these high prices, the payoff derived from leisure activities is greater than the payoff derived from working. The price at which the animal will no longer work at the lever varies depending on the animal that is being tested. A rat with a particularly good electrode placement in the medial forebrain bundle will work for the reward at very high prices. The highest STD price to support robust responding is around 10 s for some subjects, but can go up to 20 s for other subjects. Therefore, the number of experimentally derived points on the subjective-price function is limited.

The graphs of the individual conditions for B7 (Appendix A, Figures 33, 38, 39) reveal that time allocation initially increased as the price increased, the opposite of the behaviour that is usually seen. This low time allocation at low prices may be attributable to the putative side-effects of the stimulation such as forced movements, reward inhibition, or aversion. In other words, if the rat has an induced motor effect from the electrical stimulation, this will inhibit its physical ability to respond to the lever although the electrical stimulation may still be rewarding.

Experiment I: Individual rats

Most rats were indifferent to changes in very low prices and revealed a transition phase

Experiment I revealed that almost all rats showed indifference to changes in price when the price was sufficiently low. In 4 out of 5 subjects, the 95 % confidence interval around the CP included the frequency value of the STD for the lowest price pairs, 0.125 s vs. 0.25 s which implies that no frequency change is needed to compensate for a price change of 0.125 s to 0.25 (Figures 14-19, Appendix A, Figures 32F-35F). In other words these two prices are subjectively equivalent. For the one subject, B1 (Figure 15, Appendix A, Figure 32F) in which the STD frequency fell outside the CP confidence interval, the CP was close to the confidence limit of the CP. (Rat Y6 was not tested in condition 0.125 s vs. 0.25 s, but in the next highest price condition, 0.25 s vs. 0.5 s, the confidence interval around the CP included the STD frequency which implies that 0.25 s and 0.5 s are subjectively equal (Appendix A, Figure 36E).)

Experiment I also revealed a transition phase that was thought to occur before the scalar region of the subjective-price function derivative (Figure 2). This transition phase is illustrated by the growth region of the subjective-price function in Figure 2 that occurs between the part of the function in which the rate of change is 0 (first flat region) and the part of the function in which the rate of change is again constant (second flat region). This transition phase was demonstrated in Experiment I in all subjects by the increase in compensatory frequency change as the price pairs (differing always by the same proportion, 2) are increased.

Frequency-scaling did not reveal a scalar region for most rats

It was also predicted in this experiment that as the price pairs are increased past a certain price, the compensatory frequency change would eventually level-off indicating that the subjective differences between the price pairs would be equivalent at higher prices. This prediction was similar to the prediction in Experiment II in which past a certain price, the objective proportional price changes were predicted to be equivalent. The compensatory frequency change was predicted to level-off somewhere.

In the function estimated in Experiment I (analogous to the derivative of the subjective-price function shown in Figure 2) the prices are scalar when the curve is flat over a range of high prices. Note that on the derivative function there are two flat regions, one where the derivative is 0, indicating the range in which objective prices are equal to each other (rate of change = 0), and the region in which the derivative is constant, at the highest prices. To determine whether the subjective-price function begins to become scalar, there must be at least two prices on this flat range of high prices, what is plotted is the compensatory frequency change as a function of the price condition, a range of prices always varying by a constant of 2 (i.e. 1 s vs. 2 s, 2 s vs. 4 s). To determine where the function becomes scalar, equivalent compensatory frequency changes must be observed for at least two adjacent pairs of prices. In 2 out of 6 rats, (rats B6 and C27), equal compensatory frequency changes were noted for the two highest pairs of prices. Rat C27's two highest points are equivalent but the frequency change for ~ 1.4 s (condition 1 s vs. 2 s.) is higher than the last two points (~2.8 s and ~ 5.7 s) (Figures 14-19). This result was odd because the prediction was that as prices increased, frequencies would increase until the objective-subjective relation became scalar as illustrated by equal compensatory frequency changes. The frequency shifts for this rat were small (relative to the other subjects), and the variability was high. Thus, the apparent spike in the compensatory frequency change in the middle of the price range could be due these small shifts and large error bars. B6's data show a steady increase in frequency and then the predicted leveling-off the frequencies, indicating the scalar range.

The other rats did not show a proportional frequency change that reached a plateau. Perhaps the function becomes scalar for the other rats beyond the range of prices that were tested in Experiment I. As explained above, to infer that the function is scalar, equal compensatory frequency changes would have to be noted for at least two adjacent pairs of prices. Therefore, for B6, it appears that the function becomes scalar at around 3 s. Specifically, equal frequency changes occur in the 2 s vs. 4 s (denoted by the midpoint ~ 2.8 s) and the 4 s vs. 8 s condition (denoted by ~ 5.7 s), and thus it is inferred that past ~ 2.8 s the function is scalar. Perhaps the function for some rats becomes scalar at prices higher than 3 s, such as 4 s, 5 s, or 6 s. This scalar relationship at higher prices would not be revealed the way Experiment I was conducted because the highest price pairs that were tested was 4 s vs. 8 s, denoted by the 5.7 s point on the subjective-price function graph. If the function did become scalar at ~ 6 s, this relationship would only be revealed when testing higher-price conditions such as 8 s vs. 16 s (which would be denoted by 11.3 s on the subjective-price function curve).

The use of the fVI schedule and the undersampling at high prices may have also contributed to rendering the data more noisy which will be discussed later.

Experiment II: Individual rats

An equal compensatory price change was observed in most rats past a given price. The price after which the compensatory price changes became equal differed for each subject; however, these prices did not vary to a very large extent. This variation in the point at which the function becomes straight was to be expected because each subject is assumed to have its own subjective-price function.

This experiment entailed determining the changes in price that offset the difference between the STD and ALT frequencies. In the first phase (Phase A) in Experiment II, the frequency spacing was 0.2 log units, and in the second phase (Phase B), the frequency spacing was 0.1 log units. Comparisons of the 0.1 and 0.2 log unit frequency spacing phases will be discussed later. For now, the 0.2 log unit spacing will be considered as the more reliable condition and thus the better condition to estimate the scalar range of the function. In the 0.2 log unit frequency spacing phase, the objective prices after which the objective-subjective price relationship became scalar were 3 s for B6, 5 s for B7 and B9, 14 s for C27 (Figures 23-28). The only rat in which the compensatory price changes did not become equivalent was rat Y6 (Figure 26). For rat Y6, the CP shift became increasingly smaller which is illustrated in the shift summary graph (Figure 26) where the last two CPs are practically on top of each other for both conditions. Y6 was the first rat to be tested in this condition, and was the oldest rat of the group; perhaps it was unable to learn the task as well as the other rats. The price at which the proportional changes became equivalent to each other for rat C27, 14s (Figure 27), was higher than for the other rats, 3 s to 5 s (Figures 23, 24, 25).

In principle, curve-fitting could be used to estimate the price after which the subjective-price function becomes scalar; this would entail examination of the fitted function (the derivative of the subject-price function) to find where it approaches a value of one. That approach will be adopted in the case of the stronger data set obtained in Experiment III, but is beyond the scope of the analyses reported here. Instead, the lower limit of the scalar portion of the subjective-price function was estimated by simple visual inspection of the summary graphs. For example, the lower limit can be estimated to be for B6 in the 0.2 log unit phases at 3 s in Figure 23A, and for B7 at about 5 s in Figure 24A.

Deriving the subjective-price function using two frequency spacing conditions

Two frequency spacing phases were used in order to derive the subjective-price function; the methods were the same, only the size of the frequency ratio differed. In the first phase (Phase A) in Experiment II, the frequency spacing was 0.2 log units, and in the second phase (Phase B), the frequency spacing was 0.1 log units. It was expected that in the larger spacing phase (0.2 log units), the proportional price changes, denoted on the graphs as the distance between the log CPs, would be larger than in the smaller frequency spaced phase (0.1 log units). Specifically, a large compensatory price change would be required to compensate for a large frequency difference, whereas a small compensatory price change would be required to compensate for a small frequency difference. In all subjects except for B7, the proportional compensatory change was larger in the 0.2 log unit phase than in the 0.1 log unit phase for the first condition in which the STD price is set to 0.25 s. For the rest of the conditions, the proportional price changes of the larger frequency spacing condition were generally larger than that of the smaller frequency spacing condition for subjects B6 and B9 (reflected in the steeper slope of the curve in the smaller frequency spacing condition). The larger compensatory proportional price change differences in the larger frequency spacing condition were expected because it is thought that under the definition of payoff, the greater the frequency difference, the more the rat would be required to compensate for this difference with a greater change in price. For rat B7, proportional price changes were equivalent across the two frequency conditions even in the first condition. It is difficult to make valid comparisons for rat Y6 because of the odd data obtained (for possible reasons mentioned above), although, it can be noted that the initial compensatory price change (STD of 0.25 s) in the 0.2 log unit frequency phase was larger than in the 0.1 log unit phase. Nor was it possible to make valid comparisons for C27 because it only completed the 0.2 log unit phase and the first condition of the 0.1 log unit phase.

The unexpected equivalent proportional price change across the two frequency conditions for B7 may be explained by the use of frequency instead of reward intensity to infer compensatory price changes. Although the frequencies are set to 0.2 log units apart or 0.1 log units apart, the actual spacing between reward intensities is unknown because the reward-growth function has not been derived in these rats. For instance if 60 HZ and 38 Hz are used in the first 0.2 log unit spacing condition, the frequency spacing in the 0.1 log unit spacing phase would be 48 Hz and 38 Hz. The frequency spacing of the two conditions differed (the 0.2 log unit difference is twice that of the 0.1 log unit difference). It is the STD frequency (lower frequency) that remains constant in the two conditions. Because frequency and intensity do not vary in direct proportion with each other, the actual proportional difference between the two reward intensities would not be the proportion that is set by the frequency pairs, a doubling (0.2 log units is twice that of 0.1 log units). For instance, the corresponding reward intensity for 60 Hz may be at the asymptote of the reward-growth function, and the corresponding reward value for 38 Hz may be on the growth part of the reward-growth function. In the next condition, 48 Hz may correspond to a reward intensity at the asymptote of the reward-growth function as well. To the rat, 48 Hz and 60 Hz would have the same reward intensity. Therefore, the reward intensity difference between 38 Hz and 48 Hz is not half that of the difference between 38 Hz and 60 Hz as it is the case for the frequency values. The differences in reward intensity would actually be equivalent in the two conditions. Therefore, the proportional differences in frequency spacing conditions may not correspond to the same proportional differences in reward intensity. Because the definition of payoff takes into account reward intensity rather than frequency, CP shifts reflect the differences in reward intensity which may help explain the equal proportional price difference across Phases A and B. Consequently, the two experimentally derived subjective-price functions for both conditions look identical for B7. Had B7 survived long enough, it would have been possible to test whether the reward-growth function indeed saturated as proposed here.

Advantages of the 0.2 log unit and 0.1 log unit frequency spacing phases

Two frequency spacing conditions were used to estimate the subjective-price function in order to assess the reliability of the data. Both of these frequency spacing conditions have advantages and disadvantages. In the 0.2 log unit phase, because the contrast in the reward signal is strong, the rat is more likely to perceive a significant difference in the reward signals. The proportional price changes the rat will make in order to compensate for the significantly differing reward intensities will thus be more reliable. The advantage of the 0.1 log unit spacing is that there would be more points plotted on the subjective-price function than in the 0.2 log unit phase.

The limitation of the 0.1 log unit phase is that the reward intensity contrast is not large and therefore the rat may not make reliable compensatory price differences. The bar graphs in Figure 28 showing the proportional price changes as a function of the condition as denoted by the STD price illustrate that the results from the 0.1 log unit phase were less reliable than the 0.2 log unit phase. It was predicted that the proportional changes would decrease systematically and then become equal past a given price. Equivalent proportional price changes are inferred by the equal height of the bar graphs. If the 95 % confidence intervals of the bar graphs overlap, it is inferred that the price changes are not statistically significantly different. For the 0.2 log unit phases, for most of the subjects the proportional price changes decreased and eventually remained the same size. For the 0.1 log unit phase, the bar graphs seemed to increase and decrease sometimes in a nonsystematic fashion (Figure 28B) suggesting that the reward intensity contrast may not be great.

