

INTERMODAL STIMULUS COMPOUNDING WITH AMBIENT ODORS

PRODUCES AVERAGING IN RATS

Sophia B. Kirkland, B.S.

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APPROVED:

April Becker, Committee Chair
Jesús Rosales-Ruiz, Committee Member
Daniele Ortu, Committee Member
Manish Vaidya, Chair of the Department of
Behavior Analysis
Nicole Dash, Dean of the College of Health
and Public Service
Victor Prybutok, Dean of the Toulouse
Graduate School

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In an organism's natural environment, there are always an uncountable number of stimuli, and stimulus features, available to gain control over behavior. When these component stimuli are presented simultaneously, this new stimulus compound can occasion a previously unseen effect on behavior. Stimulus compounding is a method used to better understand how variables in stimulus features may impact the final effect on an organism's responding when presented with a stimulus compound. While stimulus compounding experiments are often conducted using intermodal tone and light stimuli, it is conducted far less often using intramodal stimuli, potentially due to the competing stimulus features of same-modality stimuli. Even less conducted research has been done using two odor component stimuli, despite the large impact odor has on many species' behavior. The purpose of this study was to conduct a stimulus compounding experiment using intramodal ambient odor stimuli in rats, to see what kind of effect a mixed odor compound would have on the subject's behavior. This was done using a wind tunnel designed operant chamber, where both subjects were trained to respond to independently presented odor stimuli. Following training a compound mixture of both component odors was presented to the subjects. The results of this study demonstrated an averaged effect on behavior, producing a response rate under the compound mixture that was intermediate to the response rates under each independent component stimulus. This may be due to several factors, including the efficacy of initial training procedures, the efficacy of the apparatus, and the merging of the component stimuli's features.

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INTRODUCTION

Behavior is a function of an organism's environment, and the environment's arrangement of stimuli. In behavior analysis, this simple truth often focuses on the control exerted on behavior by consequences. Antecedent conditions, however, can hold powerful control over behavior as well by occasioning the organism's reflexive behaviors and previously conditioned operant behaviors. Stimulus control occurs when a stimulus gains control of an organism's behavior due to previous contingency changes with respect to a behavior altering consequence (Perez, 2018). The organism's natural environment always contains multiple stimuli and stimulus features available to gain control of behavior. These features can be divided or combined in near immeasurable sequences throughout the organism's learning history. Thus, stimulus control over the same response can develop from multiple antecedent stimuli or features in complex environments. This project's primary aim is to investigate a particular phenomenon related to this complexity: stimulus compounding. Stimulus compounding occurs when two previously learned stimuli or stimulus features are combined and produce more exaggerated behavior (summation) or averaged behavior (averaging). This phenomenon has not often been addressed in rats using their primary sensory modality: olfaction. I therefore want to see if a mixed odor compound will produce either summation or averaging, following independent training of responses under each individual odorant component.

Stimulus compounding occurs in many everyday environments. For example, human organisms often communicate with vocal speech, which includes fluctuations in tone, as well as the words spoken. Both the speaker's tone of voice and the content of their words can individually evoke certain responses from a listener. A parent wanting to stop their child's screaming may do so by vocalizing a wordless, scolding sound. The tone of the sound itself may

be enough to occasion an alternate, more appropriate response from the screaming child. The independently whispered word “stop” may also be sufficient in occasioning this response. The combination of both the scolding tone, and the word “stop” however, might be found to be much more effective at decreasing the rate or intensity of the child’s screaming. The independent presentations of the scolding tone, and the word “stop”, are component stimuli. When presented simultaneously in the child’s environment, these stimuli create a compound stimulus that occasions a higher probability of the appropriate response than before.

An organism's behavior can be affected in several different ways when presented with multiple stimuli simultaneously after training with each stimulus individually (Weiss, 1972). While stimulus compounding nomenclature can vary, for the purpose of clarity, this paper will use nomenclature from Weiss’ 1972 review paper. Weiss (1972) describes the definitions of additive summation, averaging, and suppressive summation. These definitions are key to describing the effects of stimulus compounding on an organism’s behavior. Additive summation is defined as when the response rate under the presence of the compound stimulus is higher than the response rates under the presentation of each component stimulus. Averaging is defined as when the response rate under the presence of the compound stimulus is between or intermediate to the response rates under the presence of each component stimulus. Suppressive summation is defined as when the response rate under the compound stimulus is less than the response rate under the presence of each component stimulus. A component stimulus is one of the individual stimuli that comprise a compound stimulus. A compound stimulus is the simultaneous presentation of more than one component stimulus. This can happen in several ways, including presenting the components overlapping on one another, presenting the components simultaneously but separated spatially, or combining the components together creating a mixture.

When the component independently learned stimuli are presented simultaneously as a compound, the effects are referred to as the merging of learning histories. These learning histories may summate to produce a higher or lower response rate, or they may compete to produce an averaged response rate. Compounding is an important phenomenon to consider when trying to understand how an organism reacts to the overall complexity in its natural environment pertaining to the presentation of component and compound stimuli (Perez, Martin, & Soto, 2018).

Stimulus compounding experiments are typically conducted by either using an unconditioned response (UR) under the control of two independently presented unconditioned stimuli (US) / conditioned stimuli (CS), or (under operant procedures) teaching a discriminated response separately to two antecedent stimuli. Past studies demonstrate that either classical or operant conditioning procedures can produce additive and suppressive summation (Weiss, 1969, 1971, 1972). However, some studies (e.g., Ayden & Pearce, 1997) have shown that operant training using contingent reinforcement more reliably produces summation compared to classical conditioning, perhaps because operant procedures more explicitly track and condition the discriminative function of the previously neutral stimulus (Aydan & Pearce, 1977; Holth & Arntzen, 1998; Weiss, 1972). Both positive and negative reinforcement histories can produce additive summation. Miller (1969) demonstrated additive summation using negative reinforcement by pairing independent presentations of light and tone component stimuli with the delivery of a shock. When the subjects crossed over a line on the floor, the tone or light (T, L), was terminated along with the shock. When the two components were presented simultaneously as a compound (T+L), the subject's response latency decreased below its initial rate under the presentation of either component stimulus. Kearns, Weiss, and Panlilio (2002), used operant

conditioning to produce suppressive summation of cocaine seeking behavior in rats. They did this by training rats to press a lever contingent on the delivery of cocaine on a VI schedule. Following this training, the independent presentations of both tone and light component stimuli were paired with the delivery of a shock. The delivery of this shock resulted in a decreased response rate. When these stimuli were presented as a compound, the subjects' response rate decreased below their response rate under the component stimuli.

Both Rescorla & Wagner (1972), and Pearce (1987), have developed quantitative accounts to conceptualize how the behavioral control of stimulus features may sporadically carryover from either a compound stimulus to its component stimuli or vice versa. Both accounts were originally based on classical conditioning techniques, but more recent research has tested their models using operant conditioning, producing similar results (Pearce, 2002; Weiss, 1972). Rescorla and Wagner developed an "elemental" account, emphasizing that the control held by a compound stimulus is also held by the individual compound "elements" (component stimuli). This account states that when a stimulus compound (A+B) is conditioned to control a behavior, this control (C^C) is held in the compound's unique stimulus feature (C^{FC}). This feature is unique to the compound stimulus, and its existence is dependent on the specific variations in the component stimuli's features (A^F, B^F). When these component features (A^F, B^F) are contained in the stimulus compound in the moment of conditioning, they are also conditioned alongside the compound stimulus' features (C^F), and consequently gain their own, individual control over the response (A^{FC}, B^{FC}). Based on this assumption, Rescorla and Wagner postulate that the behavioral control held by the compound stimulus' features (C^{FC}) is equal to the combined total control of both component stimuli's features ($A^{FC} + B^{FC} = C^{FC}$). This implies that the production

of additive summation, subtractive summation, and averaging, is dependent on the previously held control of a compound stimulus' component features.

This elemental view of stimulus features is contrasted by the “configural” account produced by Pearce (1984). This account states that the behavioral control of a compound stimulus (C^C) is held in the specific configuration of the component stimuli. When each component stimulus (A, B) is presented independently during conditioning, this independent arrangement functions as a stimulus feature (A^F , B^F), gaining control over the subject's behavior. Consequently, these stimulus features and their behavioral control can be lost in the presentation of the compound stimulus. When the component stimuli (A, B) are presented together as parts of a compound stimulus (A+B), both the component stimuli's features (A^F , B^F) and the stimulus control held by those features, dissolve together to become a new, compound stimulus feature (C^F). This new stimulus feature is unique to the compound because it is only produced due to the merging of specific component stimulus features, and therefore its control over behavior is dependent on the control previously held by each component feature.

Kehoe & Gormezano (1980) and Kehoe (1980) had a similar approach to conceptualizing compounding stimulus compounding outcomes. They describe the combination law and the interaction law. The combination law suggests that the control of the component stimuli to the behavior “combined”, resulting in an increase in responding under the presence of both compounds (Kehoe & Gormezano, 1980). This implies that the stimulus control held by each component stimulus carries over when the components are presented as a compound. Therefore, the behavioral control of both components merges into a greater control on responding. The interaction law, on the other hand, implies that the control of each compound stimuli interacted with the other, resulting in a non-summative behavior under the compound stimulus (Kehoe,

1980). This implies that the stimulus control held by each component stimulus may not completely carry over when the components are presented as compound. Therefore, some of the behavioral control of either component is lost, resulting in an equal, or lower control on responding.

While these quantitative and conceptual approaches provide a framework for organizing research outcomes, an alternative (or perhaps a complimentary) approach is to identify which unconsidered variables in stimulus compounding experiments may influence the production of summation vs. averaging. Two of these potential variables include the conditioning histories paired with each independent component stimulus (Weiss, 1972), and the use of either intermodal or intramodal component stimuli (Kehoe et al., 1994; Miller, 1971, 1974; Pluta et al., 2011; Rowe, 2005; Weiss, 1964).

Determinants of Compounding

Component Conditioning Histories

Weiss (1969) developed the concept of a "composite continuum" to better understand the relationship between the contingencies paired with the individual component stimuli and the response rate produced during the total presence or absence of those component stimuli. The composite continuum represents the available combinatorial variations involving not only the presence, but also the absence of stimulus components. One can think of it as a sliding scale in which one side is the complete absence of all relevant component stimuli (e.g., $\bar{T} + \bar{L}$: no tone, no light), and on the other is the complete presence of all the relevant component stimuli (e.g., $T + L$). Between these two ends is the range of potential compounds that could be present or absent.

Previous studies have demonstrated that when the individual presentation of a component

stimulus (either T or L) is trained in a discrimination paradigm that includes extinction under the absence of either stimulus, (\bar{T} , \bar{L}) the presentation of the compound stimulus (T+L) produces a higher rate of summation, compared to when a response is conditioned without a discrimination paradigm (Weiss, 1972).-These results were produced in studies in which either the extinction of the experimental response and/or the differential reinforcement of other behaviors (DRO) occurred in the absence of either stimulus \bar{T} or \bar{L} . Both DRO and extinction in the absence of either \bar{T} or \bar{L} produces summative results (although the use of DRO produced slightly lower rates of summation compared to the use of extinction (Weiss, 1971, 1972)). While full extinction is not necessary for summation of responding to occur, it does increase the likelihood of summation being produced by the presentation of the compound stimulus.

Weiss (1972) proposed the interpretation that summation occurs because when a single component stimulus is presented to an organism, there is also a simultaneous "presentation" of the absence of the other component stimulus. The absence of the second component stimulus may gain some control over responding. If so, this absence also holds partial control over responding as an Sd. Therefore, when both stimuli are presented as a compound, these "absent stimulus" features are missing, and the compound does not contain all controlling stimulus elements. However, during extinction or DRO condition with both stimuli absent, these "stimulus absent" features may lose their control over the response and become SAs, permitting unhampered summation to the compound stimulus.

Weiss (1969) explored this theory by testing the symmetry of the composite continuum. He first trained subjects to discriminate between the presence of each individually presented component stimulus (tone and light), and an extinction condition signaled by the presence rather than the absence of both component stimuli (T+L). After this training period, the subjects were

tested with randomized presentations of either T, L, T+L, or $\bar{T}+\bar{L}$. Results showed that the subject's response rate in the $\bar{T}+\bar{L}$ condition was significantly higher than in the presence of either T or L; i.e., summation occurred to the compounded absence of stimuli. The simultaneous presentation of T+L resulted in almost no responding at all. These results demonstrate that either the presence or absence of stimuli in a discrimination paradigm can determine which side of the composite continuum summation of responses will occur. This confirms Weiss' idea that both continuum extremes are symmetrical, in the sense that they can gain equal control over responding.

Weiss & Emurian (1970) also demonstrated the symmetry of the composite continuum by training suppressive summation on responding under $\bar{T}+\bar{L}$. In their experiment, subjects were trained to a baseline rate of lever pressing using a VI schedule of reinforcement under the presence of both T+L. Following this training, either T or L was removed from the T+L compound, resulting in the independent presentation of either T or L component stimulus. Both the independent T or L component stimuli were then paired with an unavoidable presentation of shock, which suppressed responding under both T and L component stimuli. When tested with randomized presentations of T, L, T+L, and $\bar{T}+\bar{L}$, the subjects showed summative suppression during the $\bar{T}+\bar{L}$ condition. This means their response rate was lower in the absence of all stimuli than in the presence of either or both component stimuli. These results demonstrate that responses can summate under either end of the composite continuum, as also demonstrated in Weiss's (1969) study.

The composite continuum provides a generalized way for researchers to discuss the competing effects of the behavior-altering contingencies that are paired with each component stimulus, when merged in a stimulus compound. The composite continuum is compatible with

the paradigm of Pryor (1984/1999), who proposed a four-contingency approach to training true discrimination. This view postulates that training a single discriminated operant, such as responding and non-responding under the presence and absence of a stimulus, is an incomplete discrimination. This incomplete discrimination may produce insufficient control over the organism's behavior. Pryor's four-contingency approach states that in addition to training a response (R1) under one stimulus (S1), and the absence of that response in the absence of that stimulus, two additional contingencies must be established, and tested including extinguishing R1 under any other stimulus (S2), and extinguishing any other response (R2) under the S1. This ensures that true discrimination is established, gaining complete control over the organism's behavior, leading to only R1 occurring under S1, and not under S2, or R2 occurring under S1.