Other experimental factors affecting the results

Schedule of reinforcement: fVI and FCHT

The schedule of reinforcement used may have influenced the results. In Experiment II, the proportional price changes required to compensate for a constant frequency difference became equal for most rats; however, the absolute price changes (shifts) that eventually became equal to each other at high prices were smaller than predicted. Different factors involving the way in which the experiment was conducted may have caused these smaller than predicted price shifts. The schedule used may have influenced the size of these shifts. An fVI schedule in which the rat must be holding down the lever at the end of an unpredictable interval was used in order to provide greater control over the price than a traditional schedule of reinforcement. At higher prices, however, this schedule may be difficult for the rat to learn. Estimating prices in a price sweep is probably not an easy task for the rat; although the STD price remains the same, the ALT price varies from trial to trial, and on every trial, the rat must make an estimate of the price. The rat is required to be able to estimate in some cases unpredictable intervals that can be as high as 100 s (on the ALT lever). To make matters worse, the fVI is a variable schedule, and thus the rat must somehow extract the mean of the distribution of varying prices to which it is exposed.

In order to better estimate the average interval, the rat would probably need many encounters with the reward because the distribution (exponential) of prices includes a wide range of prices, from very low to very high and therefore the rat would have to "experience" a lot of these intervals within a session in order to make an accurate estimate of the average price. The number of encounters with the reward, and therefore the number of time interval estimates the rat makes depends on the length of the trial which may not have been long enough for the rats in Experiment II. Perhaps the a scalar region was not revealed in most of the rats in Experiment I partly because the animals may not have been able to correctly estimate the price presented. Furthermore, the somewhat non-systematic results seen in rat B6 in the 0.1 log unit phase of Experiment II (Figure 28B) may also be attributed to the same reasons.

In some cases the STD frequency may not have been rewarding enough to support stimulation at very high prices and this would cause the rats to consider the reward too "expensive" and therefore resulting in a breakdown of at higher prices because the rat would not be allocating much time to the lever. How rewarding the most rewarding frequency is depends on the placement of electrode.

Experiment III was conducted in order to obtain "cleaner" data; the factors described above were adjusted to make the task easier for the animal to learn. Instead of the fVI schedule, the fixed cumulative handling time schedule (FCHT) was used. On this new schedule, the rat is required to hold the lever for a cumulative experimenter-set amount of time. For instance, if the FCHT interval were set to 8 s, the rat would be required to hold the lever for a cumulative time of 8 s; it could hold the lever for 2 s, release for 1 s, hold again for 6s, and then obtain the reward (after a cumulative time of 8 s). This schedule was thought to be easier to learn because it is a fixed schedule rather than a variable schedule; therefore, the rat is not required to estimate the average of a distribution of time intervals. Although the fVI schedule is an improvement over the classical VI schedule for controlling the cost of the reward, the FCHT is even better because it directly sets the amount of time the animal is required to work (hold the lever) to earn a reward. Furthermore, the trial times were increased so that the rat would have enough encounters with the reward to permit it to compute an accurate estimate of the experimenter-set interval. Data for B10 were only collected for the 0.2 log unit frequency spacing condition. B10's data show that the CP shifts are relatively large compared to those observed in Experiment II. These larger price shifts may be due to the rat's improved ability to estimate the interval at higher prices due to the fixed schedule and the ample opportunity (increased trial time) to estimate the interval. Also, this rat worked particularly well at higher prices indicating a good electrode placement; at 8 s the time allocation to the STD lever was 0.5, and at 23 s, the highest price, the rat was still working at a time allocation of around 0.3. It appears that the function for B10 becomes scalar after about 3 s (Figure 30A), however the histogram (Figure 30B) reveals a slight decrease in the proportional compensatory price change for the last condition, past about 20 s. This slight decrease past 20 s probably does not mean that the function begins to be scalar at around 20 s, but may be due to the breakdown of responding (although better than the other rats) at this very high price.

Deriving the CPs in Experiment II

The results in Experiment II may have also been influenced by the way the CPs were experimenter-estimated. After a condition of the experiment is complete, such as the first condition in which the STD price is set to 0.25 s, the CP of the curve must be estimated because the STD price in the next condition is set to the CP price of the previous condition. Initially, the curve fitting method had not yet been developed, and the CP was estimated by eye from the raw data. When the experiments were complete, the models were fit to the data, and the CPs were derived. When comparing the CPs estimated from the raw data to those derived by means of curve fitting, there was often a degree of discrepancy. Because the STD prices must be set to that of the CP price in the previous conditions in order to develop the function as described, having the proper value of the CP is crucial. Therefore, the subjective-price function estimated is not completely accurate, yet close to what would have been derived if the CPs were determined initially using the model.

Experiment I and Experiment II complement each other

Experiment I and Experiment II both estimate the subjective-price function. Experiment I estimates the derivative of the function while Experiment II directly estimates the function itself. These two methods of estimating the function each offer different strengths in obtaining the various parts of the function. Experiment II (conjoint-measurement, price scaling) is the better method for estimating the scalar range of the function. The method employed in Experiment I is best suited for finding the range over which the rat is indifferent to price changes (the range over which the derivative of the subjective-price function is zero).

Experiment II also estimates the part of the function in which the scalar relation breaks down. The region of the function that is not scalar is illustrated by the larger proportional price changes compared to a series of equal proportional price changes that occur over a high range of prices. The limitation of Experiment II is that the method of price scaling cannot directly illustrate that this function is flat over the lowest range of prices. A flat range of prices can only be assumed by the initial large compensatory price change ranging from 0.25 s to a price outside of the flat range. Only one point can be positioned on the flat part of the curve because the task of the rat is to choose a price that is subjectively different from the STD price (which is 0.25 s in the first condition) in order to offset the two differing frequencies. A price that is subjectively different than 0.25 s will not lie on the flat part of the subjective-price function. Where the next CP after 0.25 s falls depends on the ratio of the reward intensities produced by the two trains; the CP will fall at least at the first price that is not on the flat part of the curve, but does not necessarily have to be at that exact price. If the reward intensity is great, then the CP will fall well past the point at which the function begins to be non-flat.

The strength of the frequency-scaling method is that it can confirm that the subjective-price function is flat over the domain of very low prices. The frequency-scaling method actually demonstrates pairs of prices that are interpreted as subjectively the same, and therefore lie on the flat range of the subjective-price function. As well, the frequency-scaling method is useful for determining the price at which the function begins to bend. The price in which the function is no longer flat is revealed when the CP shifts from the STD frequency, that is, the prices at which the confidence interval does not include the frequency of the STD. The price at which the CP shifts (increasing compensatory frequency) is generally seen at the price of 0.75 s and continues to 6 s. This increasing frequency as prices are increased is analogous to the transition part of the derivative of the scalar function (Figure 2), after the first flat part (where the derivative is 0) up to the second flat part of the function where the derivative is constant. The frequency-scaling method was unable to capture the scalar region of prices; perhaps the procedural problems (fVI, undersampling at high prices) stood in the way. Replicating the experiment under the adjusted factors may reveal a scalar region.

Comparing rats in Experiment I and Experiment II

The advantage of estimating the function by two different means in the same rats is that one can compare the reliability and strengths of the methods. One experiment measured the compensatory frequency change required to offset a price difference, the other experiment measured the compensatory price change required to offset a given frequency difference. In theory, the subjective price functions developed by these two methods should be the same, namely, the scalar range and where the scalar relation breaks down should be equivalent for both of the estimations of the function.

The frequency experiment (Experiment I) can be compared with Phase A of the price scaling experiment (the more reliable condition of Experiment II) for the individual rats. For B6, both the frequency scaling and price scaling method illustrated that the subjective-price function is scalar after 3 s. For B7 and B9, the frequency scaling method did not reveal a scalar relation whereas the price scaling method revealed the function to be scalar after about 5 s. Perhaps another condition in the frequency-scaling experiment (testing of higher prices) would reveal a scalar relationship. For C27, the frequency scaling method showed that the function is scalar after 3 s, but the price scaling method showed that the function is scalar after 14 s. For Y6, neither the frequency scaling nor price scaling method revealed a scalar relation.

Implications

The present experiments test a fundamental assumption about opportunity cost in organisms that has only assumed and has never been tested: that the relationship between subjective and objective opportunity costs is scalar. From a biological perspective, the assumption that subjective and objective prices are directly proportional makes intuitive and obvious sense: it would be detrimental to the animal if it could not accurately interpret objective costs. The present experiments support the implicit notion that the relationship between objective and subjective costs is scalar over a range of prices. The test of the scalar relationship of objective and subjective opportunity costs is important because it has not previously been conducted and it is the basis for the most generally accepted method for scaling reward value (matching) (Miller, 1976). Furthermore, it was revealed that at very low opportunity costs, this scalar relationship breaks down which has not previously been shown and has practical importance in choosing parameter values for experiments. The tests for determining at what prices the scalar relationship breaks down are important because subjective opportunity costs are used to scale other variables, such as reward intensity. If reward intensity is measured under the assumption that objective and subjective costs are equivalent, when in fact they are not, then this renders the scaling of reward intensity inaccurate. In experiments that entail price scaling, a test such as the one performed here should be carried out to determine whether the "price ruler" is straight. Generalizing from the findings in this thesis, prices of at least 5 s would be an appropriate value to use in experiments that use price as a parameter to scale other values.

Although opportunity costs are the focus, the animal's ability to estimate time intervals is assumed when developing the subjective-price function. The subjective-price function did indeed break down at low prices, indicating that opportunity costs are considered subjectively equal to each other at low prices. The function became scalar at higher prices indicating that objective opportunity costs are proportional to subjective opportunity costs over a range. Because estimates of opportunity costs are based on estimates of time intervals, and opportunity cost is scalar over a range of prices, then this implies that the relationship between subjective and objective time intervals is scalar over a range as well and thus supports the scalar theory of interval timing, at least for a higher range of time intervals.

These experiments also suggest that rats have the ability to perform complex computations. In the present dual-operant paradigm, rats behaved as if they had divided the reward value by the subjective price of a train of electrical stimulation while at the same time doing the same calculation for another train of electrical stimulation and then comparing the two payoffs to determine which is greater! These simultaneous calculations and decisions are impressive for a non-symbolic creature. The evidence that rats are performing a multiplicative computation while concurrently making comparisons is derived from the consistent shifts of the CP in the predicted direction, the eventual scalar relation and the reliable behaviour of the animal for each condition. It is thought that the calculation the rat makes is an automatic, innate process.

Applications

This scalar combination of subjective price and subjective reward intensity provides a straightforward way to estimate the reward-growth function. For example, the spacing between the frequencies triggered by both levers (as in Experiment II) can be varied such that the compensatory proportional price change can be determined at various frequency spacings. As the frequency spacing becomes larger, the proportional price changes are expected to become larger. If the compensatory price changes are equivalent from one frequency spacing condition to the other, then it can be inferred that saturation of the reward-growth function (upper asymptote) has been reached at these frequencies. Once the reward-growth function is derived, it will play an important role in studies aimed at determining the roles of different cells and systems in BSR. Different physiological manipulations can be used in combination with this function such as lesions, dietary restrictions, single unit recordings, and measures of neurotransmission. For instance, changes in dopamine transmission alter performance for BSR but their role in BSR is not yet fully understood. By measuring dopamine release (via microdialysis) and knowing how reward grows with increasing frequency (via the reward-growth function) the role of dopamine in BSR can be determined. That is, does dopamine release continue to increase when reward-growth saturates (which would imply that the input from the stimulated neurons to the dopamine neurons occurs before the computation of the rewarding effect has been made, suggesting that dopamine is involved in the experience of reward). Alternatively, does dopamine release increase and saturate in parallel with the reward growth (which would imply that the input from the stimulated neurons to the dopamine neurons occurs after the computation of the rewarding effect has been made, suggesting that dopamine is involved in another process that occurs following the computation of the rewarding effect). Another example of how the reward-growth function can be used in combination with physiological manipulations is the use of recording methods. For instance, one can record the activity of nearby neurons trans-synaptically activated by the experimenter. If the neuronal firing of a recorded neuron saturates at a much higher frequency than the subjective rewarding effect, then one can infer that it is unlikely that the neuron in question contributes significantly to the rewarding effect. Similarly, lesioning particular neurons and examining the effect of this manipulation on the reward-growth function would allow the experimenter to determine if a particular neuron is necessary in the experience of reward.