Davidson and Nevin (1999) extended Pryor's approach, by proposing that adding an additional contingency, by conditioning the R2 under the S2 would create a conditional discrimination consisting of two conditioned stimuli (S1 & S2), and four contingencies (S1 – R1 – Sr+) (S2 – R1 – EXT) (S1 – R2 – EXT) (S2 – R1 – SR+). Davidson and Rosales-Ruiz (2022) later used this conditional discrimination method to successfully reduce the jumping behavior in a dog by teaching discrimination between jumping and mouthing under two separate stimuli.

Intermodal vs. Intramodal Component Stimulus Features

Most studies on stimulus compounding have used intermodal compounds, which consist of component stimuli from different sensory modality systems. These stimuli interact with different sensory systems within an organism, including the visual (sight), auditory (sound), olfactory (smell), gustatory (taste), and tactile (touch) systems (Jaeger & Gabbiani, 2022; Meredith, 2002). To date, the most commonly utilized intermodal component stimuli used in stimulus compounding research are auditory (tone) and visual (light) stimuli (e.g. Weiss, 1964).

While combinations of component stimuli from other modalities are less common, some have included flavors (Delwiche & Heffelfinger, 2005; Wilson, 1977), vibrations (Kehoe & White, 2004), and smells (Cohn & Weiss, 2007).

Fewer studies have used intramodal compounds, which consist of component stimuli of the same sensory modality that interact with the same sensory systems. While intramodal compounding has been shown to produce summative effects on behavior (e.g., Huntsberry 2006, experiment 2), intermodal component stimuli seem much more reliably produce additive results than intramodal stimuli (Candy Rowe, 2005; Ghirlanda, 2022; Kehoe et al., 1994). This has been shown with many species, including rabbits, rats, pigeons, and humans, and using both classical and operant conditioning methods. An example of an experiment that demonstrates success in producing summative effects on responding to an intermodal compound, and failure with intramodal stimuli, is Kehoe (1994). Kehoe measured an eye blink reflex in rabbits after classical training under independent presentations of tone (auditory), light (visual), and noise (auditory) component stimuli. These stimuli were then presented in T+L, N+L, and T+N compounds. Results showed that additive summation occurred under the presence of the T+L compound and the N+L compound but not under the presence of the T+N compound.

While fewer published stimulus compounding studies have used intramodal stimuli, the overarching theme from the results of these studies indicates that, while additive summation can be produced using the compound of two unimodal component stimuli, the component stimulus features play an important factor in the success of producing summation (Miller, 1971; Weiss, 1972). For example, Aydan and Pearce (1995) conducted a series of visual intramodal compounding experiments, each attempting to produce additive summation in pigeons using autoshaping, after failing to do so in 1994. They manipulated several different procedural factors,

including the reversal of component contingencies, presenting a “control” stimulus compound, presenting component stimuli for longer durations during training, and delivering food at varying interval during component presentations. Out of all these factors, only the component duration helped to produce summation, although the authors considered this summation statistically insignificant. The authors then tried again (Aydan and Pearce, 1997) by conducting several extensions of their previous experiments, which included several more procedural and environmental changes. These changes included the use of operant conditioning, spatially separating component stimuli, using both intermodal and intramodal compounds, and changes in the background color of the presented stimuli. The use of operant conditioning produced a statistically non-significant level of summation and was used in the following experiments to test the remaining factors. These experiments did not produce intramodal summation using spatially separated components but found that the background color of the presented component or compound stimulus has a significant impact on the production of summation.

The difficulty with producing summation in these and other studies (e.g. McDevitt & Fantino, 1996) may be related to the fact that intramodal stimulus compounds don't always retain all features (and may add new features) compared to training stimuli. For example, presenting two visual stimuli together may change visual properties related to background, position, or overall luminescence of stimuli. It may be difficult to predict the features that will be important for particular stimuli since subjects may come under control of various properties probabilistically (Mackintosh, 1974). In other words, combining intramodal stimuli may alter the properties of the components more than intermodal combinations. The complexities of potentially altered features of olfactory stimulus combinations might be difficult to assess for

humans, who rely little on olfaction (Nielsen et al., 2015; Sinding et al., 2015; Yeshurun & Sobel, 2010).

Stimulus Compounding using Odorants

While summation has been shown reliably across many modalities and species, one modality that is often underused in stimulus-compounding studies is olfactory stimuli, despite the importance of olfactory stimuli across a variety of species (Ache & Young, 2005; Auffarth, 2013; Batsell, 2005; Kurian et al., 2021) and despite the fact that rats (an ever-popular species in the laboratory) have an extremely well-developed olfactory system (Ache & Young, 2005; Kaupp, 2010; Staubli et al., 1987). The olfactory system begins with the binding of odorant particles to odor receptors, which create and send numerous signals through many complex neural pathways (Kurian et al., 2021; Stockhorst & Pietrowsky, 2004; Wilson & Stevenson, 2003, 2010). While the general/overall structure of the olfactory system is consistent across species, the systems of certain species are more complex and developed than others. For example, the olfactory system of human animals contains around 12 million olfactory receptor neurons (ORNs), with around 350 different receptor types (Batsell, 2005; Yeshurun, 2010; Glusman et al, 2001; Moran et al, 1982). While this may seem like an incredibly large number, it pales when compared to the systems of other non-human animals such as rats, which contain around 1430 receptor types, and dogs, which contain around 1070 receptor types. This is because unlike humans, many non-human animals throughout history have primarily depended on olfactory cues to guide their behavior in their natural environments (Auffarth, 2013). This is seen across many species, a small sample of which includes dogs (Hepper & Wells, 2005; Moser et al., 2022), cats (Ellis & Wells, 2010), lemurs (Sündermann et al., 2008), lobsters (Grasso & Basil, 2002), and rats (Wesson et al., 2009).

In short, the ecological importance of olfaction justifies systematic expansion of stimulus compounding studies into the area of olfaction. To date, only a few studies have examined olfactory summation, and still more have explored relevant stimulus-mixing effects other than summation.

Stimulus Compounding and Odor-Mixing Studies in Olfaction

Odors can be concurrently presented in several ways. Two odorants can be combined, creating an evenly blended mixture. This mixture presents the molecules of the component odorants spatially together. Alternatively, odors could be concurrently presented from different sources, causing a spatially uneven mixture of odorants that might be detectable by advanced olfactory systems. Several studies on odor signaling provide clues about how olfactory stimuli tend to function in fully mixed compounds.

Grossman (2008) used various ratio mixtures of odors to train digging responses in mice. After training, mice were presented with either the previously tested mixture, one of the component odors, or a novel unconditioned odor. While all subjects engaged in longer durations of digging in the previously conditioned odor compared to the novel odor, their duration of digging each component odor fluctuated according to the previously conditioned ratio mixture. Frederick et al., (2009) later found similar results using the same paradigm with seven compound odorant mixtures, each containing two components of varying similarity. In these studies, subjects responded more to mixed compounds of previously trained odors compared to a novel odorant, implying that the stimulus features present in the conditioned components continued to hold some level of control while presented in a mixed compound.

Conversely, Hopfield and Gelperin (1998) conducted an experiment that seems to indicate the opposite: that mixed odors may typically function as a new olfactory stimulus rather

than as a compound stimulus. They sought to see how leopard slugs would respond to presentations of two component and one compound odor stimulus (A, B, A+B) after these odors had been previously paired with an aversive stimulus while presented as either a mixed (A+B) or spatially separated (A/B) compound. Component response rates to A and B were similar to the trained composite only when the training was conducted with unmixed A/B compound. The results of this study may indicate that when odors are mixed rather than concurrently presented from spatially separate sources, the stimulus acts more as a novel stimulus than as a compound of component stimuli. Thinking of this in terms of other modalities seems to follow; a mixture of a red and a blue stimulus looks like a purple stimulus rather than a compound. The question of whether spatial distinction is necessary for compounding to occur could be both a species-specific, modality-specific, and stimulus-property specific question.

Despite the significant influence that odor plays on the behavior of rats, stimulus-compounding studies have rarely utilized an odorant stimulus in that species as part of the stimulus compound. Still, some studies have established that at least intermodal summation can work with odorants. Cohn and Weiss (2007) created a stimulus compound by training rats to respond under the independent presentations of both a tone and an ambient odor. Their results demonstrated an additive summation effect, where response rates were higher under an odor + tone compound, compared to the individual odor and tone components. These results are consistent with other stimulus-compounding research using non-rodent subjects, including Delwiche and Heffelfinger (2005), who presented a taste and odor compound to human subjects, demonstrating additive summation effects on responding.

No studies to date have examined intramodal olfactory stimulus summation in rats, however some studies have used compound and component olfactory stimuli in ways that

indicate that olfactory stimulus mixing may be complex for the species. Yoder (2015) trained trial-based discrimination in rats between independent presentations of two odorants. Correct responses were reinforced for licking the odor delivery port that contained the Sd odor. When the odors were mixed at different ratios and presented to the subjects, the rat's latencies in the presence of the compound stimulus increased compared to the single odorant presentations. Near-even mix ratios such as 60/40 even resulted in complete removal of the nose from the olfactory port. These discrete trial results (higher reaction times and nonresponding) seem to foreshadow that mixed compound odor stimuli could even negatively summate under free operant conditions, perhaps because the stimulus mixture functions as a third odorant rather than a true compound. These results are consistent with studies using human verbal reports in which odorant mixtures were reported as being perceived as different odor compared to each odor individually (Batsell, 2005).

The Challenges of Stimulus Summation using Odorants

Several challenges related to the selection and use of olfactory stimuli may underlie the rarity of odorant-based summation research. First, odors are logistically challenging to work with, and difficult to present or remove in a short timescale. Ambient odors are made up of odorant particles housed in the air. The presence of these particles is dependent on the airflow in the air of the environment and the stickiness of the particles or how readily they cling to surfaces in the environment (Cohn & Weiss, 2007). This makes controlling the presence and absence of ambient odorant particles in a controlled environment difficult, as it requires the control of the airflow in the experimental environment. Odorants that are contained within another stimulus, such as a cup or sand pit, are easier for researchers to manipulate in the subject's environment, but the container they are held in creates additional stimuli that could unintendedly gain control

of the subject's responding (Brushfield et al., 2008; Devore et al., 2013). Nose poke ports also complicate experimental procedures by limiting the availability of the stimulus to a specific location or area in the operant chamber, often requiring an explicit response on the part of the animal to come into contact with the stimulus.

The use of odorant stimuli in compounding studies also requires the researcher to make judgements about what constitutes a “different” component odor stimulus, which can be complex (for reasons reviewed above). Odorant categorization and classification to date has been based on multiple factors, including chemical properties, human-reported similarity of perceived odorant qualities, and behavioral impact. These factors have often been found to contest one another, in the sense that two odors with different chemical compounds successfully trained as independent discriminative stimuli may not evoke a verbal report of having different qualities, and vice versa. The physical features of the odorants may also modulate odor discriminability; Yoder, et al. (2014) reported higher discrimination in rats between odorants with wider ranges of carbon atoms, than odorants with smaller ranges of carbon atoms. Complicating the issue, the rat's biological structures and the chemical structure of the odor stimulus may be less relevant to defining stimuli than the contingencies that rodents have encountered in relation to odorant stimuli, which can in turn alter biological responsiveness (Asahina, 2008; Auffarth, 2013; Shams, 2011; Wilson & Stevenson, 2003). Rats naturally detect variations of odorants in their environment, such as the presence or absence of many different categories of odor, for a wide variety of reasons, including navigation, socialization, identification, recognition of predators, food acquisition, and avoidance of aversive stimuli. Previous research has shown that rats will often use odors to track the passage of other rats and track their previous paths to navigate through a novel environment to find their way back to their home (Wallas et al., 2002). Studies

have also shown that rats will use odors as cues to identify and avoid other rats in their community that are sick (Arakawa et al., 2010). Rats will use scent marking to identify and select mating partners based on factors such as health and fertility (Bakker et al., 1996; Ferkin, 2018; Lydell, 1972). Rats will make food selection choices using scents from other littermate's saliva (Galef, 2002) and will avoid/escape both conditioned and unconditioned predators (Hubbard et al., 2004; Takahashi et al., 2005; Wallace & Rosen, 2000). Using such natural odor stimuli (or accidentally using similar stimuli) as “different” odors may carry the advantage of previous discrimination conditioning and salience but may also introduce confounds should these reinforcement histories interact with stimulus compounding pretraining procedures.

In short, a systematic expansion of our understanding of intramodal stimulus compounding using olfactory stimuli requires a researcher to consider and/or address both the logistical and the conceptual challenges of intramodal olfactory compounding procedures.

Current Study

This study aimed to determine whether rats would show summation or averaging to ambiently presented intramodal odor stimulus compounds. The subjects were trained to respond to individual component odors, and then tested with the presentation of an odorant mixture compound. Given the contradictory results from intramodality studies and the lack of published results on intra-modal odorant stimulus compounding, I wished to see if a mixed odor compound will produce either summation or averaging following independent training of responses under each individual odorant component. If a summative effect on responding is produced, this may indicate that most of the original component stimulus features, and the control over behavior they previously held, carried over in the presence of the compound stimulus. If an averaged effect on responding is produced, this may indicate that some of the original component stimulus

features were either lost or impacted by one another in the compound stimulus.

Establishing an initial empirical assessment of intermodal olfactory stimulus compounding in the rat first required the development of an odor-presenting apparatus that could present and remove odor stimuli on a similar time course compared to audiovisual summation studies. Also, similarly to audiovisual scenarios, the apparatus needed to present stimuli in a manner that is detectable from anywhere in the chamber instead of requiring a nosepoke or other restricted positioning. Once I created this apparatus, I validated it by showing that it could create and control olfactory discrimination for rat subjects. Next, I used the apparatus to establish an initial olfactory compounding data set.

METHODS

Apparatus Development

I created an operant chamber that could effectively function as an odorant delivery and removal system. The system was required to control the presentation and extraction of odorant particles in a way that was effective enough for reinforcement and extinction contingencies placed during the presence and absence of the odor to shape discrimination in the rat subject's response. The apparatus underwent many early design changes that are not described here. This development process resulted in the apparatus described below. My fellow researchers and I first tested the efficacy of the chamber using our own olfactory systems. I then subsequently validated the apparatus with two rat subjects to demonstrate the discriminability of the odorant presentation system and to guide further apparatus improvements.