Summary

One of the principal goals of psychophysics is to describe the functions that transform the objective variables into their subjective equivalents. The present experiments estimated the function that transforms objective opportunity costs into subjective opportunity costs. In Experiment I, the change in frequency required to offset a constant proportional change in price was determined. In theory, this provides an estimate of the first derivative of the subjective-price function. In Experiment II, the change in price required to offset a fixed change in frequency was determined. In theory, this provides an estimate of the subjective-price function itself. The two different methods complement each other. The price scaling method revealed the scalar range of the objective-subjective price relationship. However, this price-scaling procedure cannot place more than a single point on the flat portion of the subjective-price function and thus, cannot tell us whether this portion is flat. The frequency-scaling method (Experiment I) provided this information, thus complementing what is learned from the price-scaling data.

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Appendix A

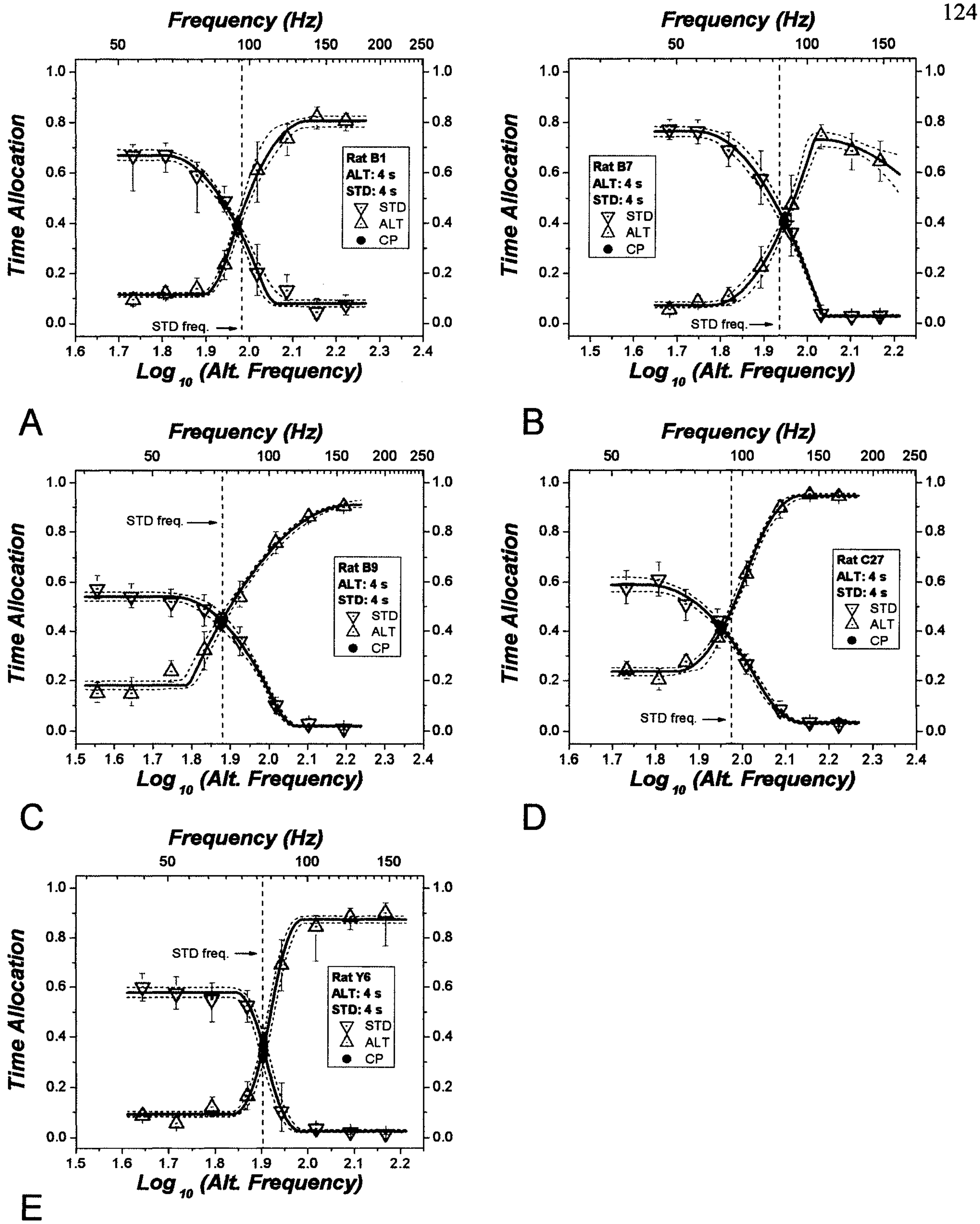


Figure 31. The 4 s vs. 4 s condition is a training condition and check to determine whether the rat had learned the task. The CP 95% CI includes the frequency value of the STD for rats Y6 and B9. For the other rats, the STD frequency was very close to the CP 95% CI.

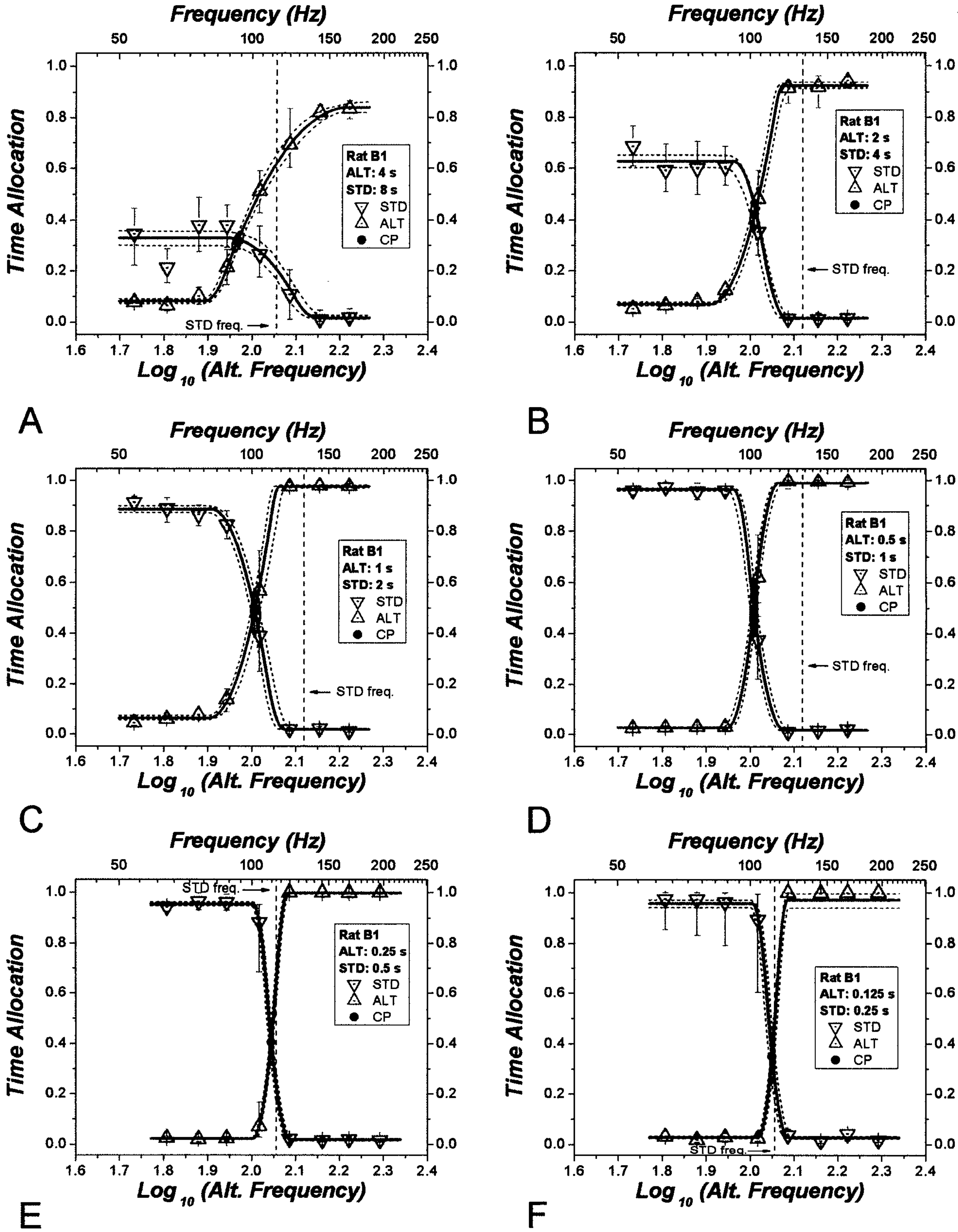


Figure 32. Graphs A-F are the results obtained for the experimental conditions for rat B1. As the price pairs are decreased throughout the conditions, the CP shift from the STD frequency diminishes which implies that the compensatory frequency change diminishes. This reduction in frequency occurs because small prices are thought to be subjectively similar and therefore less frequency is required to compensate for the price difference at smaller prices. Error bars represent 95% confidence intervals.