Main Chamber

The apparatus was 21cm wide, 25cm long, and 21cm tall. The main part of the apparatus, where the subject was placed, was made of 1/8" red plexiglass, with red acrylic blockers placed along the bottom edges of the chamber from the front corners to the back corners. This prevented the air stream from being caught in the edges and corners of the chamber, instead directing air flow through the chamber and out through the back fan. At the front of the chamber (see Figure 1) there was a 60mm x 60mm x 25mm axial fan connected with dryer tubing to the vivarium's air filtration system, supplying 28 cubic feet per minute of filtered air into the chamber. Below the fan sat an input valve connected to a set of custom tubing, which allowed the input of either unscented or scented air into the chamber. Located directly to the left and right of the scented air input, there were two inputs for additional filtered air connected to 32W air pump, which supplied 60 liters of air per minute. Attached to the back of the chamber was a 8.94" by 6.3" by

10.9” fan capable of moving 185 cubic feet of air per minute. Overall, the chamber functioned as a horizontally oriented wind tunnel, maintaining a constant air flow through the subject’s experimental environment.

Olfactory Delivery and Removal System

The presentation and discontinuation of the odor stimulus was controlled by a series of tubing and solenoids (Figure 2). Air from the main air pump was pushed through a main tube that separated into two secondary tubes and connected to two separate solenoid valves. Each solenoid valve could be turned on or off to control the flow of air, and only one was open at a time. Following each solenoid valve was a chamber filled with 100% cotton. One chamber functioned as an olfactory storage unit that dispensed the odorant, and the other was used as a control without odorant to maintain consistent air pressure across both conditions. The air on either side was then directed through one-way air valves, which prevent backflow and cross contamination of odorant particles, and then into a single tube that connected to the chamber.

Because the back fan was capable of moving 185 cubic feet of air per minute, the flow of the scented air was continually being removed from the chamber, meaning that once the olfactory solenoid was closed and the filtered air solenoid was opened, the odorant was quickly eliminated from the chamber. To test the time scale of air clearing in the apparatus, we used a fog machine. After filling the chamber with fogged air, we recorded the time that it took for all visible fog to clear. We placed paper with a set of sharpie marks on the far end of the chamber while performing this test so that we could use the contrast and resolution of the lines to better discriminate the moment of complete clearing. We measured the air clearing time as 5s.

In order to minimize any lingering odorant particles on the inside the scented air input valve or on other areas of the chamber, we thoroughly cleaned the scented air input valve,

olfactory device tubing between sessions with a 3% hydrogen peroxide solution designed to disinfect animal cages, and then with a 70% ethanol solution.

My fellow researchers and I successfully detected the presentation and removal of the odorant stimulus immediately after the programmed stimulus change while sniffing near the rat's planned position in the chamber. As a result, no temporal delay of contingency schedules was programmed to correct for lingering odorants.

Apparatus Validation

During apparatus development, researchers first assessed the detectability, intensity, and fluctuations of the odorant stimulus by sniffing near the area that rats would eventually occupy. This approach was used to test certain variables of the apparatus, such as types of fan motors, air pumps, solenoids, odorant delivery methods, material types, and more. Researchers then tested the final effect by routinely sampling the air exiting from the back fan of the chamber, and pressing an external lever when they detected the presentation or removal of the odorant. During these tests, the researcher pressing the lever did not know when the odor would be on or off. Figures 3, 4, and 5, display the results of these tests, conducted before beginning apparatus validation with animal subjects.

Apparatus Validation Subjects

Two, experimentally naïve, female Long-Evans rats from the same litter were recruited to validate the apparatus, to test for discrimination. Both subjects were housed together when not in use, in a 19" (45.7cm) by 9" (22.9cm) by 8" (20.3cm) home cage kept in an air filtered animal housing system. The vivarium lighting was set to a 12-hour reverse light schedule, where the house lights remained off from 9am-9pm, and on from 9pm-9am. The vivarium contained a pressurized air filtration system, which would exchange 100% of the room's volume of air 12

times per hour. Subjects had free access to food and water before, between, and after all experimental sessions. Subjects were kept at 100% of their free feeding weight throughout the experiment. The study was approved by the University of North Texas' Institutional Animal Care and Use Committee (IACUC) prior to any experimental sessions.

Experimental Subjects

Two female Long-Evans rats from the same litter were recruited for the experimental compounding study from a previous behavioral study, that included handling and clicker training. Neither subject had ever pressed a lever. Both subjects were one year and four months old when initially introduced to the operant chamber for the acclimation phase. Both subjects were housed together when not in use, in a 19" (45.7cm) by 9" (22.9cm) by 8" (20.3cm) home cage kept in an air filtered animal housing system. Housing, light cycle, and other variables for these rats were identical to those of subjects 2 & 3.

Acclimation: All Subjects

All Subjects were given time prior to training to acclimate to the chamber with the purpose of decreasing exploration and habituating to novel (and potentially aversive) air current stimulation enough for training to begin.

During the first phase of acclimation, each subject was placed individually into the main chamber of the apparatus. All fans, air pumps, and solenoids were off, so no additional noise or wind was generated by the apparatus. Sweetened condensed milk was smeared on the left wall of the apparatus, where the feeder attaches to the chamber. Each rat was left in the chamber for 10 to 30 minutes at a time, alternating between subjects.

Once rats' exploration and escape responses decreased to a level where they were engaging with the sweetened condensed milk more than they were engaging in exploration

responses, they were moved on to the second phase of acclimation.

During the second phase of the acclimation, each subject was placed individually into the main chamber of the apparatus, with all fans and air pumps turned on to their lowest settings. This placed the rats into a chamber with a moderate level of noise and a moderate amount of wind. Sweetened condensed milk was freely available non-contingently, through the feeder port. Each rat was left in the chamber for 10 to 30 minutes at a time, alternating between subjects. Once subjects no longer showed high rates of exploration or nervous body language and were showing increased interaction with the sweetened condensed milk, they were moved to the third phase of acclimation.

During the third phase of the acclimation, each subject was placed individually into the main chamber of the apparatus, with all fans and air pumps turned on to their highest settings. This placed the rats into a chamber with a high a level of noise and wind. Sweetened condensed milk was freely available non-contingently, through the feeder port. Each rat was left in the chamber for 10 to 30 minutes at a time, alternating between subjects. Once subjects engaged in few to no exploration responses, the acclimation phase was considered complete.

Magazine Training

Magazine training for validation subjects occurred in their respective Sd conditions (subject 2 odor on, subject 3 odor off). Experimental subjects had magazine training under no-odor conditions. The presentation of a 100 millisecond 440 hertz tone was followed by the delivery of 1-2 drops of sweetened condensed milk from the feeder located on the side of the chamber. Once animals were responding reliably to the tone by orienting to the feeder, they were moved on to lever press training.

Lever/Response Training

Rats were then trained to press the lever for reinforcement. All subjects were shaped by hand, using differential reinforcement of successive approximations of the final response. The reinforcement system consisted of a lever housed at the front of the chamber. Pressing the lever was immediately followed by the activation of tone and reinforcer delivery. The feeder was located far enough away that the subjects were forced to completely let go of the lever in order to contact the reinforcement. The final response consisted of orienting head and/or body towards feeder immediately following the presentation of the conditioned stimulus, approaching the feeder, and consuming the sweetened condensed milk within two seconds of presentation. This method of reinforcer delivery was used for the remainder of the training and experiment.

Validation Subjects

The lever training procedure used for both validation subjects was conducted under their Sd odor conditions (the same as in magazine training); subject 2 was trained in the presence of the odor (lemon oil) and subject 3 in the absence of the odor.

Experimental Subjects

All lever training for experimental subjects was conducted in the presence of either rosemary oil, or orange oil in separate sessions. These odorants were selected based on previous literature demonstrating their safety when presented overextended periods of time to rat and mouse subjects (Anadón et al., 2008; Ceccarelli et al., 2004; Dosoky & Setzer, 2018; Horváthová et al., 2010; Leite et al., 2008). Lever training sessions for experimental subjects lasted from 20-90 seconds. This length of time was chosen based on previous habituation literature, showing that habituation of neurons began at 50 seconds (Wilson, 1998). The decision was also based on our previous testing and validation, which showed breakdown of human discrimination behavior

(when experimenters tried to discriminate odor by positioning the face just above the chamber) and less than ideal performance in validation rats when longer periods were used. Lever presses in the presence of the odor were followed immediately by the presentation of a 100-millisecond long presentation of a 440 hertz tone, and the delivery of 1-2 drops of sweetened condensed milk from the feeder. This phase did not have any time period in which odor was not present.

Lever pressing was hand shaped on an FR1 schedule, by manually reinforcing successive approximations of the response cycle: presses the lever, orients to feeder following the conditioned stimulus, consumes the delivered reinforcer, and orients back to the lever to continue pressing. The experimenter reinforced approximations by manipulating the lever from outside the chamber until the subjects were responding independently and sufficiently to close the switch. Both subjects were trained on an FR1 reinforcement schedule, which continued until they were pressing at a minimum rate of 8 presses per minute.

Odor Discrimination Training

Validation Subjects

Validation subjects were taught to discriminate between the presence and absence of lemon essential oil. The presence of the lemon odor was conditioned as an Sd for subject 2, and as an S Δ for subject 3. Discrimination training alternated between the presence and absence of odor until the validation phase of training was completed. Both subjects received training on the same scent, at the same time, and were switched to the second scent synchronously. Subjects were trained using a two-ply schedule, including an FR1 reinforcement schedule during the presence of odor, and extinction of reinforcement in the absence of odor. Initial discrimination training began with odor on (FR1) and odor off (extinction) conditions lasting 30-45 seconds, with trial lengths lasting approximately 3 minutes. When this procedure produced poor

discrimination performance, both subjects were switched to more discrete, extended odor on, odor off, AB conditions, consisting of a 30-60 second presentation of the odorant S^D , followed by an extended S^{Δ} odor off condition, which lasted until the subject decreased responding. The lengths of these AB conditions gradually increased to their final length of 3-5 minutes. Reinforcement using this training procedure began on an FR1 reinforcement schedule and was gradually increased to a VI 5-minute schedule. Once discrimination was established, the validation was complete, and validation subjects did not undergo any further procedures.

Experimental Subjects

Discrimination training for experimental subjects was modified based on what I had learned from the results of validation training. Initial discrimination training sessions consisted of a single sequence of odor on and odor off, and early in training we added an initial odor-off condition to the sequence so that a single session consisted of odor off, odor on, and another odor off condition. The first phase was implemented later in training (once I realized that this order was better) and consisted of a few seconds of time in which the air stream had neither odor present. The odor was then turned on contingent on the rat performing alternative behavior (not lever pressing) for at least 2-3 seconds. Odor was then presented for 20-90 seconds during which lever presses were reinforced on an FR1 schedule. This was followed by the removal of the scent, which was replaced once again by filtered air, and any lever presses were placed on extinction. This extinction condition lasted until the rate of lever presses had extinguished for a minimum of five seconds, and the session was terminated. During the training process, experimenters realized that training would progress best if non-lever behaviors were explicitly trained in the absence of the odor, and so this contingency was added to the odor-off sections of the session. Criterion for the non-lever pressing response started as any non-lever pressing

response during the odor off condition. These responses were manually reinforced by the researcher using a button outside of the chamber that controlled the primary reinforcement system, activating the 440 hertz tone, and delivering 1-2 drops of sweetened condensed milk. The response captured in both rats was a head-bobbing behavior (moving the head back and forth from left to right), and subsequently only this alternative behavior was reinforced during odor-off conditions. Head bobbing was reinforced during odor-off at a ratio as similar as possible to the operative odor-on ratio for the session. As the subject's discrimination improved, additional odor and non-odor phases were added to the training sessions, resulting in a repeating ABAB design lasting from 3-5 minutes. Despite the availability of reinforcement for head-bobbing during odor-off conditions, rats encountered many non-reinforced trials of lever pressing during the training process (i.e., they both encountered at least some extinction trials in odor-off).

Once the subjects reached at least a 0.8 discrimination index, the reinforcement schedule gradually increased. For Subject 6 it was increased from FR1, to an FR5 schedule, and then switched to a VI5 second schedule in both orange and rosemary conditions. For subject 6, the final discrimination index in rosemary oil was 0.83, and the final discrimination index in orange oil was 0.9. For Subject 5 the 0.8 discrimination index requirement was not met due to time constraints in the laboratory. Therefore, rosemary oil was trained to a VR3 with a 0.9 discrimination index, and orange oil was trained to a VI5 second schedule with a 0.7 discrimination index.

Additive Summation Testing

After discrimination training was complete, I tested both subjects to see if the rate of lever pressing in the presence of a rosemary-orange compound stimulus would be higher, lower,

or intermediate compared to the rate of lever pressing in the presence of each individual odor. During this phase, subjects experienced alternating periods of rosemary oil, orange oil, or the rosemary-orange compound oil. The compound stimulus was made using equal proportions of both rosemary and orange oil in a 50/50 ratio. One large batch of the compound mixture was made prior to testing, and was the only mixture used for the entirety of the experiment. Sessions lasted 3-5 mins each and occurred in trial blocks in a faux randomized order. Trial blocks consisted of one presentation each of orange, rosemary, and the compound odorant. I counterbalanced trial blocks by implementing them in every possible order combination. Time was given between sessions of different odors to allow the vivarium to clear of any detectable scent, ranging from 15 to several hours.

The first ten trial blocks were conducted under a VI5 second reinforcement schedule for all three condition types. Next, nine trial blocks were conducted under complete extinction, meaning no reinforcement was provided for any lever pressing under any of the three conditions. Because rates of lever pressing had diminished to near zero during the nine extinction conditions, three re-training sessions were then conducted for rosemary and orange oil separately for three sessions, until responding had returned to pre-testing levels. The reinforcement schedules for subject 5's retraining during the orange conditions were 0.08 per second, 0.06 per second, and 0.07 per second, respectively. The reinforcement delivery schedules for subject 5's retraining during the rosemary conditions were 0.1 per second, 0.02 per second, and 0.06 per second, respectively. The reinforcement schedules for subject 6's retraining during the orange conditions were 0.07 per second, 0.05 per second, and 0.06 per second, respectively. The reinforcement delivery schedules for subject 6's retraining during the rosemary conditions were 0.1 per second,

0.07 per second, and 0.05 per second, respectively. Next, an additional ten testing blocks were conducted under a variable interval ten second schedule, for all three condition types.

RESULTS

Validation Results

Overall, both validation subjects achieved discrimination between the presence and absence of the lemon odor, however they did not achieve 100% discrimination. Subject 2's final discrimination index was 0.94, with a discrimination ratio of 1:31. Subject 3's final discrimination index was 0.91, with a discrimination ratio of 1:22. Cumulative records of final discrimination performances are visualized in Figures 6 and 7.

Stimulus Compounding Study Subject 5 Results

Subject 5 Overall Results

Overall, subject 5's results, under a variable interval 5 second reinforcement schedule, show an averaged response rate under the presence of the compound stimulus was less than the orange stimulus, and greater than the rosemary stimulus, or in-between her average rates of responding to either component stimuli. This is consistent with Weiss' definition of averaging.

Under the extinction schedule, subject 5's average response rate under the presence of the compound stimulus was greater than the orange stimulus, and less than the rosemary stimulus, or in-between the average rates of responding to either component stimulus. This is consistent with Weiss' definition of averaging.

Under the variable interval 10 second reinforcement schedule, subject 5's average rate of responding under the presence of the compound stimulus was less than the orange stimulus, and slightly higher than the rosemary stimulus, or in-between her average rates of responding to either component stimulus. This is consistent with Weiss' definition of averaging.

Subject 5 VI5 Second Schedule of Reinforcement

Figure 8 shows subject 5's rates of responding during all testing sessions, and figure 9

shows subject 5's cumulative rates of responding per condition for the first trial block, using the VI5 schedule. Subject 5's lever pressing during the rosemary condition maintained a downward trend from the initial session to the final session at a slope of -0.0176 ($R^2= 0.1747$). The rates of responding in the first and last sessions were 0.21, and 0.18 presses per second, respectively. Lever pressing during the orange condition maintained an upward trend from the initial session to the final session at a slope of 0.005 ($R^2= 0.012$). The rates of responding in the first and last sessions were 0.45, and 0.33 presses per second respectively. Lever pressing during the compound condition maintained an upwards trend from the initial session to the final session at a slope of 0.017 ($R^2= 0.186$). The rates of responding in the first and last sessions were 0.3, and 0.51 presses per second respectively.

Figure 10 shows subject 5's overall mean response rates per condition, and distribution of responding per session. During the orange condition, subject 5's mean rate of responding was 0.41 lever presses per second. During the rosemary condition, subject 5's mean rate of responding was 0.35 lever presses per second. During the compound condition, Subject 5's mean rate of responding was 0.37 lever presses per second. This demonstrates that subject 5's mean rate of responding during the compound condition, when compared to its mean rate of responding during the component conditions between rosemary and orange component conditioning.

Subject 5 Extinction

Figure 11 shows subject 5's rates of responding during all testing sessions, and figure 12 shows subject 5's cumulative rates of responding per condition for the first trial block, using the extinction schedule. Subject 5's lever pressing during the rosemary condition maintained a downward trend from the initial session to the final session at a slope of -0.0165 ($R^2= 0.32$). The

rates of responding in the first and last sessions were 0.33, and 0.09 presses per second, respectively. Lever pressing during the orange condition maintained a downwards trend from the initial session to the final session at a slope of -0.0049 ($R^2= 0.1393$). The rates of responding in the first and last sessions were 0.10, and 0.04 presses per second respectively. Lever pressing during the compound condition maintained a downwards trend from the initial session to the final session at a slope of -0.0282 ($R^2= 0.36$). The rates of responding in the first and last sessions were 0.43, and 0.12 presses per second respectively.

Figure 13 shows subject 5's overall mean response rates per condition, and distribution of responding per session.. During the orange condition, subject 5's mean rate of responding was 0.09 lever presses per second. During the rosemary condition, subject 5's mean rate of responding was 0.14 lever presses per second. During the compound condition, Subject 5's mean rate of responding was 0.11 lever presses per second.

Subject 5 Re-Training

Figure 14 shows subject 5's rate of responding during all re-training sessions. Subject 5's lever pressing during the rosemary condition maintained an upwards trend from the initial session to the final session at a slope of 0.1511 ($R^2= 0.93$). The rates of responding in the first and last sessions were 0.04, and 0.61 presses per second, respectively. Lever pressing during the orange condition maintained an upwards trend from the initial session to the final session at a slope of 0.2882 ($R^2= 0.99$). The rates of responding in the first and last sessions were 0.11, and 0.42 presses per second respectively.

Figure 15 shows subject 5's mean rate and distribution of responding per condition. During the rosemary condition, subject 5's mean rate of responding was 0.32 lever presses per

second. During the orange condition, subject 5's mean rate of responding was 0.29 lever presses per second.

Subject 5 VI10 Second Reinforcement Schedule

Figure 16 shows subject 5's rates of responding during all testing sessions, and figure 17 shows subject 5's cumulative rates of responding per condition for the first trial block, using the extinction schedule. Subject 5's lever pressing during the rosemary condition maintained a downward trend from the initial session to the final session at a slope of -0.0154 ($R^2 = 0.27$). The rates of responding in the first and last sessions were 0.25, and 0.12 presses per second, respectively. Lever pressing during the orange condition maintained a downwards trend from the initial session to the final session at a slope of -0.0194 ($R^2 = 0.29$). The rates of responding in the first and last sessions were 0.35, and 0.24 presses per second respectively. Lever pressing during the compound condition maintained a downwards trend from the initial session to the final session at a slope of -0.0135 ($R^2 = 0.15$). The rates of responding in the first and last sessions were 0.29, and 0.11 presses per second respectively.

Figure 18 shows subject 5's overall mean response rates per condition, and distribution of responding per session. During the rosemary condition, subject 5's mean rate of responding was 0.17 lever presses per second. During the orange condition, subject 5's mean rate of responding was 0.21 lever presses per second. During the compound condition, Subject 5's mean rate of responding was 0.18 lever presses per second.

Stimulus Compounding Study Subject 6 Results

Subject 6 Overall Results

Overall, subject 6's results, under a variable interval 5 second reinforcement schedule, show that her average response rate under the presence of the compound stimulus was greater

than the orange stimulus, and less than the rosemary stimulus, or in-between her average rates of responding to either component stimulus. This is consistent with Weiss' definition of averaging.

Under the extinction schedule, subject 6's average response rate under the presence of the compound stimulus was greater than the orange stimulus, and less than the rosemary stimulus, or in-between her average rates of responding to either component stimulus. This is consistent with Weiss' definition of averaging.

Under the variable interval 10 second reinforcement schedule, subject 6's average rate of responding under the presence of the compound stimulus was slightly greater than her average rates of responding to either component stimulus. This is consistent with Weiss' definition of additive summation.

Subject 6 VI5 Second Reinforcement Schedule

Figure 19 shows subject 6's rates of responding during all testing sessions, and figure 20 shows subject 6's cumulative rates of responding per condition for the first trial block, using the VI5 schedule. Subject 6's lever pressing during the rosemary condition maintained a downward trend from the initial session to the final session at a slope of -0.0344 ($R^2 = 0.69$). The rates of responding in the first and last sessions were 0.58, and 0.28 presses per second, respectively. Lever pressing during the orange condition maintained a downward trend from the initial session to the final session at a slope of -0.008 ($R^2 = 0.57$). The rates of responding in the first and last sessions were 0.41, and 0.23 presses per second respectively. Lever pressing during the compound condition maintained a downward trend from the initial session to the final session at a slope of -0.0261 ($R^2 = 0.498$). The rates of responding in the first and last sessions were 0.47, and 0.24 presses per second respectively.

Figure 21 shows subject 6's overall mean response rates per condition, and distribution of

responding per session. During the rosemary condition, subject 5's mean rate of responding was 0.41 lever presses per second. During the orange condition, subject 5's mean rate of responding was 0.33 lever presses per second. During the compound condition, Subject 6's mean rate of responding was 0.35 lever presses per second. This demonstrates that subject 5's mean rate of responding during the compound condition, when compared to its mean rate of responding during the component conditions between rosemary and orange component conditioning.

Subject 6 Extinction

Figure 22 shows subject 6's rates of responding during all testing sessions, and figure 23 shows subject 6's cumulative rates of responding per condition for the first trial block, using the extinction schedule. Subject 6's lever pressing during the rosemary condition maintained a downward trend from the initial session to the final session at a slope of -0.0438 ($R^2= 0.44$). The rates of responding in the first and last sessions were 0.58, and 0.07 presses per second, respectively. Lever pressing during the orange condition maintained a downward trend from the initial session to the final session at a slope of -0.0158 ($R^2= 0.43$). The rates of responding in the first and last sessions were 0.2, and 0.01 presses per second respectively. Lever pressing during the compound condition maintained a downward trend from the initial session to the final session at a slope of -0.0202 ($R^2= 0.39$). The rates of responding in the first and last sessions were 0.29, and 0.01 presses per second respectively.

Figure 24 shows subject 6's overall mean response rates per condition, and distribution of responding per session. During the rosemary condition, subject 5's mean rate of responding was 0.12 lever presses per second. During the orange condition, subject 5's mean rate of responding was 0.07 lever presses per second. During the compound condition, Subject 6's mean rate of responding was 0.08 lever presses per second.

Subject 6 Re-Training

Figure 25 show subject 6's rates of responding during all re-training sessions. Subject 6's lever pressing during the rosemary condition maintained an upwards trend from the initial session to the final session at a slope of 0.0393 ($R^2= 0.97$). The rates of responding in the first and last sessions were 0.21, and 0.29 presses per second, respectively. Lever pressing during the orange condition maintained an upwards trend from the initial session to the final session at a slope of 0.1597 ($R^2= 0.84$). The rates of responding in the first and last sessions were 0.16, and 0.48 presses per second respectively.

Figure 26 shows subject 6's mean rates and distribution of responding per condition. During the rosemary condition, subject 5's mean rate of responding was 0.25 lever presses per second. During the orange condition, subject 5's mean rate of responding was 0.28 lever presses per second.

Subject 6 VI10 Second Reinforcement Schedule

Figure 27 shows subject 6's rates of responding during all testing sessions, and figure 28 shows subject 6's cumulative rates of responding per condition for the first trial block, using the VI10 schedule. Subject 6's lever pressing during the rosemary condition maintained a downward trend from the initial session to the final session at a slope of -0.0076 ($R^2= 0.2669$). The rates of responding in the first and last sessions were 0.22, and 0.18 presses per second, respectively. Lever pressing during the orange condition maintained a downward trend from the initial session to the final session at a slope of -0.0258 ($R^2= 0.7$). The rates of responding in the first and last sessions were 0.33, and 0.09 presses per second respectively. Lever pressing during the compound condition maintained a downward trend from the initial session to the final session at a slope of -0.0072 ($R^2= 0.05$). The rates of responding in the first and last sessions were 0.22, and 0.11 presses per second respectively.

Figure 29 shows subject 6's overall mean response rates per condition, and distribution of responding per session. During the rosemary condition, subject 5's mean rate of responding was 0.20 lever presses per second. During the orange condition, subject 5's mean rate of responding was 0.15 lever presses per second. During the compound condition, Subject 6's mean rate of responding was 0.22 lever presses per second.

DISCUSSION

Validation

Both pilot subjects achieved high levels of discrimination between the presence and absence of the odor stimulus. However, both pilots engaged in brief, low levels of lever pressing during their respective S Δ conditions. This resurgence of pressing could be due to the influence of the training procedure initially used to teach discrimination. This procedure utilized rapidly reversing, odor on - odor off conditions. Due to the short period of some trial conditions, there were instances where the condition ended before the subject contacted its contingency, or the subject would lever press immediately preceding the condition change, resulting in potential reinforcement delivery occurring under the wrong stimulus condition. This previous learning history may have produced the resurgence of lever pressing under the S Δ condition while subjects were deprived of reinforcement.

In addition to the potential effects of the initial training procedures, there is also a possibility that the resurgence of lever pressing during the S Δ condition is due to habituation; olfactory sensory habituation occurs partly on a biological level (Wilson, 1998) and may make continual, unchanging olfactory stimuli less effective in longer durations. In case this may have been happening, subsequent subjects experienced short conditions during training and testing. Apart from these considerations, the apparatus functioned to produce discrimination at high levels.

Stimulus Compounding Study

This study aimed to see how the behavior-altering effects of individual odorant component stimuli would merge when presented as a mixed compound and how their presence in that compound would impact responding. The results demonstrate that the rate of responding

under the compound stimulus was similar to or intermediate between the rates of responding under the independent component stimulus. This overall result fits with Weiss' (1972) definition of averaging. While there are many previously demonstrated factors that contribute to the failure of summation and the production of averaging in stimulus compound studies, not all of them are applicable to the current results. This study's results cannot be explained by the use of classical conditioning, non-comparable response rates held by component stimuli, or the omission of a discrimination paradigm. The use of classical conditioning does not apply to the current study, as I used reinforcement contingencies to train responses. The impact of non-comparable response rates is unlikely to apply, as the response rates of both subjects were close across conditions. I did implement a discrimination paradigm, though my odor-off condition included reinforcement of a second response. Using an extinction schedule in a discrimination paradigm reliably produces higher summation levels compared to using a DRO schedule (similar to the one I used). However, the success of previous experiments in producing summation even under DRO contingencies demonstrates that, on its own, the reinforcement of another behavior during s-delta conditions should not cause a total failure of summation. Still, this factor could have combined with other factors to produce a cumulative effect. It is possible that the combination of factors played some part in the production of averaging in the current results.

It is possible that the odor-off condition used in discrimination was not entirely absent of the odor stimulus. It is possible that due to the advanced olfactory senses of the subjects, there were detectable amounts of the odorant left in the chamber during the "odor off" conditions. If the odor-off condition contained a detectable level of the odor stimulus, the remaining low-level odor could have been re-conditioned to control nonresponding under the extinction schedule. Not only would this mean that the behavioral control of odor could be unreliable or complex, but it

would impose a lack of a totally stimulus-absent condition, which has been shown to contribute to lower levels of summation. As Weiss (1972) has demonstrated, when a component stimulus is conditioned independently, the absence of the other component may gain control over responding. In this case, if the odor was present at varied intensities across all discrimination conditions, the absence of that odor would never have been re-conditioned to hold control over non-responding. Therefore, when the odor compound was presented without the absence of a particular odor, that previously conditioned stimulus feature would no longer have been included in the compound.

One implication from previous research is that the lack of spatial separation between the component stimuli that comprise an odorant compound may have had a significant impact on the behavioral control held by the stimulus features. Responses may occur more reliably when learned under spatially separated compounds, compared to mixed compounds. While spatially separated compounds have produced summation in some studies, there have been conflicting results from other experiments (Aydan & Pearce, 1995, 1997; McDevitt & Fantino, 1996; Miller, 1971; Hamm & Meltzer, 1973, 1977; Wiltz, et al., 1973; Van Wijk, & Sabelis, 2010). This study constructed the compound by mixing equal parts of each component odorant together. Some aspects of this approach may have caused the compound to gain a unique stimulus feature, that is novel compared to the component features. Investigating this possibility will require a systematic replication of the current study using spatially separated olfactory stimuli.