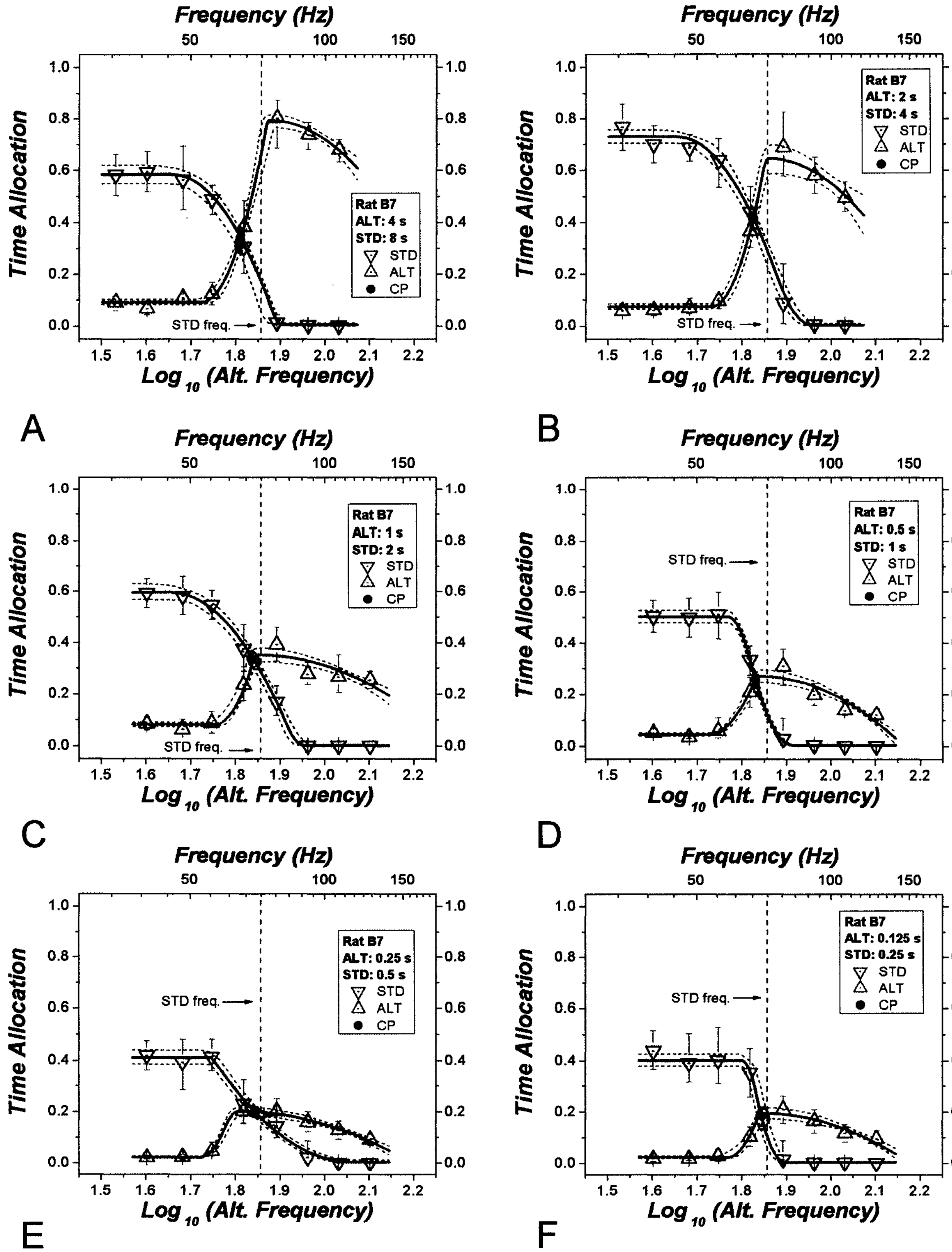


Figure 33. Graphs A-F are the results obtained for the experimental conditions for rat B7. As the price pairs are decreased throughout the conditions, the CP shift from the STD frequency diminishes which implies that the compensatory frequency change diminishes. This reduction in frequency occurs because small prices are thought to be subjectively similar and therefore less frequency is required to compensate for the price difference at smaller prices. Error bars represent 95% confidence intervals.

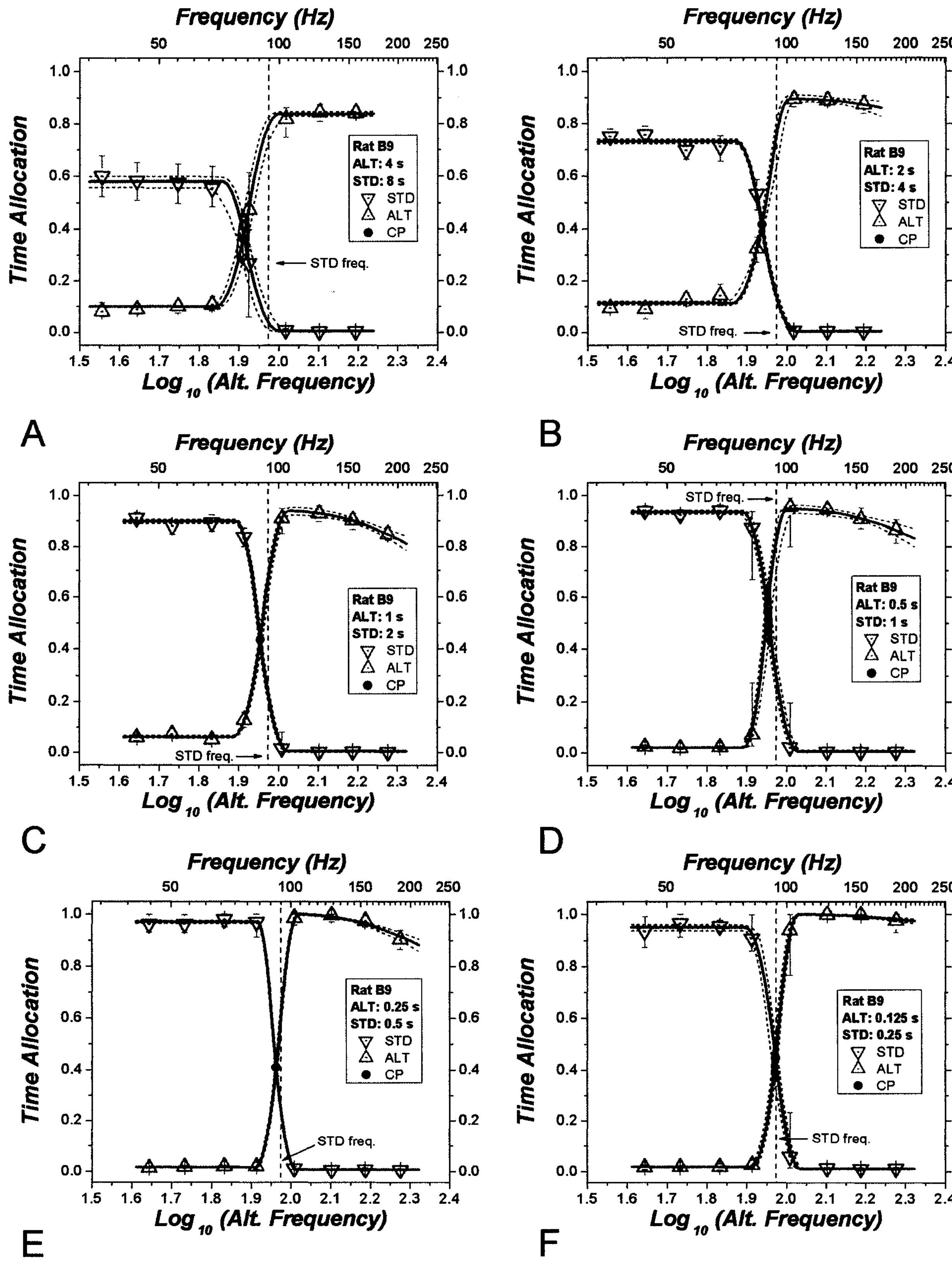


Figure 34. Graphs A-F are the results obtained for the experimental conditions for rat B9. As the price pairs are decreased throughout the conditions, the CP shift from the STD frequency diminishes which implies that the compensatory frequency change diminishes. This reduction in frequency occurs because small prices are thought to be subjectively similar and therefore less frequency is required to compensate for the price difference at smaller prices. Error bars represent 95% confidence intervals.

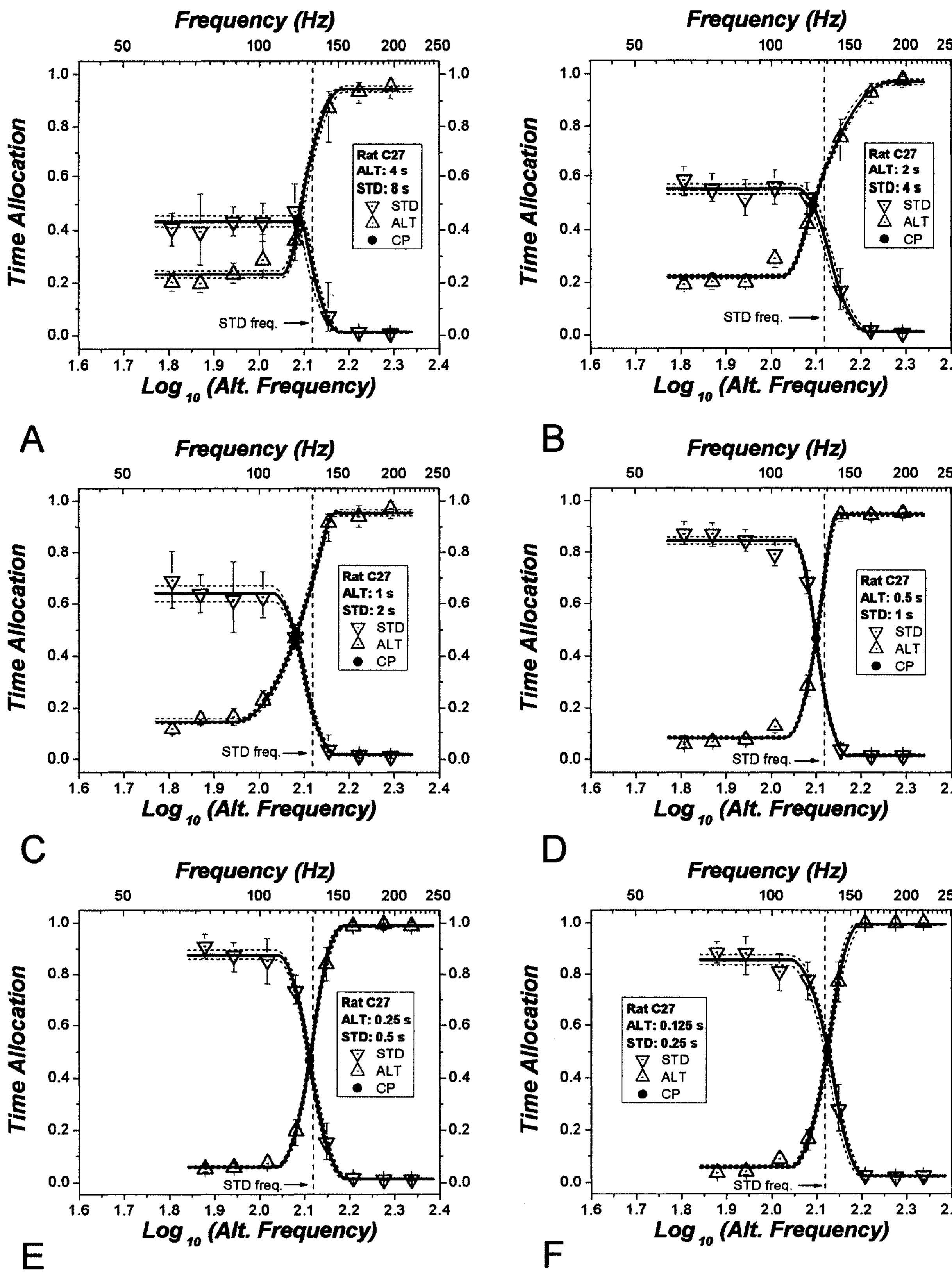


Figure 35. Graphs A-F are the results obtained for the experimental conditions for rat C27. As the price pairs are decreased throughout the conditions, the CP shift from the STD frequency diminishes which implies that the compensatory frequency change diminishes. This reduction in frequency occurs because small prices are thought to be subjectively similar and therefore less frequency is required to compensate for the price difference at smaller prices. Error bars represent 95% confidence intervals.