Another possible reason why averaging may have occurred instead of additive summation is that the compound odor may have produced a “homogenous percept”, which is when different odors synthesize to make a new odor quality, instead of a “heterogenous percept”, which is when the mixture implies that the quality of each odor component can be perceived in

the mixture (Berglund 1972, 1976). This can also mean that the stimulus features of the compound stimulus functioned as a novel stimulus when presented to the subjects. If these stimulus features were completely novel however, I would have expected the subjects' response rates under the compound to negatively summate to a lower level than in either of the component stimuli. My results indicate that the behavioral control held by the component stimulus' features maintained some control over the response, resulting in an averaged response rate.

Lack of summation could also be due to the compound odorant being delivered in the form of a mixture of both individual odorant solutions. Some previous studies, such as Hopfield and Gelperin (1998), have produced results which indicate that when odors are presented as a mixture, rather than a simultaneous presentation of two odors, they either lose the behavior altering features that were previously conditioned to the component stimuli, and/or gain a unique new feature which has not yet gained control over responding. Even without spatial separation, two odors presented from separate openings may have mixed less as the rat encountered them, which could potentially make a difference for such an odorant-sensitive species. This is difficult to test because it involves internal events/perception of odor stimulus key features. A possible way to explore this possibility is to examine the brain components of the response, or to conduct an experiment like Yoder (2015), where the rate of responding is compared to changes in the ratio of component odors present in the compound odor.

The production of averaging could also be related to the shaping methods used to teach discrimination between the presence and absence of each component stimulus. As previously proposed by Davidson and Nevin (1999) and demonstrated by Davidson and Rosales-Ruiz (2022), training a four contingency discrimination paradigm creates more error-free responding to the presence and absence of conditioned stimuli. Due to the use of a two-contingency

paradigm, there may be a lack of total stimulus control held by the component stimuli, therefore resulting in a lack of summation.

In summary, the current study constitutes the first empirical foray into intramodal stimulus compounding in rats. Two replications indicate that olfactory stimuli presented in the mixed fashion described herein produce averaging rather than positive or negative summation. Future studies should expand these results to test the various features of stimulus content, presentation, or conditioning procedures to explore whether such averaging holds over varied conditions.