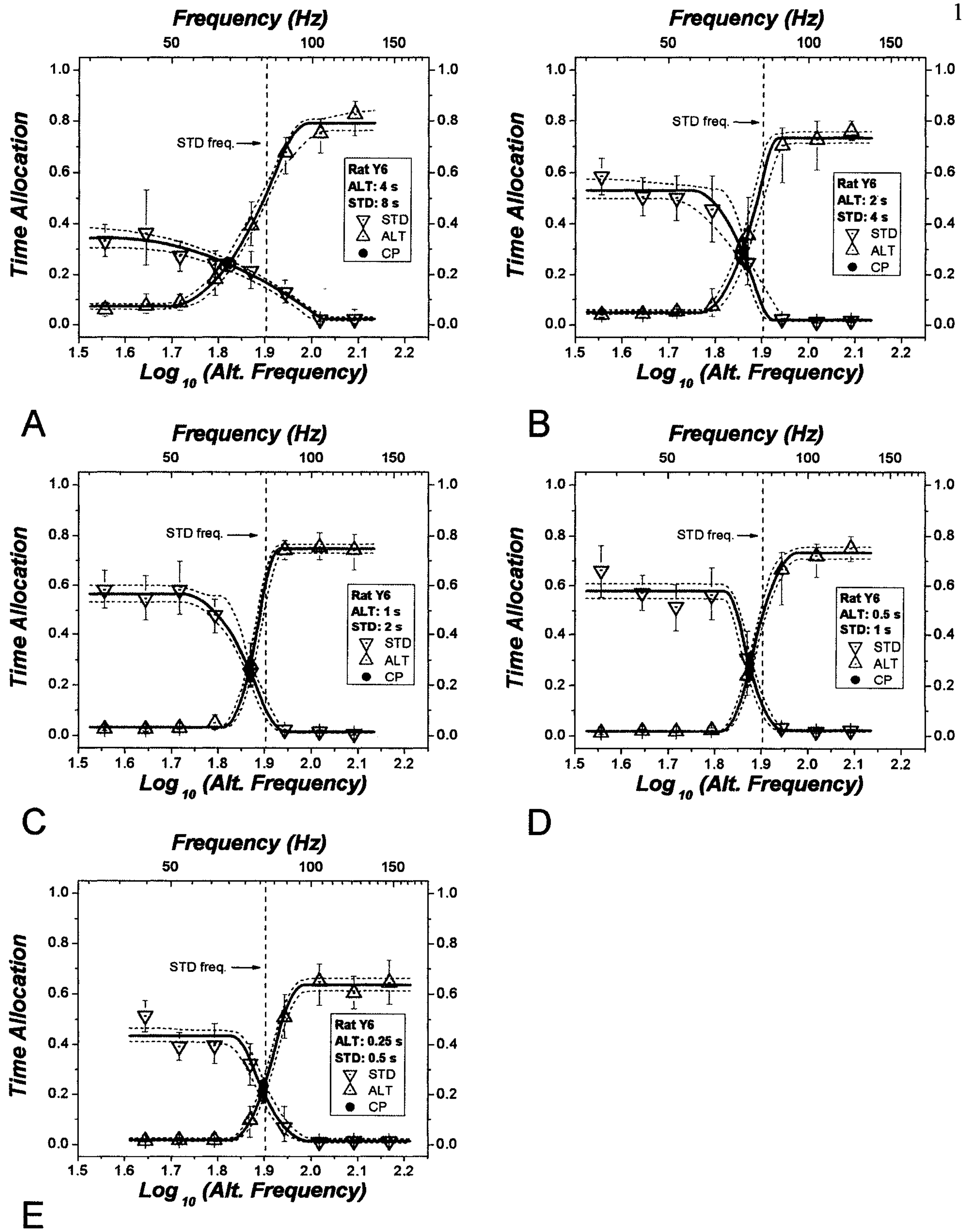


Figure 36. Graphs A-E are the results obtained for the experimental conditions for rat Y6. As the price pairs are decreased throughout the conditions, the CP shift from the STD frequency diminishes which implies that the compensatory frequency change diminishes. This reduction in frequency occurs because small prices are thought to be subjectively similar and therefore less frequency is required to compensate for the price difference at smaller prices. Error bars represent 95% confidence intervals.

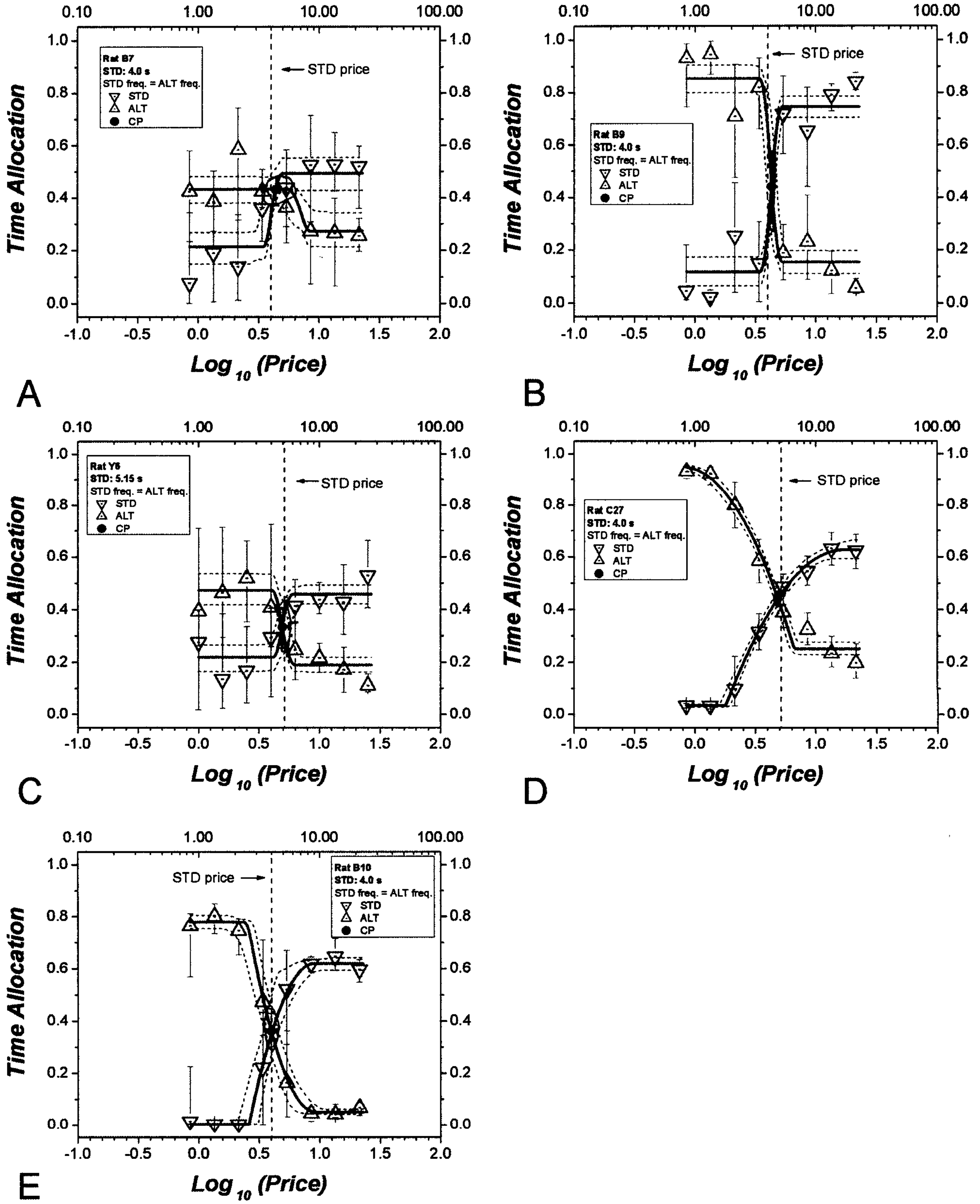


Figure 37. The price sweep condition in which the ALT frequency and STD frequency are equal is a training condition and check to determine whether the rat had learned the task. The CP 95% CI includes the STD price for rats B6 and B9. For the other rats, the STD price was very close to the CP 95% CI.

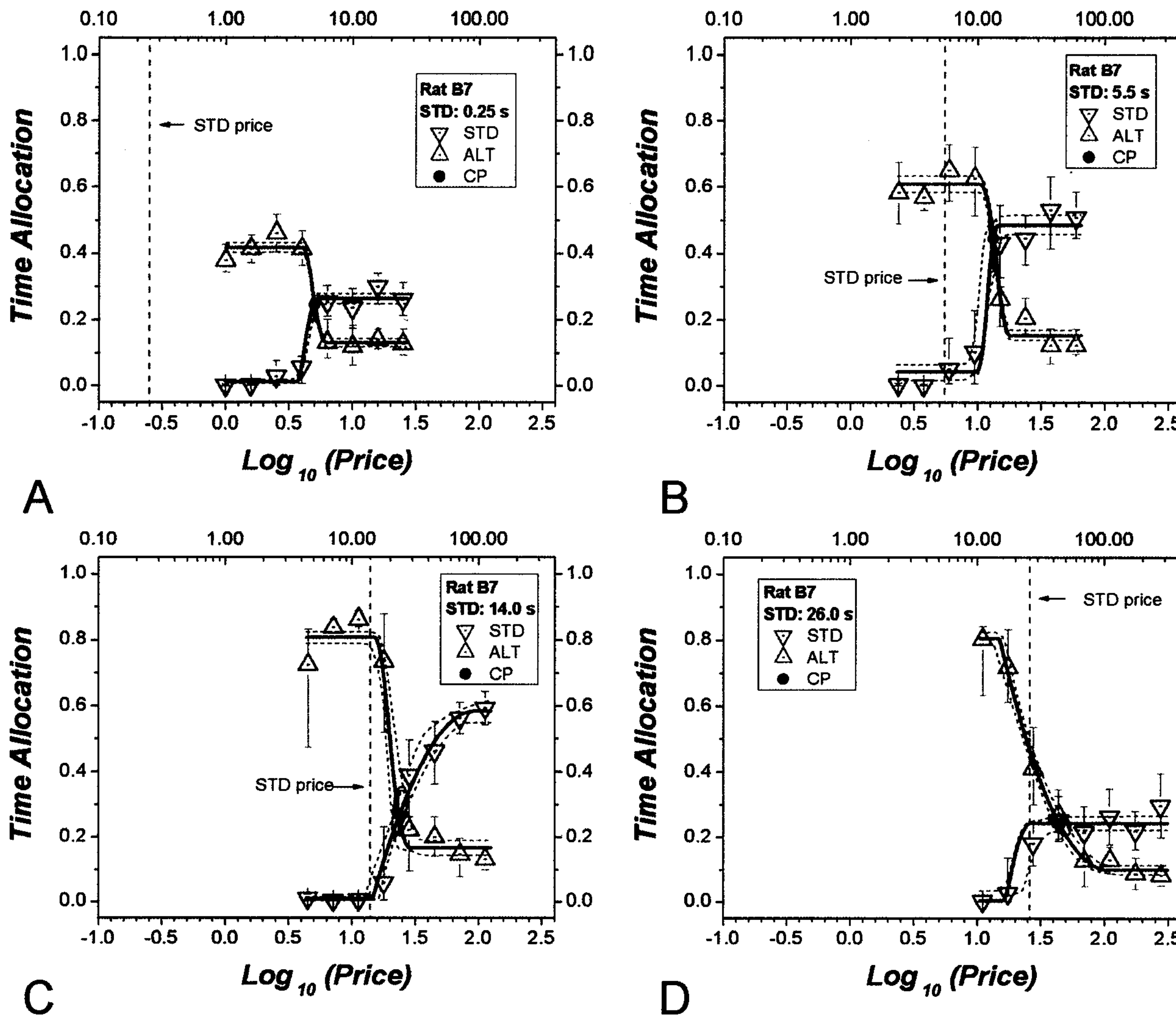


Figure 38. Graphs A to D illustrate time allocation as a function of ALT price when there is a 0.2 log unit spacing between the two frequencies for rat B7. The CP price shift is initially large in Condition A, becomes smaller in Condition B, and then becomes even smaller in Condition C, and stays almost the same in Condition D.