Figure 1

Front Panel of Apparatus Main Chamber

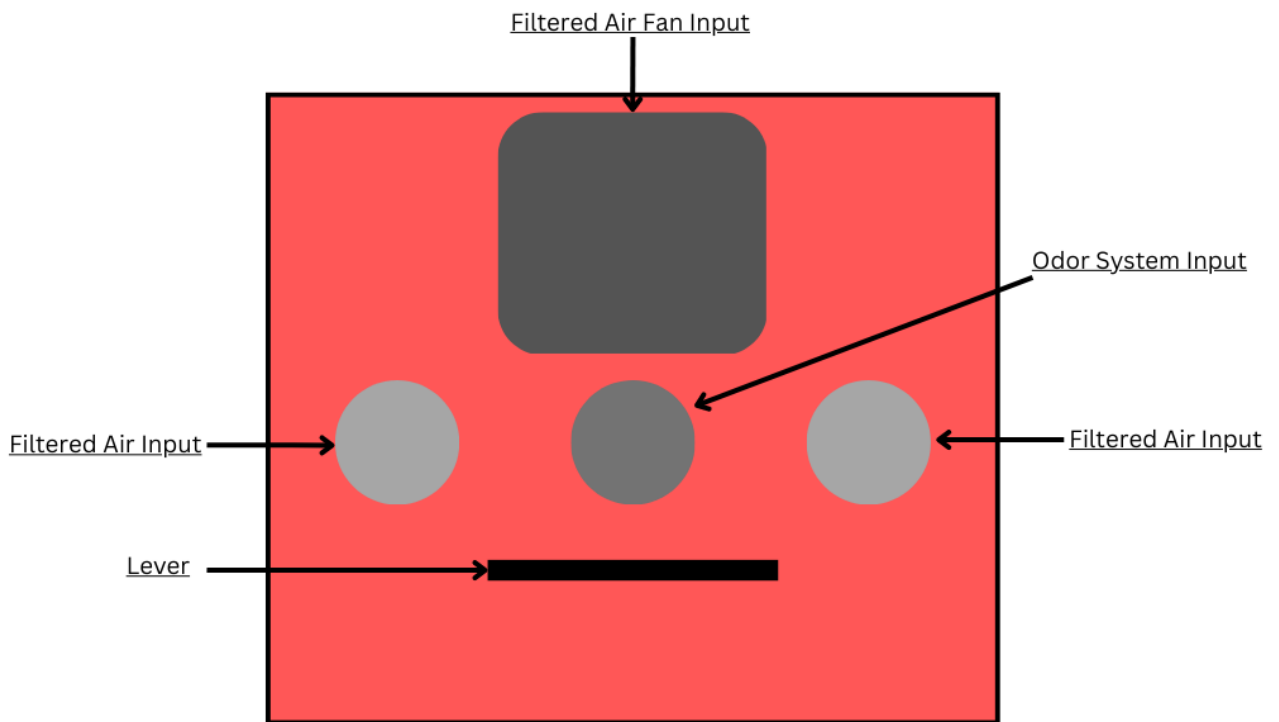


Figure 2

Olfactory Delivery System

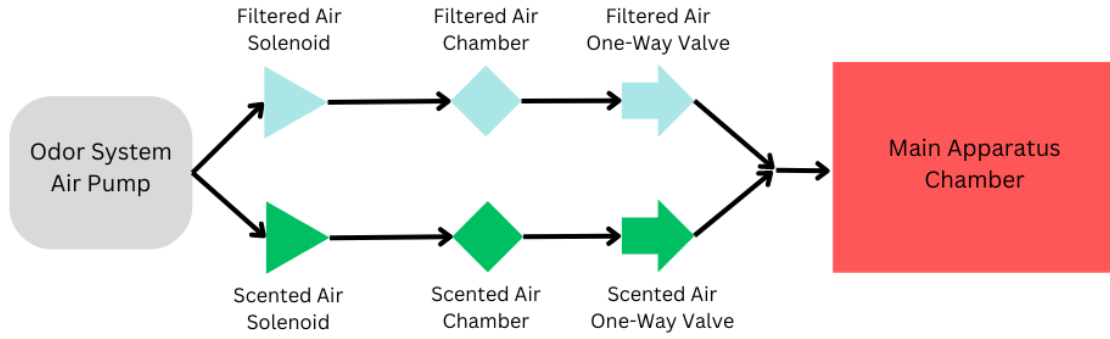


Figure 3

Apparatus Development: Results of Experiment 1

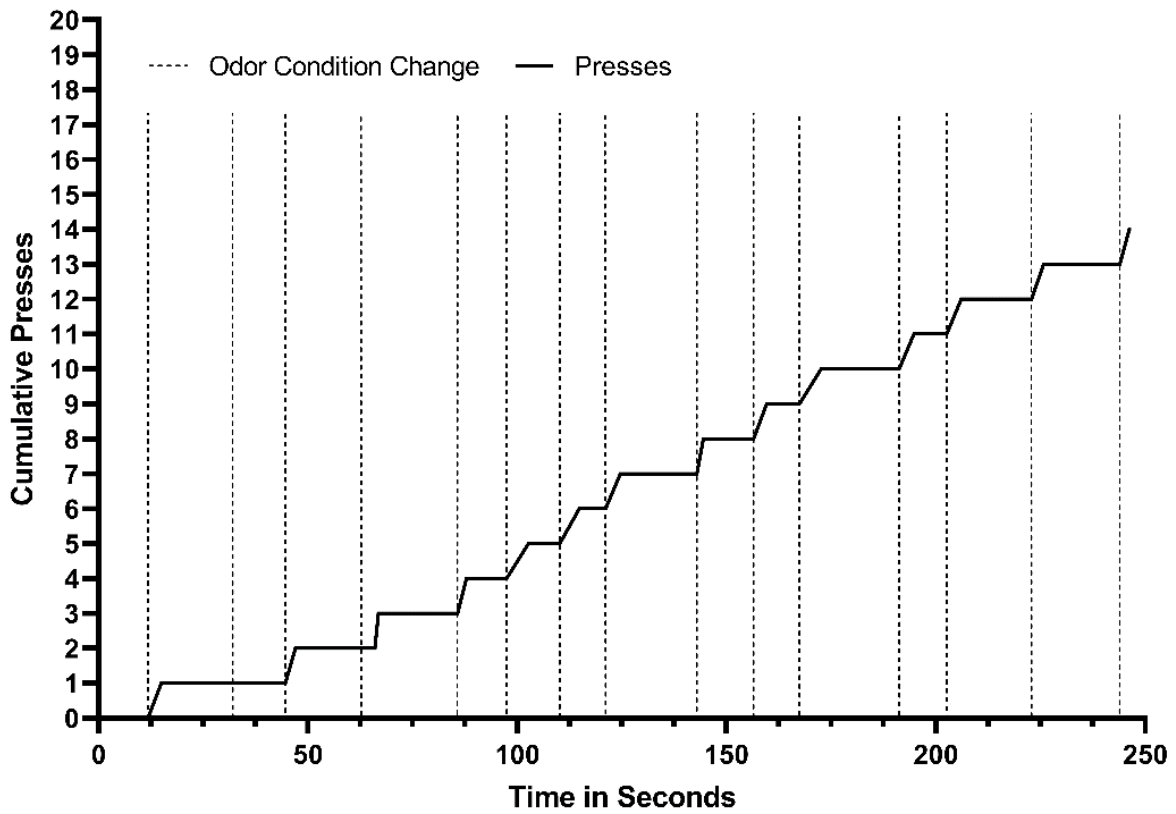


Figure 4

Apparatus Development: Results of Experimenter Test 2

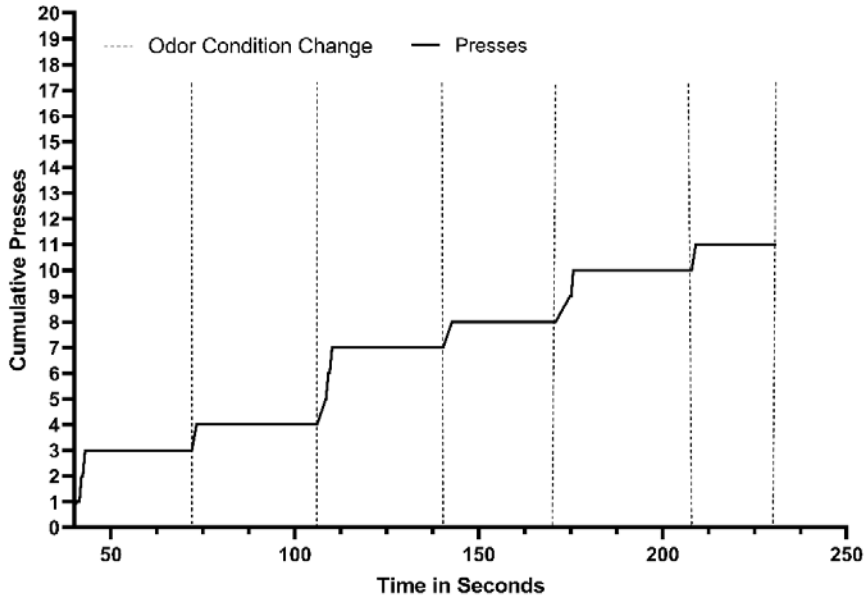


Figure 5

Apparatus Development: Results of Experimenter Test 3

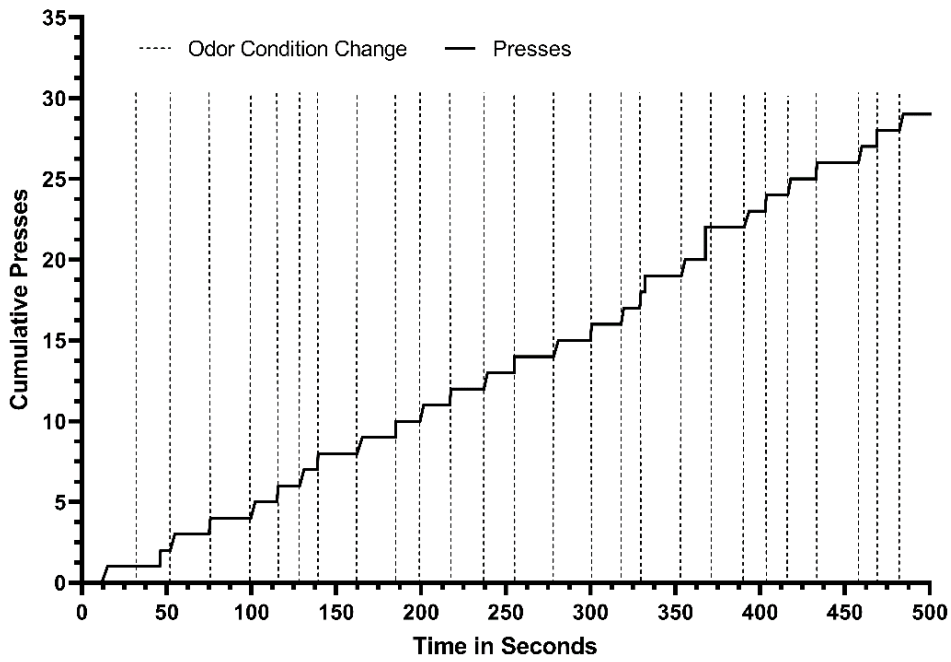


Figure 6

Subject 2 Final Cumulative Record

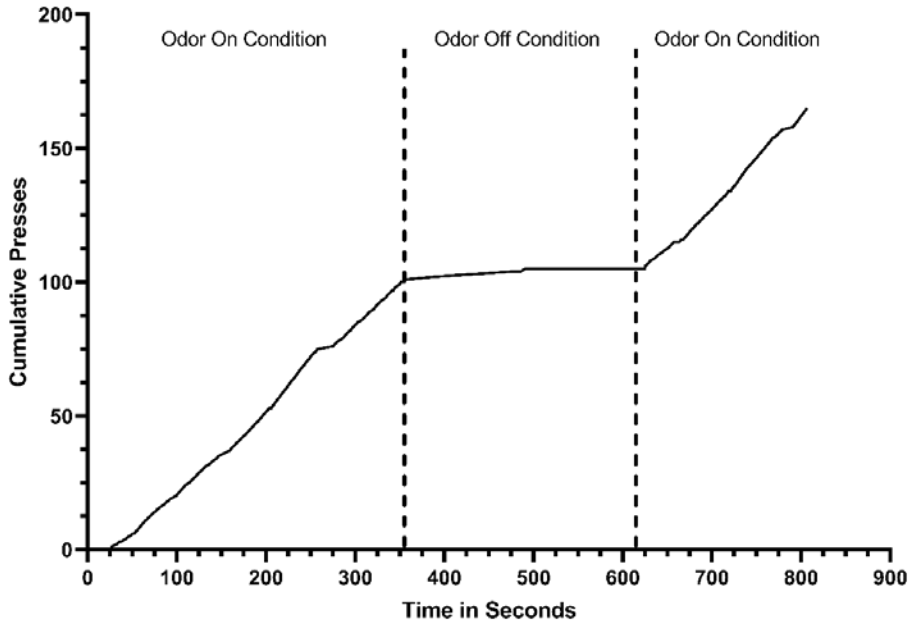


Figure 7

Subject 3 Final Cumulative Record

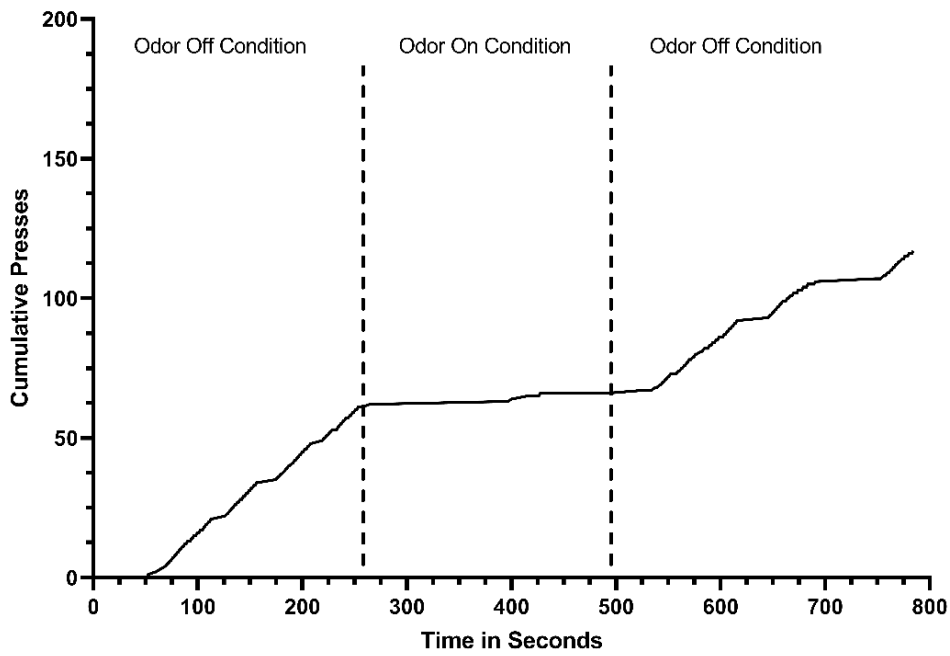


Figure 8

Subject 5 Rate per VI5 Test Session

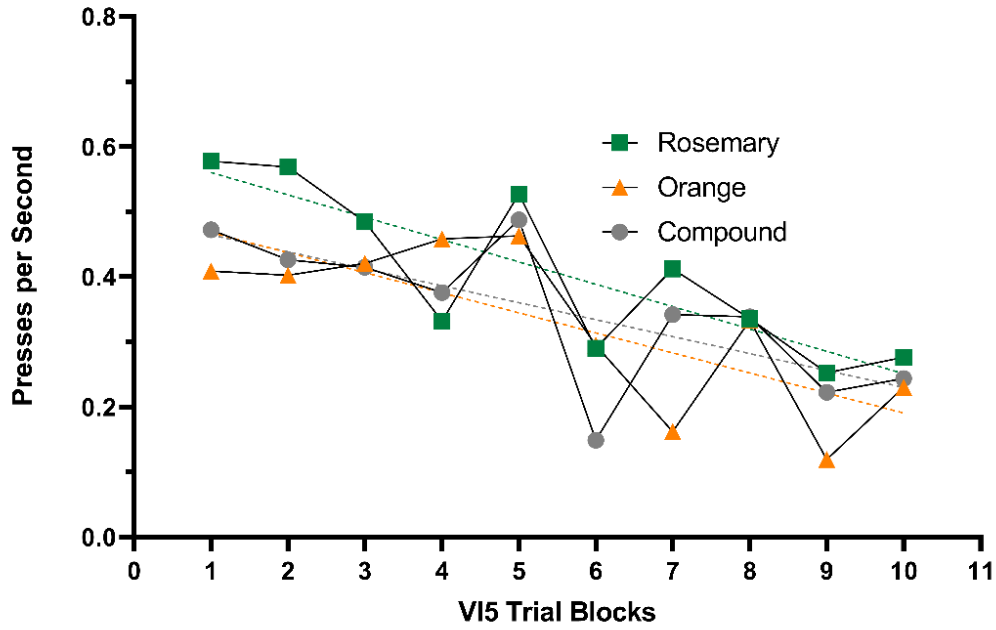


Figure 9

Subject 5 Cumulative Rates of First VI5 Test Block

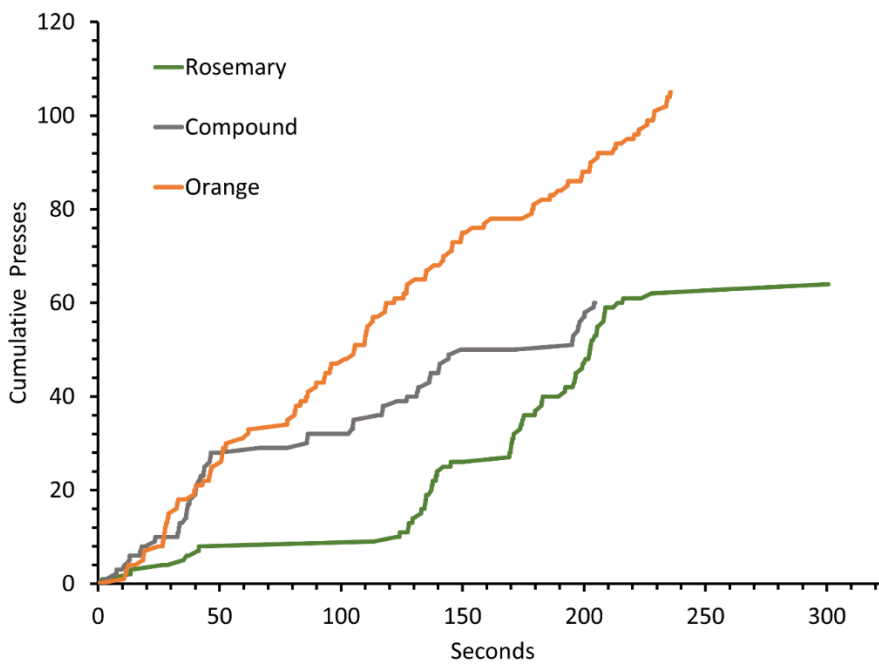


Figure 10

Subject 5 Response Distribution of VI5 Test Rates

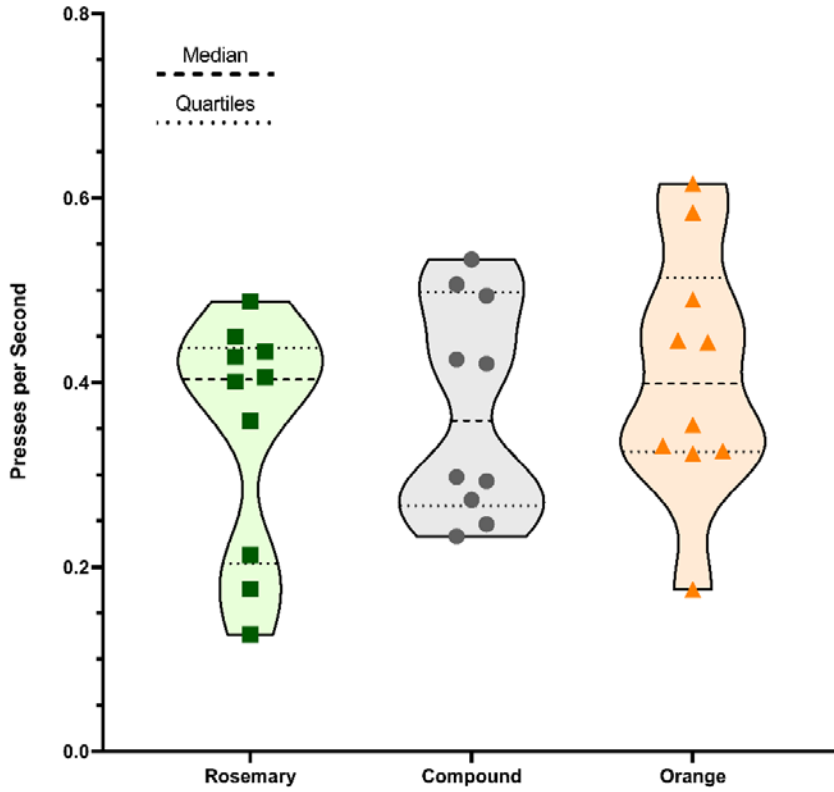


Figure 11