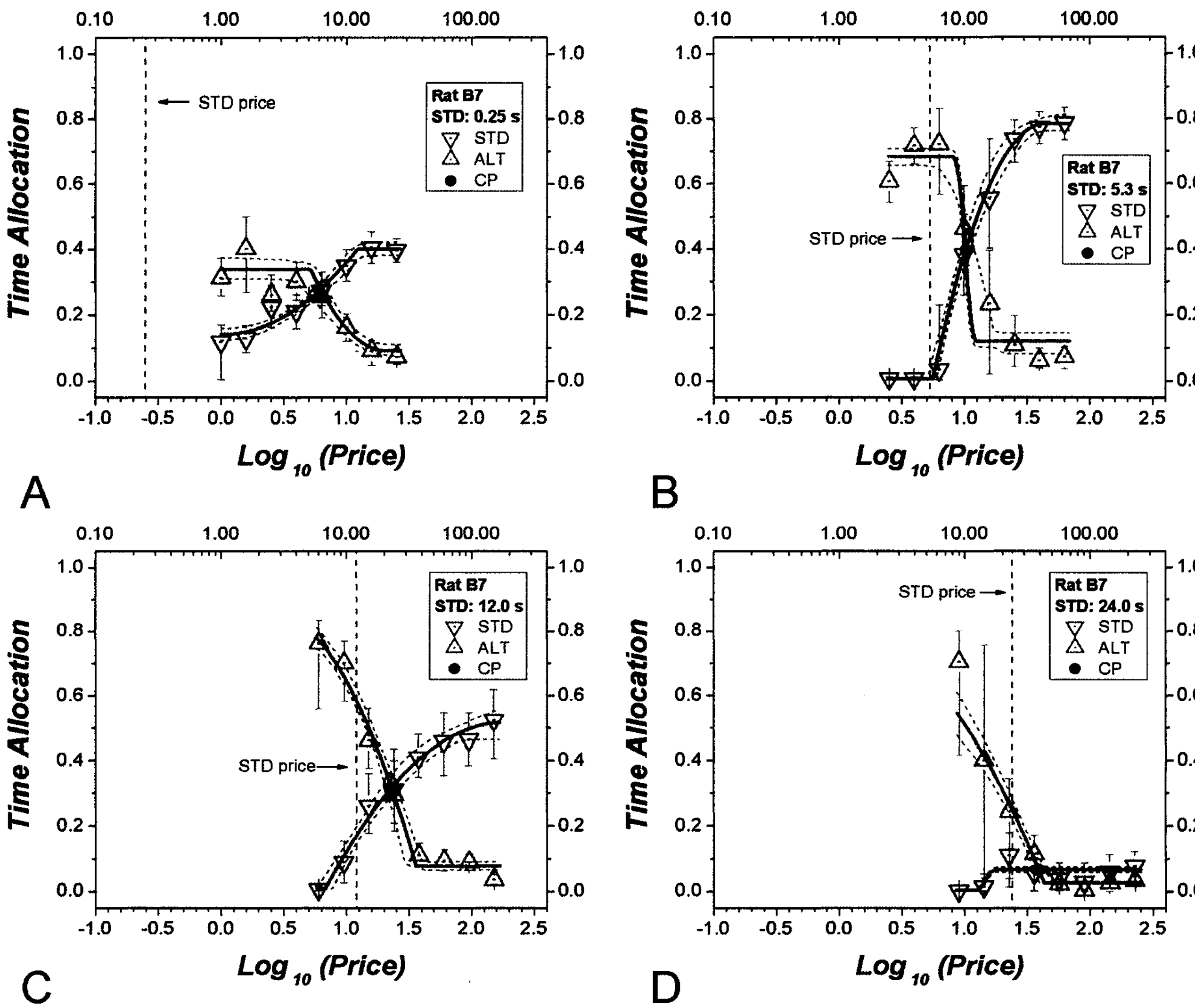
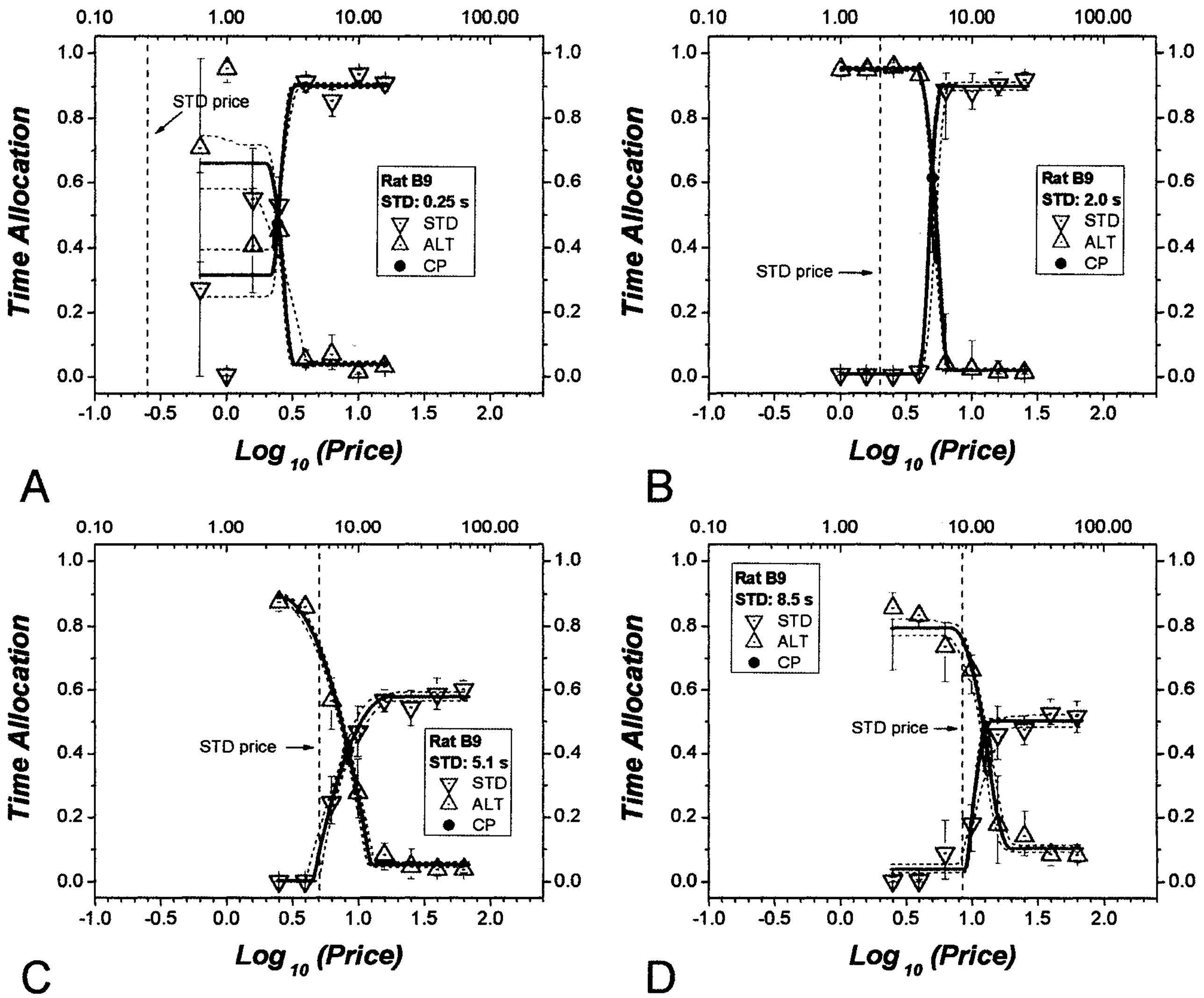


Figure 39. Graphs A to D illustrate time allocation as a function of ALT price when there is a 0.1 log unit spacing between the two frequencies for rat B7. The CP price shift is initially large in Condition A, becomes smaller in Condition B, and then becomes even smaller in Condition C, and stays almost the same in Condition D.


A
Rat B9
STD: 0.25 s
STD
ALT
CP
STD price
B
Rat B9
STD: 2.0 s
STD
ALT
CP
STD price
C
Rat B9
STD: 5.1 s
STD
ALT
CP
STD price
D
Rat B9
STD: 8.5 s
STD
ALT
CP
STD price
Time Allocation
Log 10 (Price)
0.10
1.00
10.00
100.00

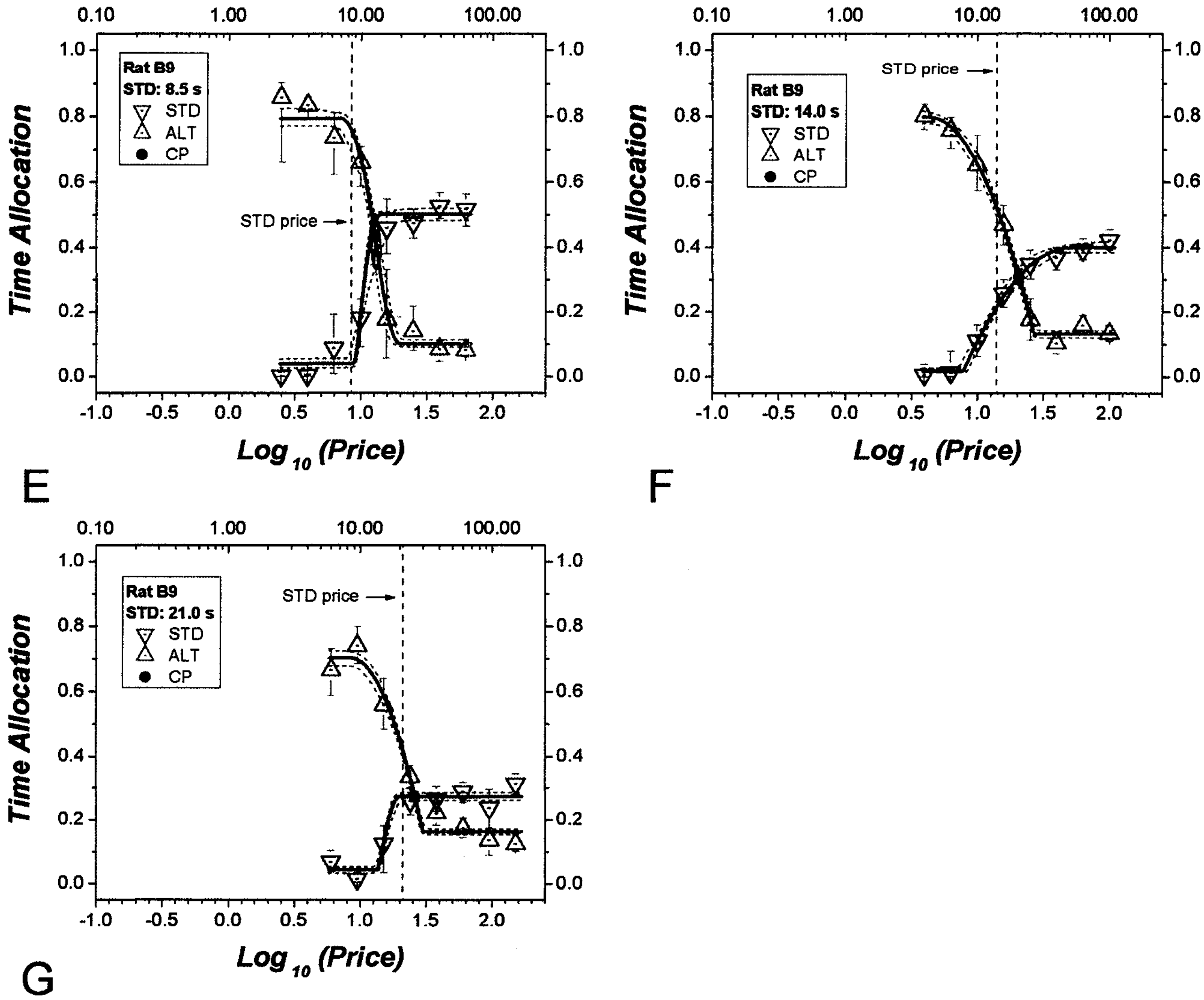


Figure 40. Graphs A to G illustrate time allocation as a function of ALT price when there is a 0.2 log unit spacing between the two frequencies for rat B9. The CP price shift is initially large in Condition A, becomes smaller in Condition B, becomes even smaller in Condition C, and levels off until Condition F, when it somewhat decreases in Condition G.