Subject 5 Rate per Extinction Test Session

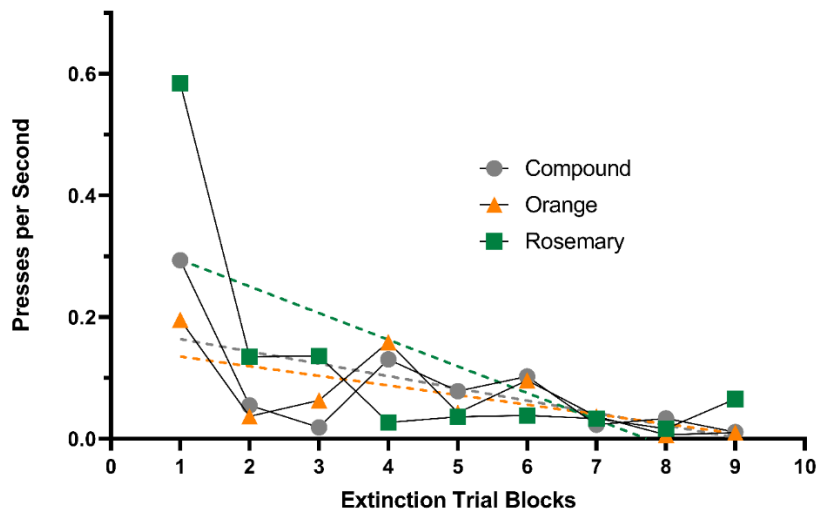


Figure 12

Subject 5 Cumulative Rates of First Extinction Test Block

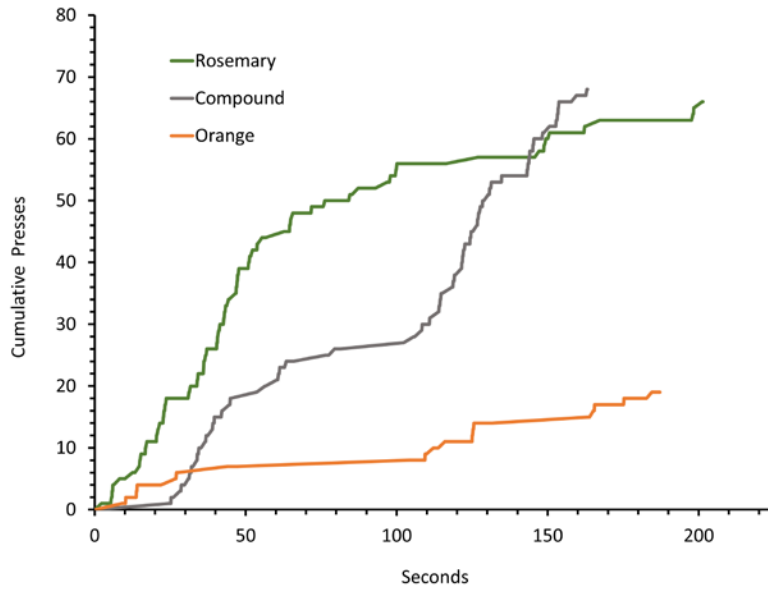


Figure 13

Subject 5 Response Distribution of Extinction Test Rates

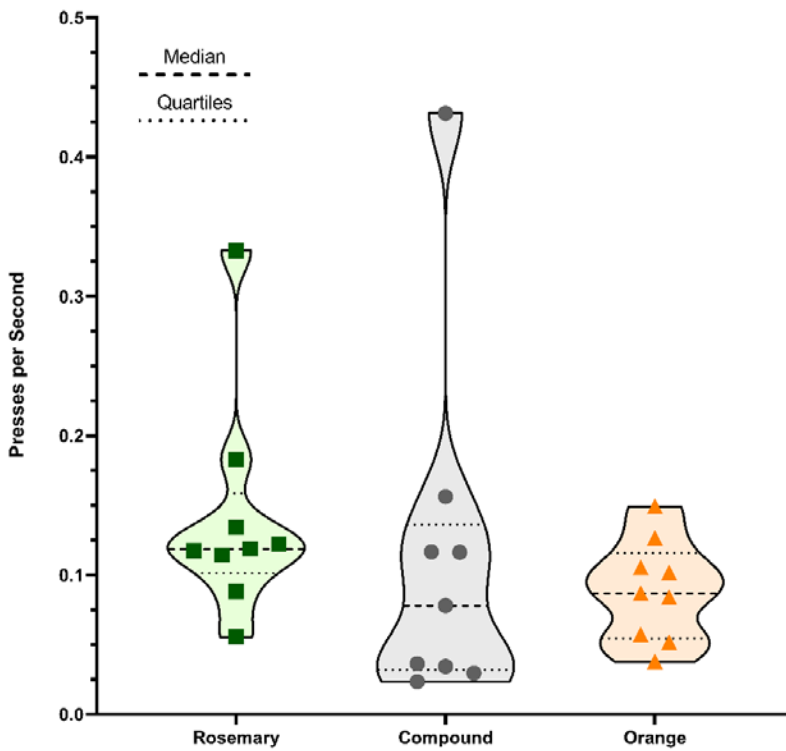


Figure 14

Subject 5 Rate per Re-Training Session

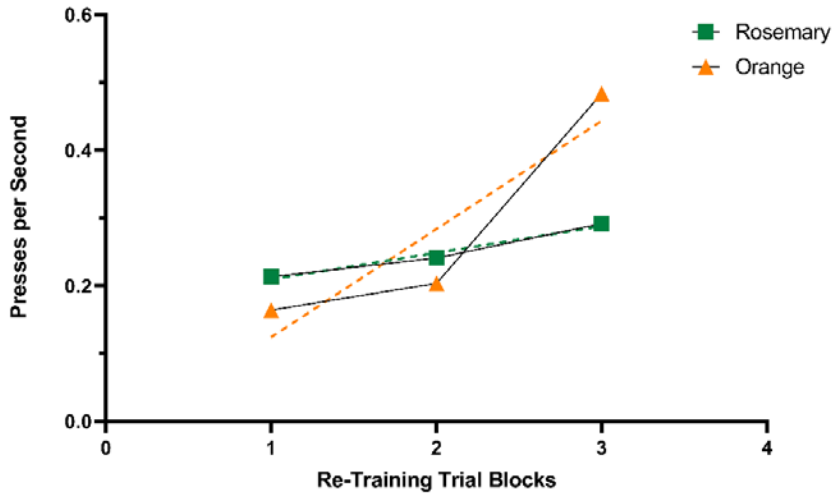


Figure 15

Subject 5 Response Distribution of Re-Training Sessions

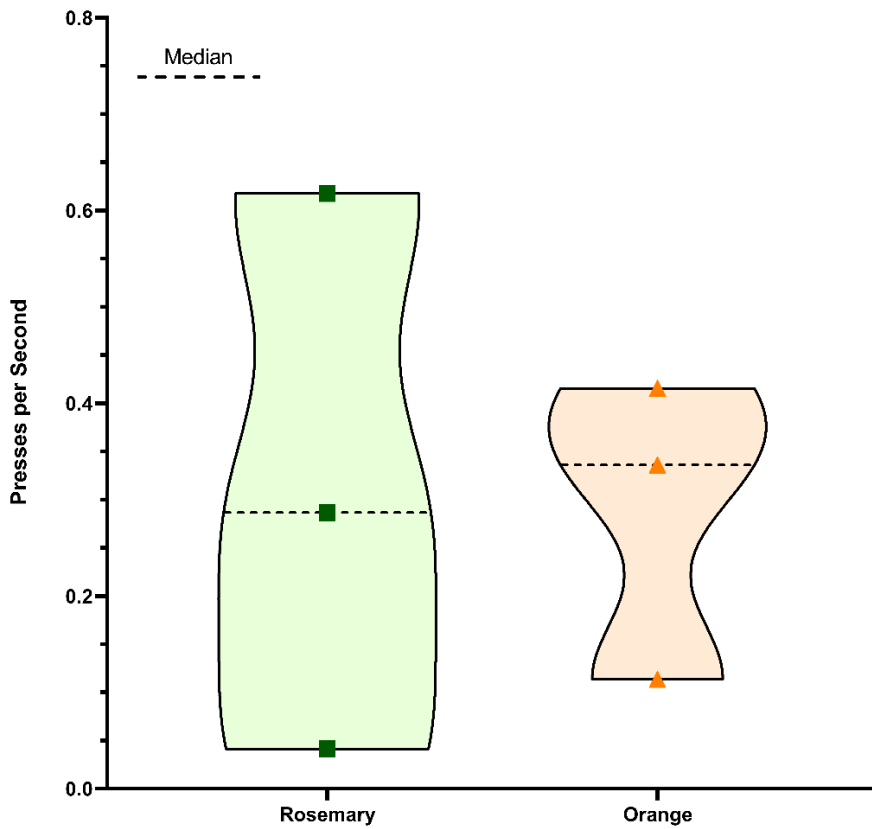


Figure 16

Subject 5 Rate per VI10 Test Session

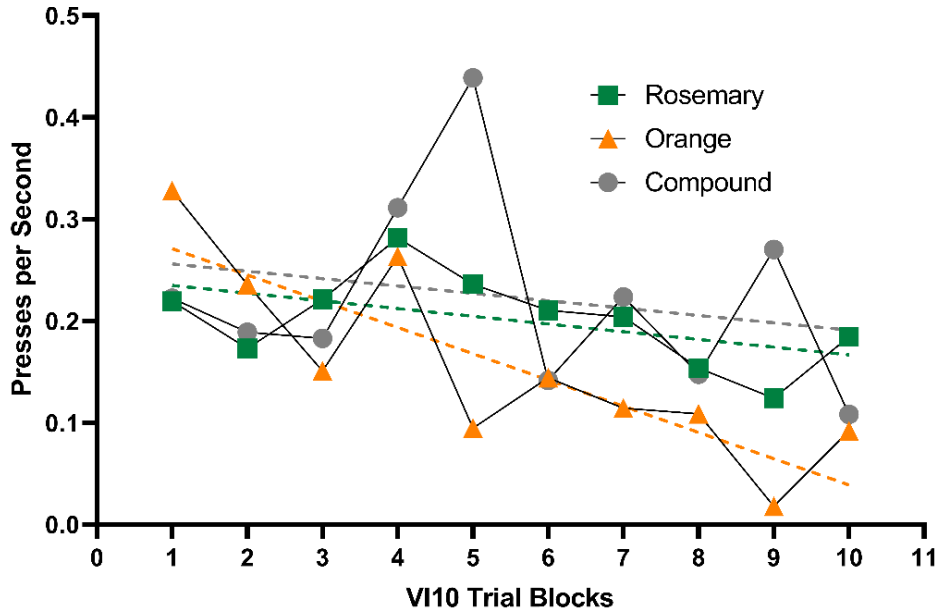


Figure 17

Subject 5 Cumulative Rates of First VI10 Test Block

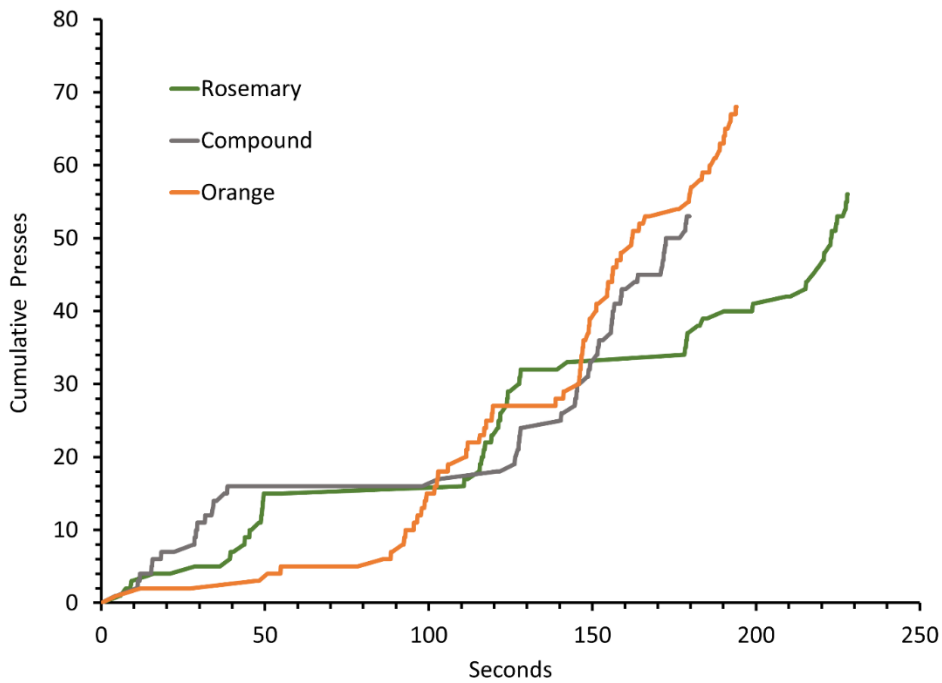


Figure 18

Subject 5 Response Distribution of VII0 Test Rates

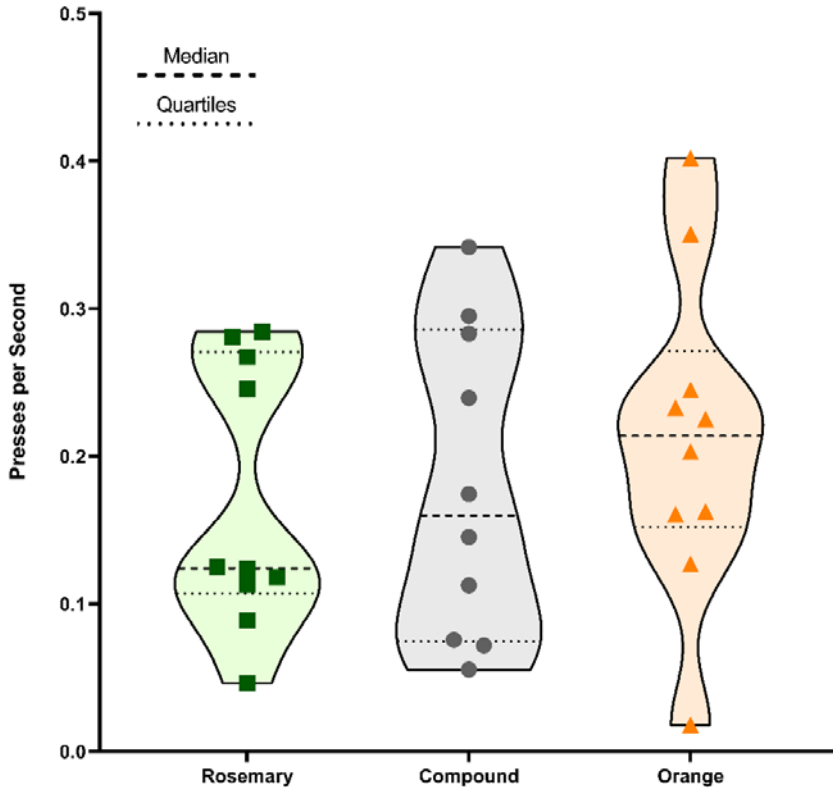


Figure 19

Subject 6 Rate per VI5 Test Session

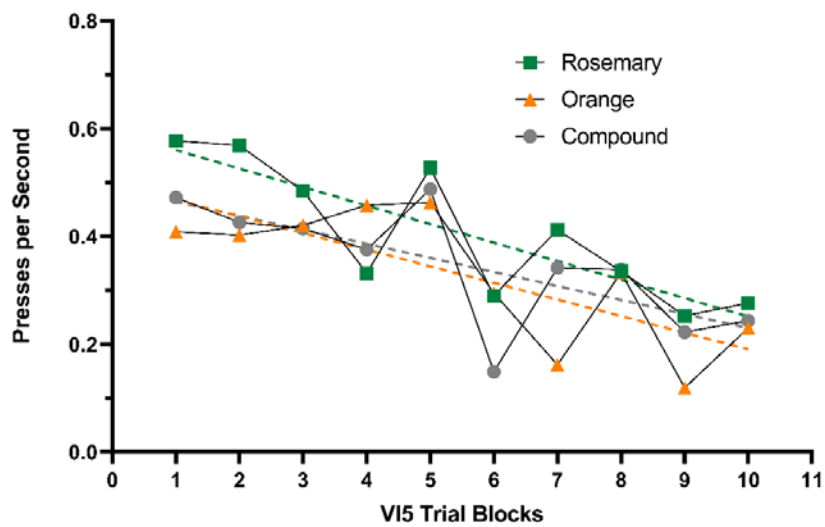


Figure 20

Subject 6 Cumulative Rates of First VI5 Test Block

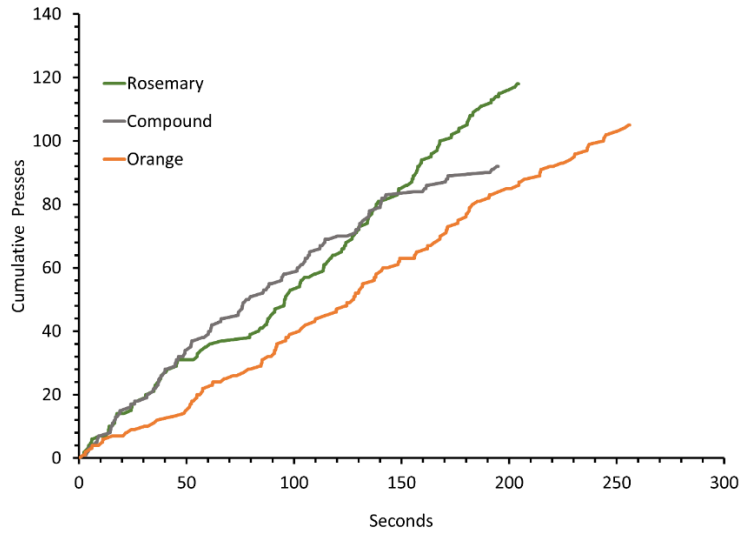