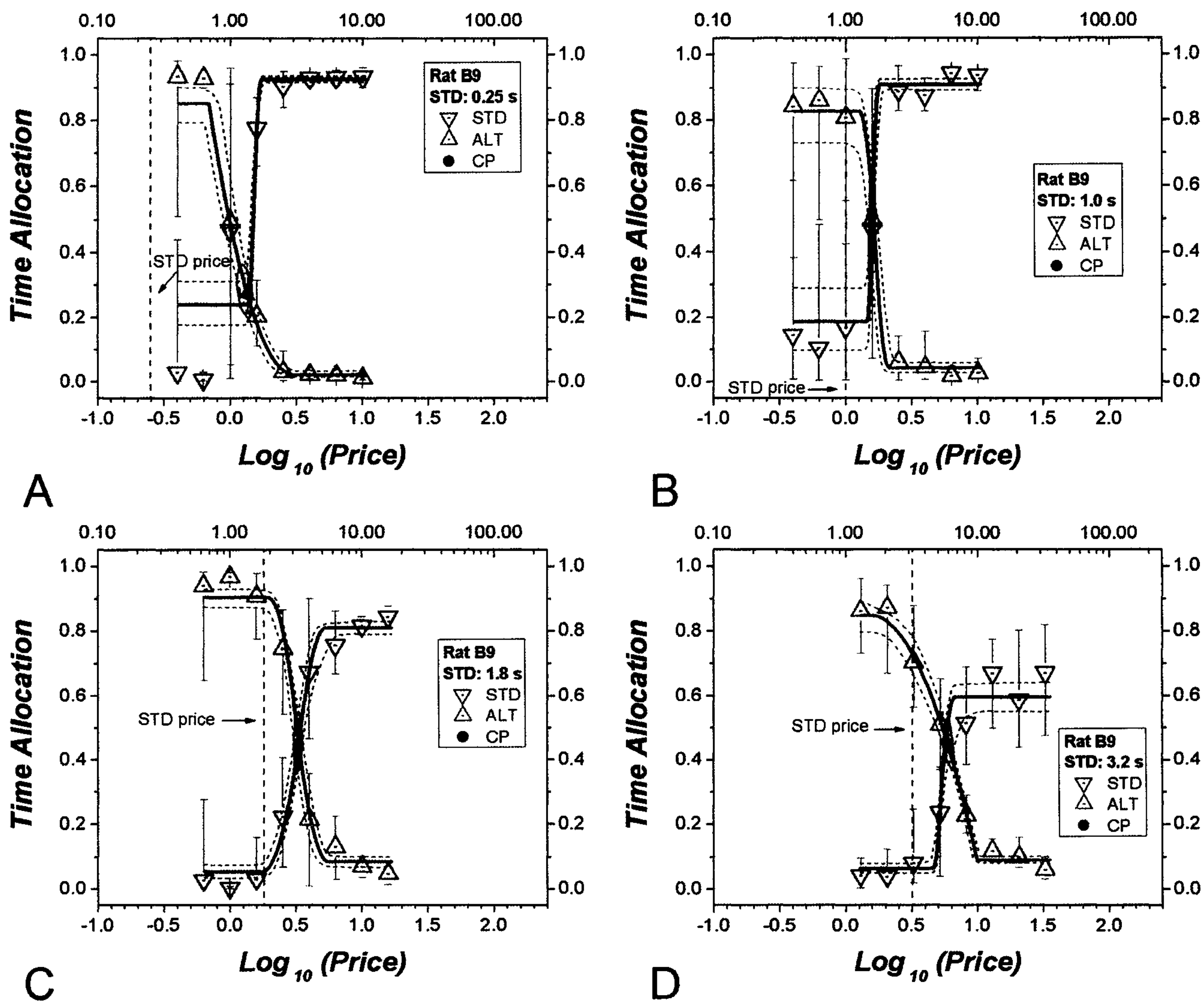


Figure 41. Graphs A to C illustrate time allocation as a function of ALT price when there is a 0.1 log unit spacing between the two frequencies for rat B9. The CP price shift is initially large in Condition A, becomes smaller in Condition B, and stays almost the same in Condition C.

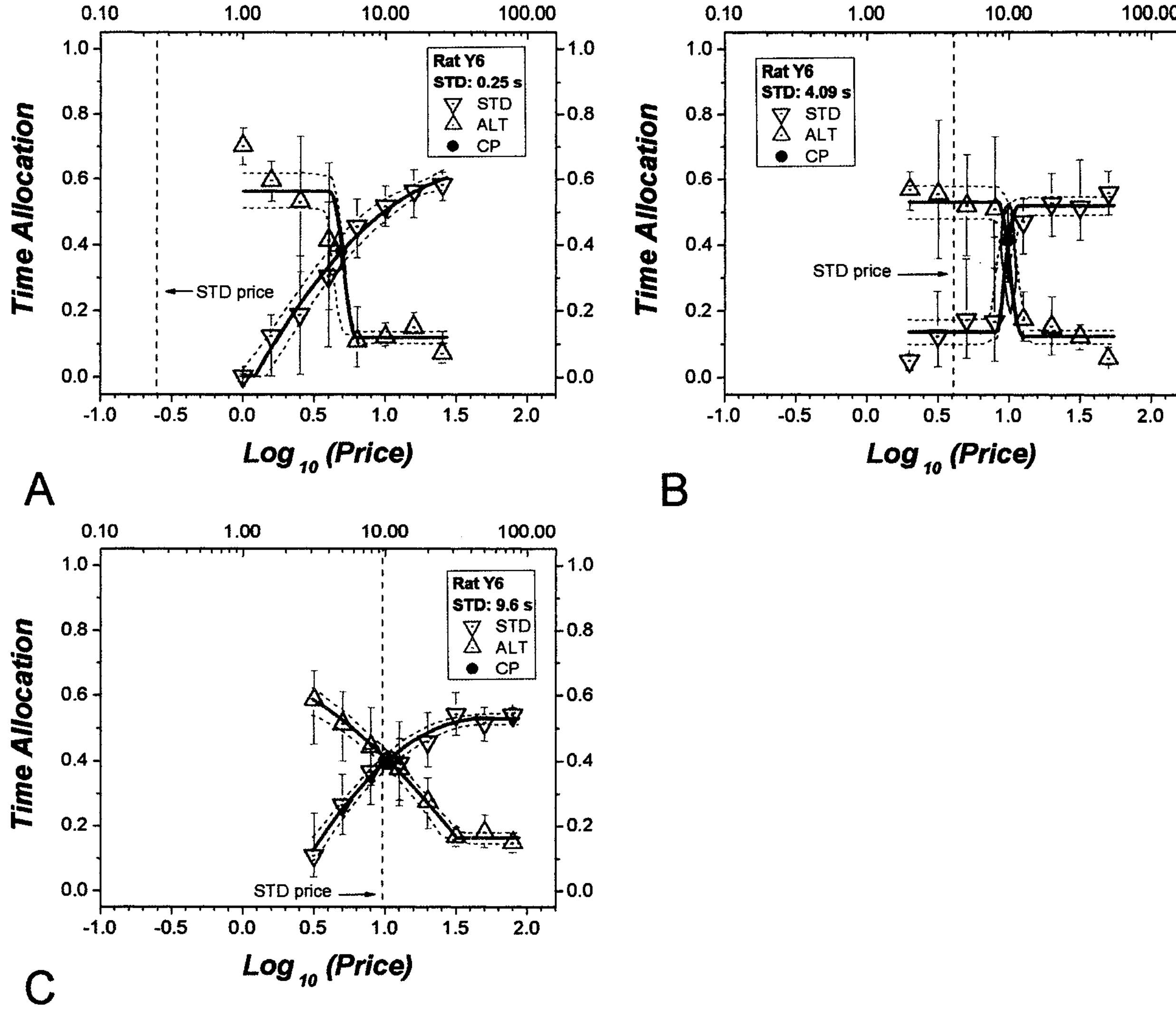


Figure 42. Graphs A to C illustrate time allocation as a function of ALT price when there is a 0.2 log unit spacing between the two frequencies for rat Y6. The CP price shift is initially large in Condition A, becomes smaller in Condition B, and becomes even smaller in Condition C, where a shift is barely seen.

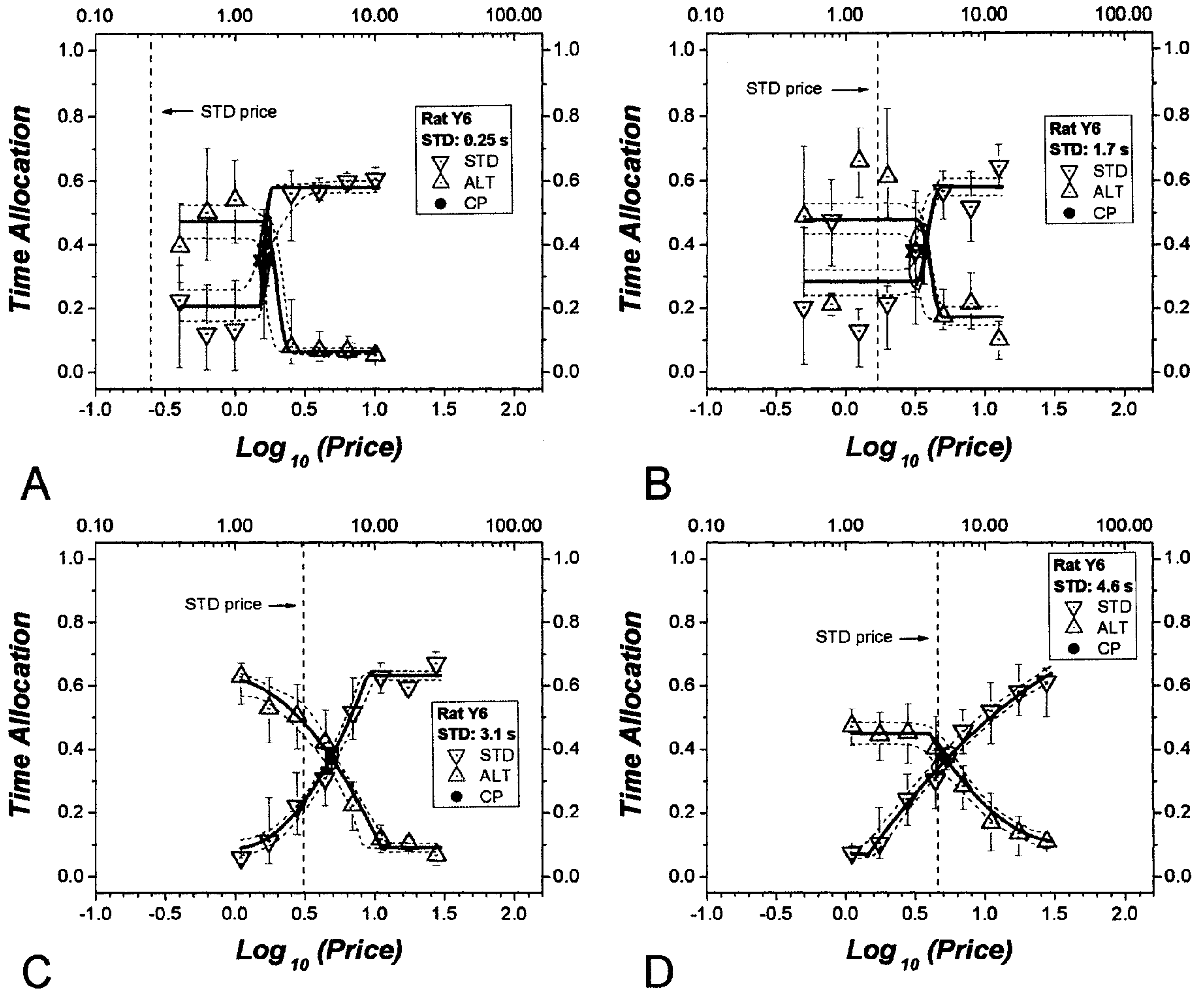


Figure 43. Graphs A to D illustrate time allocation as a function of ALT price when there is a 0.1 log unit spacing between the two frequencies for rat Y6. The CP price shift is initially large in Condition A, and decreases throughout the next four conditions.

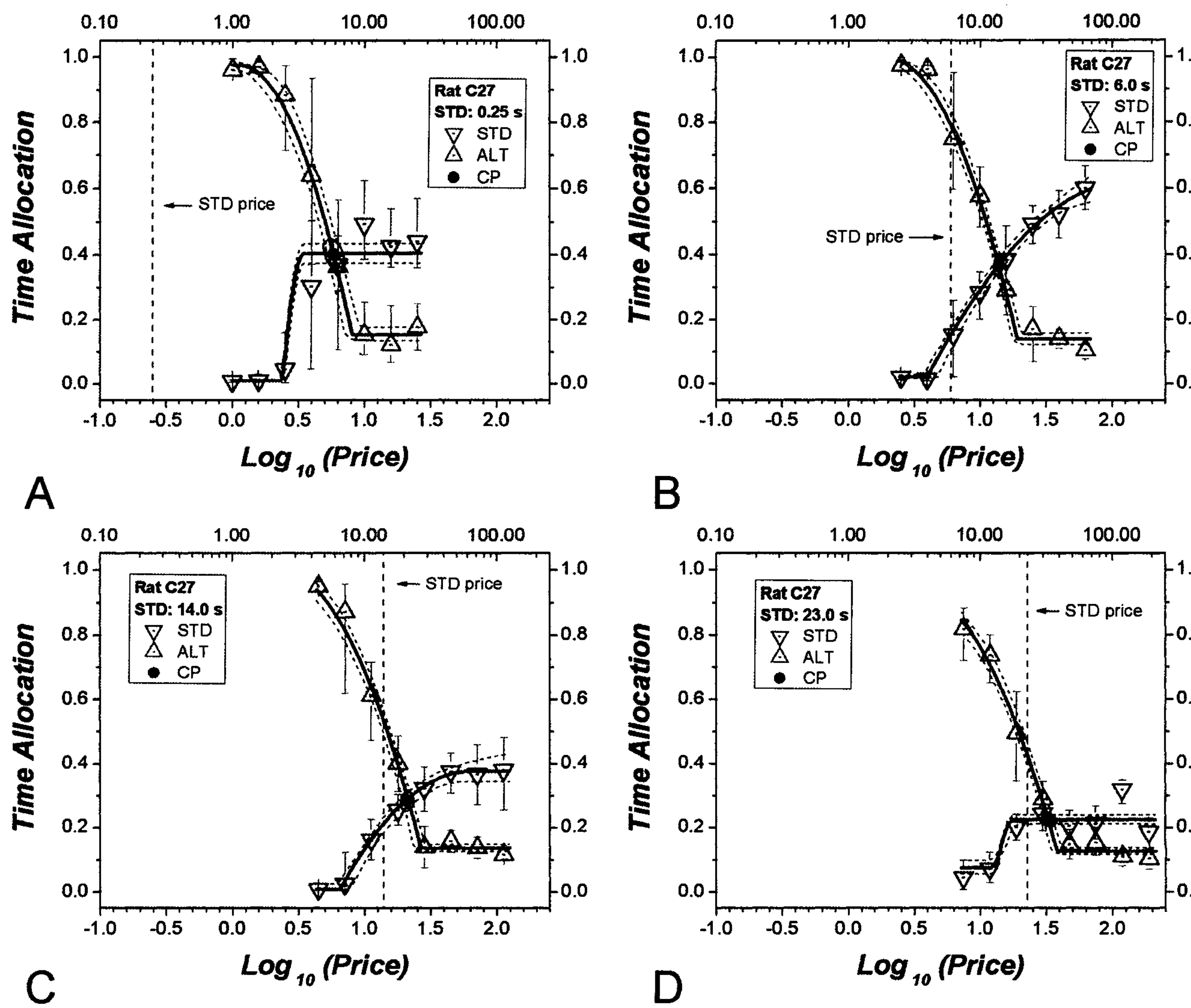
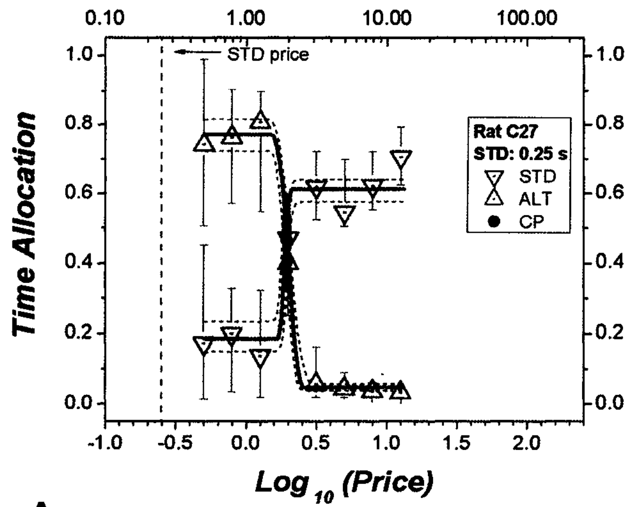


Figure 44. Graphs A to D illustrate time allocation as a function of ALT price when there is a 0.2 log unit spacing between the two frequencies for rat C27. The CP price shift is initially large in Condition A, becomes smaller in Condition B, becomes even smaller in Condition C, and stays the same in Condition D.



A

Figure 45. Graphs A illustrates time allocation as a function of ALT price when there is a 0.1 log unit spacing between the two frequencies for rat C27. The CP price shift is large in Condition A.

Appendix B

The dual quadratic model for psychophysical functions

The fitted parameters:

k_0: the knot (x-value) that joins the minimum straight line segment and the quadratic function in its accelerating phase

g_1: the growth parameter for the accelerating phase

g_2: the growth parameter for the decelerating phase

y_{min}: the minimum y-value (the minimum time allocation)

y_{max}: the maximum y-value (the maximum time allocation)

A function that accelerates implies that the slope is increasing. A function that decelerates implies that the slope is decreasing.

The derived parameters:

k_1: the knot (x-value) that joins the quadratic function in its accelerating phase to the quadratic function in its decelerating phase

k_2: the knot (x-value) that joins the quadratic function in its decelerating phase to the maximum straight line segment

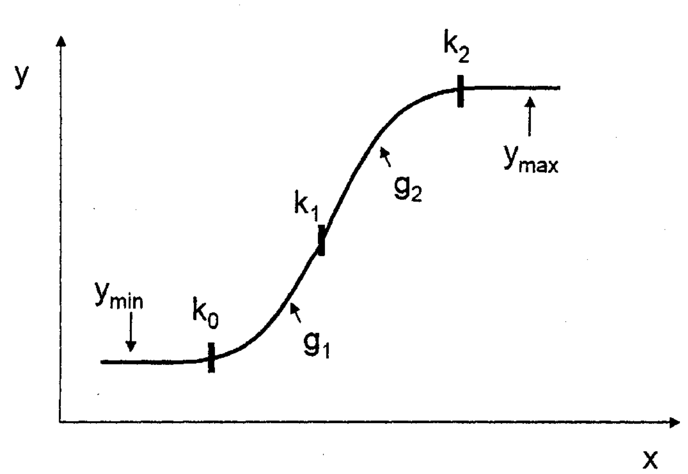


Figure 45. The total parameters of a dual quadratic function.

The dual quadratic function divides the x-axis into four domains

$-\infty < x < k_0$
$k_0 \leq x < k_1$
$k_1 \leq x < k_2$
$k_2 \leq x < \infty$

The dual quadratic equation can be expressed as follows

$y = y_{min}$, for $-\infty < x < k_0$
$y = y_{min} + (y_{max} - y_{min})\,(g_1(x - k_0)^2)$, for $k_0 \leq x < k_1$
$y = y_{min} + (y_{max} - y_{min})\,(1 - g_2(x - k_2)^2)$, for $k_1 \leq x < k_2$
$y = y_{max}$, for $k_2 \leq x < \infty$

Calculating the cross-point

The x-value of the cross-point is the most important value derived from the curve-fitting because it is the shift of the cross-point along the x-axis that is used to estimate the subjective-price function or its derivative. To calculate the x-value of the cross-point, the y-values of the dual quadratic function for the ALT function, $f_A(x)$, are subtracted from the y-values of the dual quadratic function for the STD function, $f_S(x)$. The x-value at which $y = 0$ for both $f_A(x)$ and $f_S(x)$ denotes the x-value corresponding to the intersection of the two functions (Figure 46).

The y-value of the cross-point is determined in the same way, the x-values of $f_A(x)$ are subtracted from the x-values of $f_S(x)$. The y-value at which $x = 0$ for both functions denotes the y-value corresponding to the intersection of the two functions.

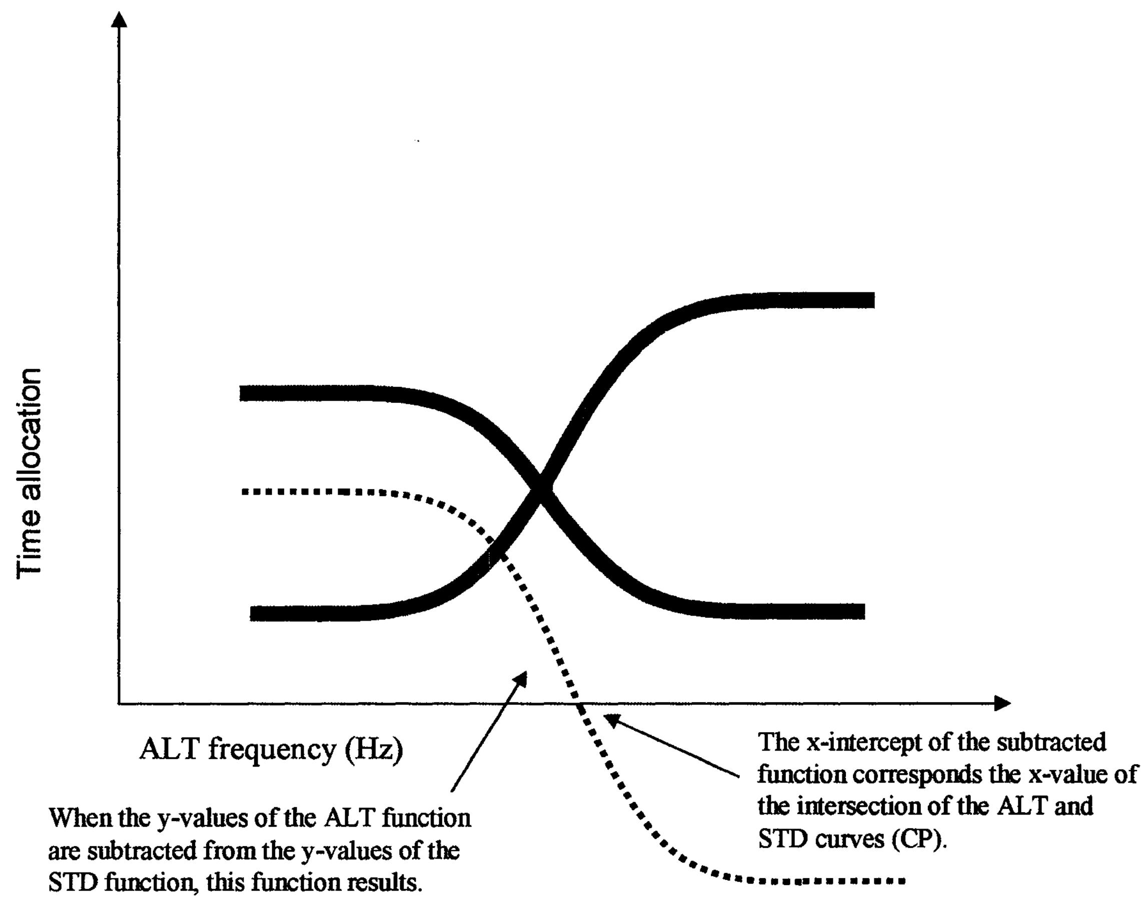


Figure 47. The x-value of the CP is found by subtracting the y-values of $f_A(x)$ from those of $f_S(x)$ and determining x-intercept of the subtracted function.