Figure 21

Subject 6 Response Distribution of VI5 Test Rates

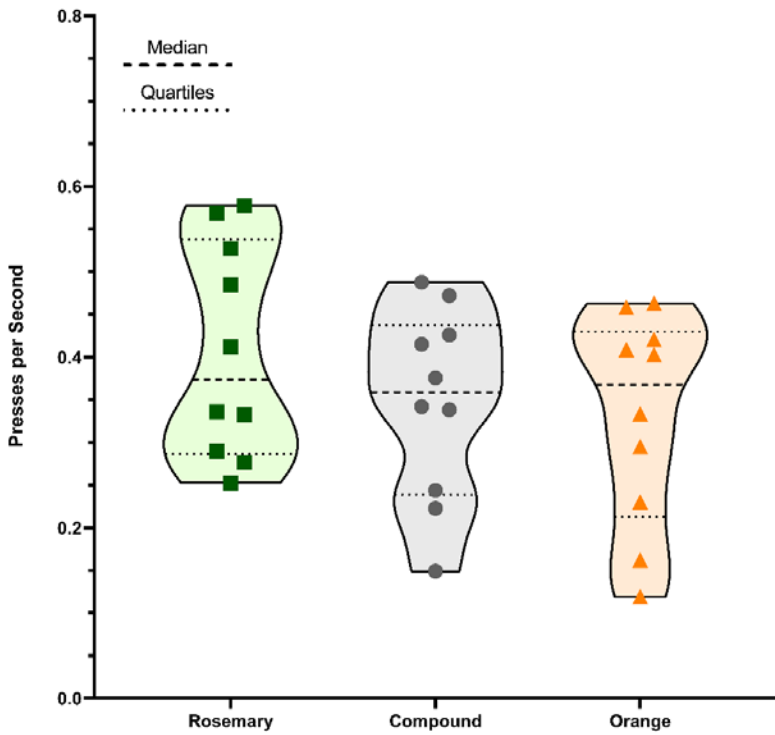


Figure 22

Subject 6 Rate per Extinction Test Session

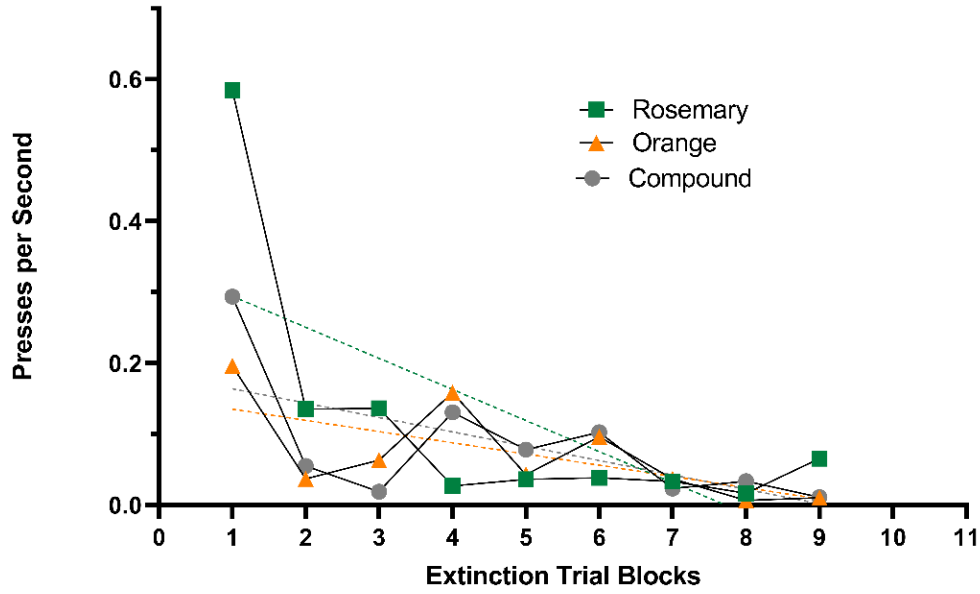


Figure 23

Subject 6 Cumulative Rates of First Extinction Test Block

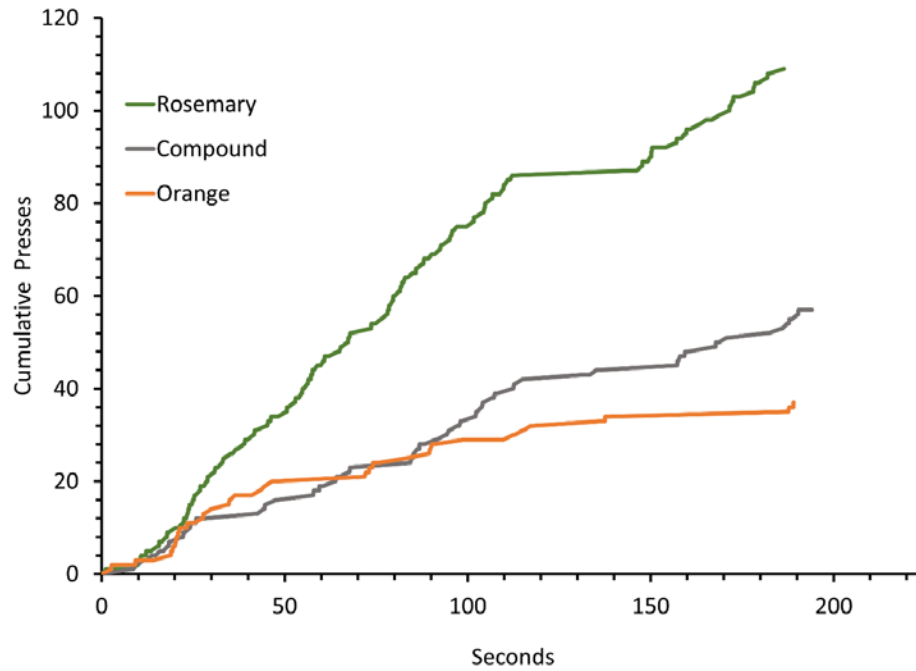


Figure 24

Subject 6 Response Distribution of Extinction Test Rates

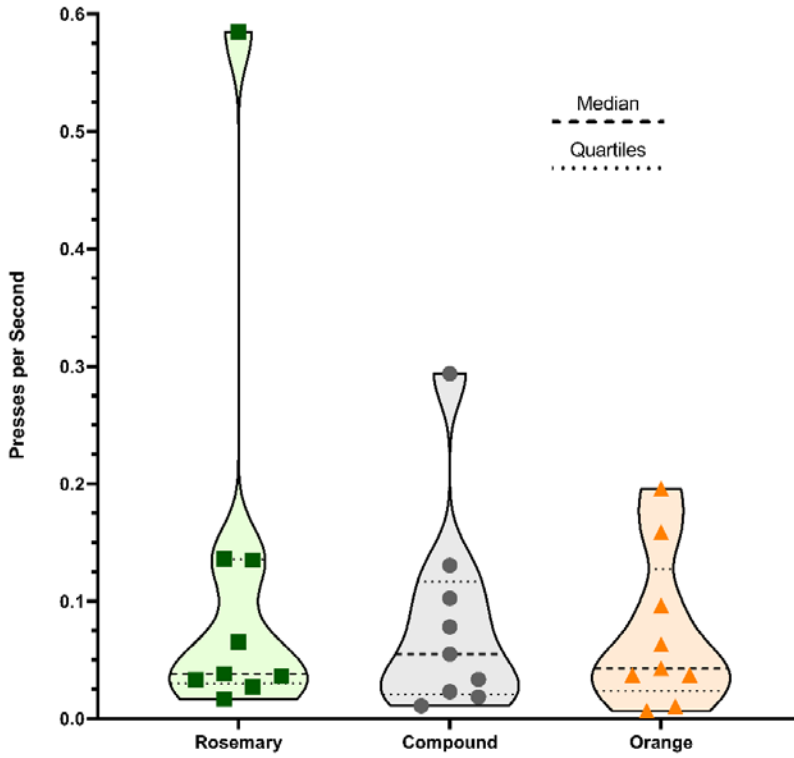


Figure 25

Subject 6 Rate per Re-Training Session

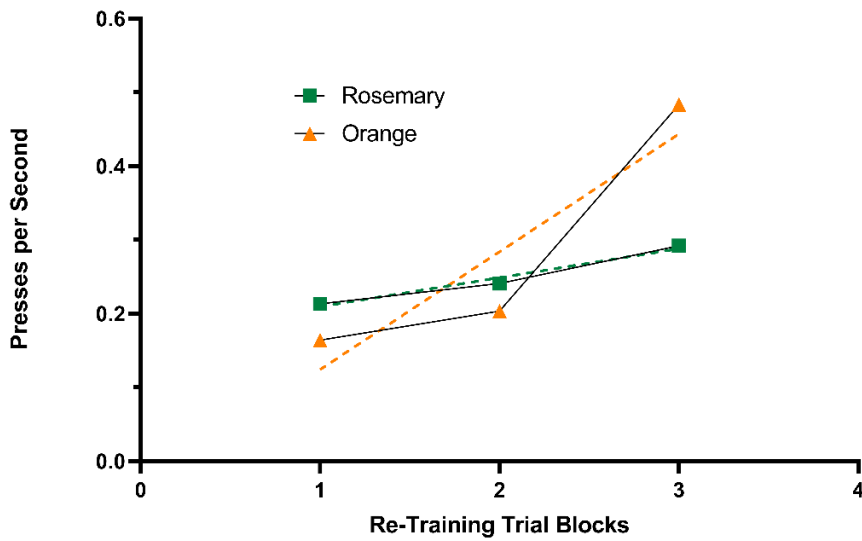


Figure 26

Subject 6 Response Distribution of Re-Testing Sessions

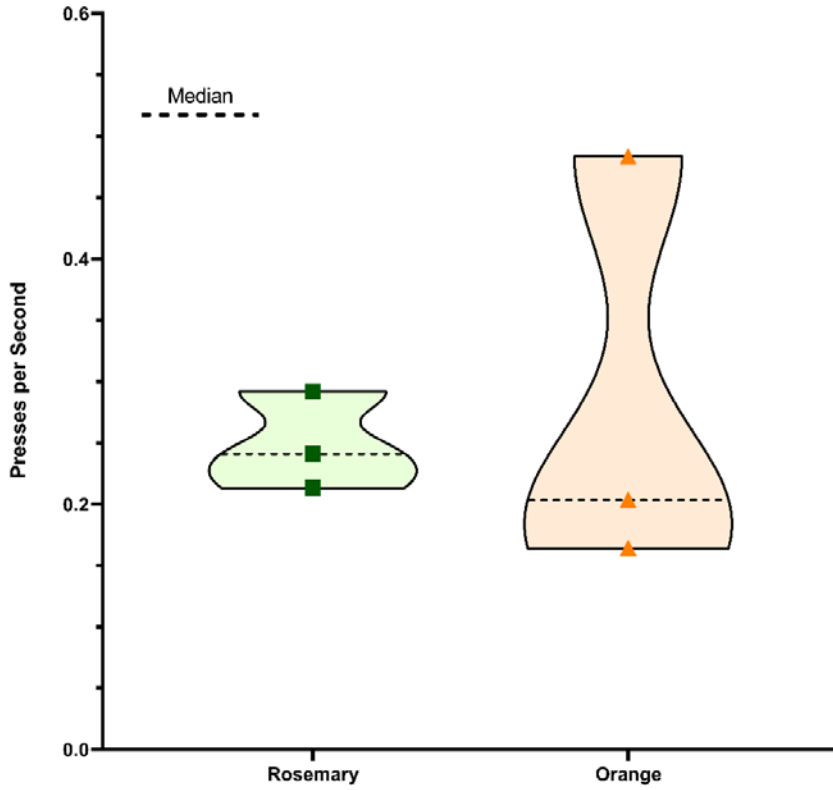


Figure 27

Subject 6 Rate per VI10 Test Session

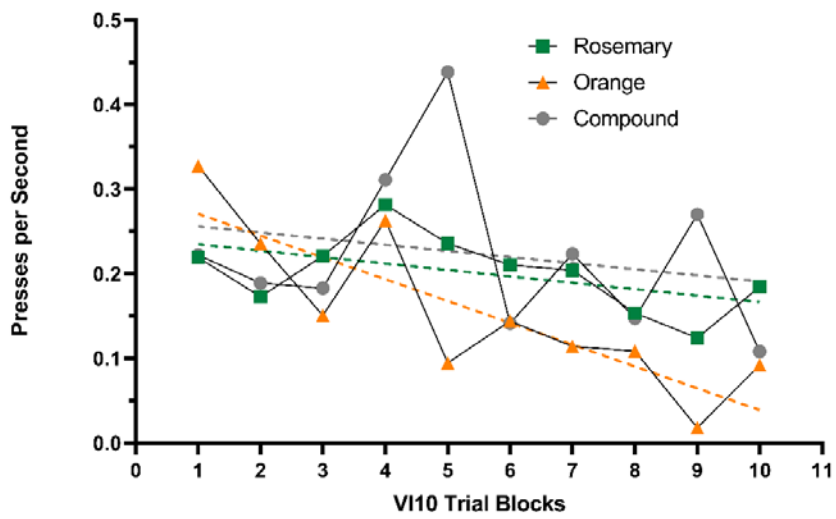


Figure 28

Subject 6 Cumulative Rates of First VII0 Test Block

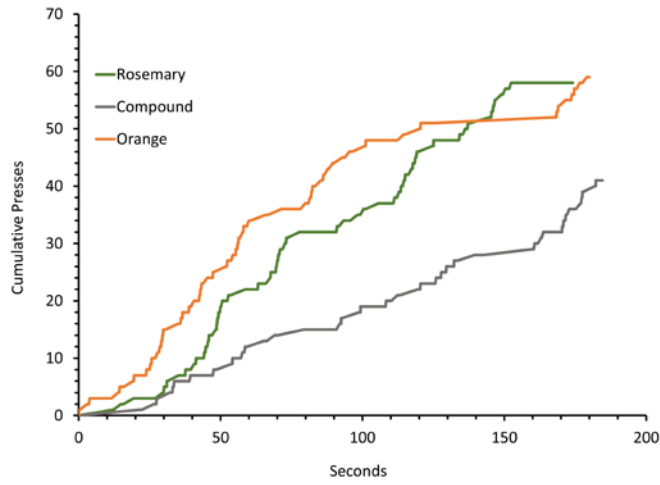
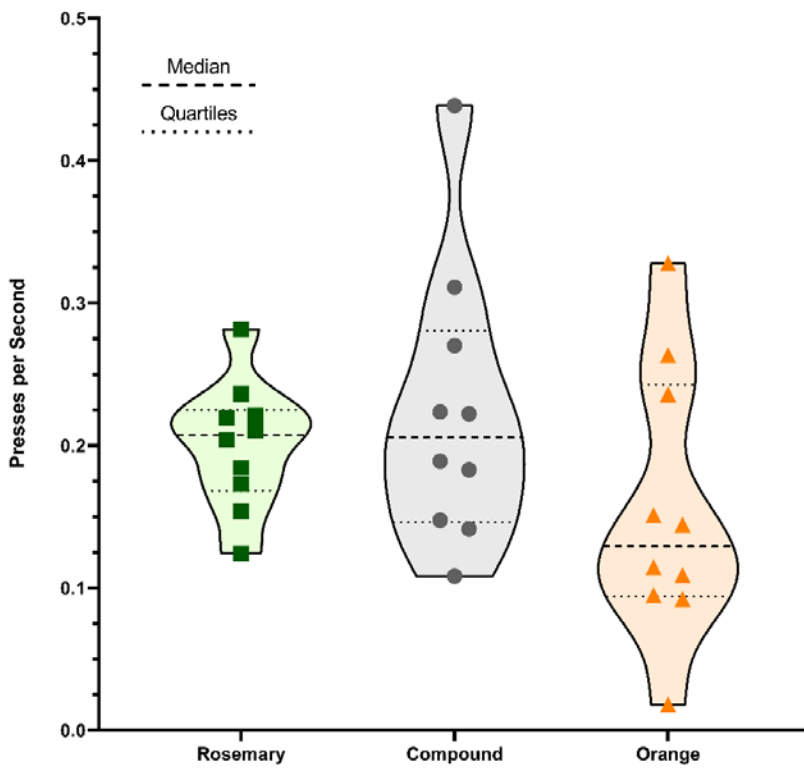


Figure 29

Subject 6 Response Distribution of VII0 Test Rates



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